Confirming QTLs and Finding Additional Loci Responsible for Resistance to Rice Sheath Blight Disease

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Abstract

Liu, G., Jia, Y., McClung, A., Oard, J. H., Lee, F. N., and Correll, J. C. 2013. Confirming QTLs and finding additional loci responsible for resistance to rice sheath blight disease. *Plant Dis.* 97:113–117.

Rice sheath blight disease, caused by *Rhizoctonia solani* AG1-1A, is one of the most destructive rice diseases worldwide. Utilization of host resistance is the most economical and environmentally sound strategy in managing sheath blight (ShB). Ten ShB quantitative trait loci (QTLs) were previously mapped in a Lemont × Jasmine 85 recombinant inbred line (LJRIL) population using greenhouse inoculation methods at an early vegetative stage. However, confirmation of ShB-resistant QTLs under field conditions is critical for their utilization in marker-assisted selection (MAS) for improving ShB resistance in new cultivars. In the present study, we evaluated ShB resistance using 216 LJRILs under field conditions in Arkansas, Texas, and Louisiana during

2008 and 2009. We confirmed the presence of the major ShB-QTL *qShB9-2* based on the field data and also identified one new ShB-QTL between markers RM221 and RM112 on chromosome 2 across all three locations. Based on the field verification of ShB evaluations, the microchamber and mist-chamber assays were simple, effective, and reliable methods to identify major ShB-QTLs like *qShB9-2* in the greenhouse at early vegetative stages. The markers RM215 and RM245 were found to be closely linked to *qShB9-2* in greenhouse and field assays, indicating that they will be useful for improving ShB resistance in rice breeding programs using MAS.

Rice sheath blight disease, caused by *Rhizoctonia solani* Kühn AG1-1A, is one of the most destructive diseases in rice-growing regions of the world (25,26). In highly intensive production systems in the United States, yield losses caused by the sheath blight (ShB) disease can reach up to 50% (14,15). ShB management typically relies on the application of fungicides in combination with cultural practices (30). Utilization of naturally occurring host resistance is the most economical and environment-friendly measure for managing ShB. The ShB pathogen has a broad host range, and no complete resistance has been identified in rice germplasm (17,20). However, substantial differences in the levels of susceptibility to the ShB pathogen among rice cultivars have been observed under field conditions (6,14–16).

Resistance to ShB is controlled by polygenic quantitative trait loci (QTLs; 20). Thus far, a number of QTLs associated with ShB resistance (ShB-QTLs) have been identified on all 12 rice chromosomes using segregating F₂, doubled haploid, and recombinant inbred line (RIL) populations (7,20,32) under field condition. Pinson et al. (20) confirmed the locations and effects of six previously identified ShB-QTLs and identified eight new ShB-QTLs in an RIL population derived from the cross of Lemont × Teqing using a field inoculation method. The accurate and reliable measurement of ShB resistance in QTL analysis under field conditions can be affected by a number of environmental factors, including light intensity, humidity, temperature (3,10), nitrogen fertilizer rate (24),

and silica level in soil (21,22), as well as plant morphology, including plant height, maturity, growth stage at infection, and plant architecture (1,2,9,11,22).

QTL mapping for resistance to ShB field evaluation methods include the use of colonized toothpicks (33) to inoculate plants and broadcasting inocula onto rice plants (4,11,24). Recently, Jia et al. (6) developed a microchamber method: a simple, rapid, accurate, and reliable method to evaluate varietal resistance to ShB under controlled greenhouse conditions. Ten ShB-QTLs were identified on chromosomes 1, 2, 3, 5, 6, and 9 using microchamber and mist-chamber assays in an RIL population derived from the cross of Lemont and Jasmine 85 (12). The major ShB-QTL *qShB9-2* on chromosome 9 co-segregated with simple-sequence repeat (SSR) marker RM245 and contributed to 24.3 and 27.2% of total phenotypic variation in ShB in the microchamber and mist-chamber assays, respectively.

The objectives of this study were to (i) confirm the ShB-QTLs previously identified using two greenhouse inoculation methods and identify additional ShB-QTLs using field evaluation methods and (ii) determine whether the greenhouse chamber inoculation evaluations correspond to disease reactions under field conditions and, therefore, are robust for breeding for resistance to ShB.

Materials and Methods

Plant materials. The RIL population derived from the cross of Lemont × Jasmine 85 (LJRIL) was developed using single seed descent, and a subset of 250 F₅ LJRILs was previously evaluated for ShB resistance under greenhouse conditions (12). Based on seed availability, 216 LJRILs were used for field evaluations of resistance to ShB disease at three locations in 2008 and 2009. The locations included Stuttgart, AR, Beaumont, TX, and Crowley, LA.

Large-scale production of inocula. Three isolates of *R. solani* AG1-1A from the southern United States were used in the field inoculation studies. Isolates RR0140, TMR-1, and LR170 were used in Stuttgart, Beaumont, and Crowley, respectively. Actively growing mycelia on potato dextrose agar (PDA) plates were transferred to fresh PDA medium and cultured in laboratory for 5 to 7

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*The e-Xtra logo stands for “electronic extra” and indicates that the online version contains a link to the USDA website.

Accepted for publication 30 July 2012.

<http://dx.doi.org/10.1094/PDIS-05-12-0466-RE>

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days at 27 to 30°C under darkness, forming fresh sclerotia as source of inoculum. The culture medium for production of inocula was a mixture of macerated corn and rye grass at a ratio of 4:3 (dry volume). First, the corn and water were mixed at a ratio of 1:1 (vol/vol), soaked for 1 h, autoclaved for 15 min at 121°C, and kept in an autoclave overnight. Then, the autoclaved corn was mixed with the rye grass by adding 250 ml of water in the autoclavable bags (30 by 36 cm). The bag opening was fixed with a cap assembly of a 15.5-cm metal band and cotton stopper and covered with an autoclavable bag. The bags of the culture mixtures were autoclaved for 50 min at 121°C and cooled slowly in an autoclave overnight. The mixtures were remixed, autoclaved for another 50 min at 121°C, and cooled. The source sclerotia on the agar plates were cut into blocks and transferred into the media bags at four to five plates per bag. The bags were closed with cotton stoppers and the inoculated media were hand mixed thoroughly to ensure even distribution of the inocula. The bags were incubated on benches and the inoculated medium was remixed to maximize colonization by the fungus. At 6 to 7 days after inoculation, the sclerotia developed. The media with sclerotia and mycelia were emptied into brown paper bags, which were laid on a metal screen rack to dry at room temperature. The inocula were ground into fine particles using a grinder before broadcasting into the field plots. A similar

procedure in inoculum production was employed at the Beaumont and Crowley locations using a mixture of rice and rice hulls at a ratio of 1:3 (vol/vol).

Field inoculation and evaluation of ShB. In Stuttgart, LJRILs were planted in a three-row plots (137 cm long and 20-cm spacing), with four replications in 2008 and three replications in 2009. LJRILs were planted in three-row plots (244 cm long and 25-cm spacing) at two replications in Beaumont. At Crowley, single-row plots (200 cm long and 25 cm between plots) were planted with three replications. The plots were arranged in a completely randomized block design. Lemont and Jasmine 85 were included in all experiments as the susceptible and resistant checks, respectively. Fertilizer was applied at 112 kg/h in a given season.

At the first internode stage of rice, approximately 30 g of inocula were broadcast at the base of the central row of each plot using a measuring cup. At 30 days after inoculation, the ShB disease severity ratings of the LJRILs were visually assessed using a 0-to-9 scale (5), with 0 to 4 as resistant and >4 as susceptible, by one person in each location, and disease rating for each line was verified afterward before harvesting.

Statistical analysis of phenotypic data. The means and standard deviation of the ShB ratings of the parental Lemont and Jasmine 85 and LJRIL population were analyzed using STAT-

Table 1. Summary of disease ratings (0-to-9 scale) of the parents and recombinant inbred lines (RILs) of Lemont × Jasmine 85 evaluated in inoculated field plots at Arkansas (AR), Texas (TX), and Louisiana (LA) in 2008 to 2009

Location-year	Parental disease ratings ^x				Disease rating of RIL population ^y		
	Range		Mean ± SD		Range	Mean ± SD	<i>r</i> ^z
	Lemont	Jasmine 85	Lemont	Jasmine 85			
AR-2008	9.0–9.0	3.0–3.0	9.0 ± 0 a	3.0 ± 0 b	2.8–9.0	6.4 ± 1.7	...
AR-2009	8.0–9.0	3.0–4.0	8.7 ± 0.6 a	3.3 ± 0.6 b	3.7–9.0	6.7 ± 1.4	0.850
TX-2008	5.0–8.0	2.0–3.0	6.5 ± 2.1 a	2.5 ± 0.7 b	1.0–8.5	4.3 ± 1.6	...
TX-2009	6.0–9.0	2.0–2.0	7.2 ± 1.5 a	2.0 ± 0 b	1.5–8.5	5.4 ± 1.5	0.522
LA-2008	7.0–8.0	4.0–5.0	7.6 ± 0.5 a	4.2 ± 0.5 b	4.7–8.4	7.0 ± 0.7	...

^x Within a location-year, means followed by the same letters are not significantly different by Fisher's least significant difference test at *P* = 0.05. Shown are averages of three or four replicates from field sheath blight disease ratings in Arkansas, two or three replicates in Texas, and two to four replicates in Louisiana; ranges of Lemont (susceptible check) and Jasmine 85 (resistant check) and mean ± standard deviation (SD).

^y RIL population sizes were 225 for evaluation locations of Arkansas and Louisiana and 216 for Texas.

^z Correlation coefficient of RIL means between years at Arkansas and at Texas.

Fig. 1. Frequency distributions of sheath blight disease ratings of 216 recombinant inbred lines (RILs) from the cross of Lemont (LMNT) and Jasmine 85 (JSMN) assayed for sheath blight resistance in inoculated field plots. Arrows show the ratings of the resistant JSMN and susceptible LMNT parents at each location.

GRAPHICS Centurion, version XV. Significant differences between the means of Lemont and Jasmine 85 within a location–year were compared using Fisher's least significant difference test at $P = 0.05$. The ShB ratings of each LJRIIL within a year–location were averaged across replications. The correlation coefficient (r) of the averaged ratings between two years within a location were analyzed on the software Microsoft EXCEL. The r values indicated strong correlation for ShB ratings between 2008 and 2009 in both Arkansas and Texas (Table 1).

QTL mapping. The previously constructed SSR linkage map was used for mapping the ShB-QTLs (12). The average ShB ratings of the LJRIILs in a location were used for the composite interval mapping (CIM). QTL analysis was performed using Windows QTL Cartographer, version 2.5 (29) with the default CIM control parameters: model 6 of standard model, five control markers, 10 centimorgans of window size, and forward regression method.

The log of the odds likelihood ratio (LOD) threshold of ≥ 2.4 was used to declare the presence of a putative QTL in order to compare with the previously identified ShB-QTL on rice chromosomes (4,7,9,12,13,19,20,23,33). Additive effect and percentage of variation explained by individual ShB-QTLs were estimated.

Results

Effects of location–year on variability of ShB severity in LJRIIL population. The ranges of the resistant control Jasmine 85 and the susceptible control Lemont in all location–years were 2.0 to 5.0 and 5.0 to 9.0, respectively (Table 1). Within an experimental location and year, the mean ShB rating of Jasmine 85 was significantly lower than that of Lemont. Lemont had relatively higher standard deviations for mean ShB ratings in Texas in 2008 and 2009 than other location–years. The correlation coefficients of the ShB ratings between 2008 and 2009 in Arkansas and in Texas were greater than 0.5 (Table 1), indicating a good association of ShB field evaluation values across years in Arkansas and Texas. Therefore, the ShB ratings were averaged across years at each location and used for CIM mapping of the ShB-QTLs. The average

field ShB ratings of the LJRIILs in all three locations were well distributed in each of the disease categories, with Jasmine 85 and Lemont at two opposite ends (Fig. 1). The ShB ratings in Texas had a wider range than the other two locations (Table 1; Fig. 1).

Confirmed and newly identified SB-QTLs in the LJRIIL population. The ShB-QTLs responsible for ShB resistance under field conditions at the three locations are summarized in Figure 2 and Table 2. Five ShB-QTLs were identified on chromosomes 2, 3, 7, and 9 in Arkansas; six ShB-QTLs on chromosomes 2, 3, 9, and 11 in Texas; and three ShB-QTLs on chromosomes 2, 7, and 9 in Louisiana. Two ShB-QTLs on chromosomes 2 and 9 were identified in all three locations (Fig. 2; Table 2). The resistant alleles for all ShB-QTLs, except *qSB11.1-TX* and *qSB11.2-TX*, originated from Jasmine 85. The SSR markers RM215 and RM245 flanked the major ShB-QTL *qSB9*, with the nearest marker being RM245. This location of *qSB9* is at the same location as *qSB9-2* identified in previous QTL analysis, using the same LJRIIL mapping population as the microchamber and mist-chamber methods (12).

Discussion

Historically, observations suggest that resistance to *R. solani* is confounded with plant height, tiller angle, and heading date (2,9,11,22). In a previous study, a subset of 216 lines selected from a random mapping population consisting of 800 recombinant individuals (Y. Jia and A. McClung, unpublished data), derived from the cross of Lemont and Jasmine 85 (after removal of the extreme individuals carrying the above-mentioned traits) was used for mapping ShB-resistant QTLs. In total, 10 ShB-resistant QTLs were identified using phenotypes collected from rice plants at an early vegetative stage under controlled greenhouse conditions, (6,12). In the present study, the same subset of RILs was used for mapping ShB resistance QTLs using phenotypic data from inoculated rice plots grown in multiple years and multiple locations.

All previously identified ShB resistance QTLs (12) were verified. Moreover, *qSB9-AR*, *qSB9-TX*, and *qSB9-LA*, identified from the three states, explained 4.6 to 11.7% of total phenotypic varia-

tion, with the additive effect of 0.15 to 0.45 (Table 2), indicating that *qSB9* is a major ShB-QTL. Previously, using two greenhouse chamber assays, *qShB9-2* was found to explain 24.3 to 27.2% of total phenotypic variation (12). The *qShB9* allele was also identified at similar chromosomal locations using different mapping populations evaluated at different global locations, suggesting that this QTL is not independently evolved or adapted (18,20,27,28, 31,33,34). The *qShB3-AR* and *qShB3-TX* flanked by RM426 and RM15824 on chromosome 3 were identified in Arkansas and Texas (Fig. 2). This finding is in agreement with our previous result that *qSB3* was mapped between RM16 and RM426 on chromosome 3 using the greenhouse inoculation methods (12). Additionally, new ShB-QTLs were identified on chromosomes 2, 7, and 11 (Fig. 2). The *qShB2* flanking between RM221 and RM112 on chromosome 2 was identified as *qShB2.2-AR*, *qShB2.2-TX*, and *qShB2-LA* in Arkansas, Texas, and Louisiana, respectively. Their LOD values ranged from 3.3 to 4.1, and the alleles explained 5.7 to 6.6% of total phenotypic variation, with the additive effect of 0.17 to 0.36 (Table 2). This ShB-QTL was located near a QTL identified using the mist-chamber method (Fig. 2). The *qShB7* allele on chromosome 7 was identified in Arkansas and Louisiana, and its resistance allele explained 7.4 to 11.5% of total phenotypic variation, with the additive effect of 0.27 to 0.42 (Table 2). The resistant alleles of ShB-QTLs *qShB11.1-TX* and *qShB11.2-TX* on chromosome 11

were from Lemont and were only identified in Texas, with LOD values of 3.2 to 3.3.

In total, 11 resistant LJRILs were identified to carry the major ShB-QTL *qSB9* (Table 3). Using ShB-QTLs that were found at more than one field site, five haplotypes were identified across the ShB-QTLs located on chromosomes 2, 3, 7, and 9 (Table 3). These were demonstrated to possess similar resistance to ShB disease using greenhouse assays (12) and the field method in the present study. LJRIL103, LJRIL158, LJRIL186, and LJRIL220 from three haplotypes with the major *qSB9* possessed comparable resistance with Jasmine 85. These lines were released as rice germplasm with improved ShB resistance (8). The rest of the LJRILs had at least three resistant alleles from Jasmine 85 (Table 3). Noticeably, *qShB2* in RIL80 and *qShB7* in RIL251 were heterozygous and both lines will be useful for fine mapping of both QTLs.

In summary, using field evaluation, we were able to identify new QTLs *qShB2-1-AR* on chromosome 2, *qShB7-AR* and *qShB7-LA* on chromosome 7, and *qShB11-1-TX* and *qShB11-2-TX* on chromosome 11. Most significantly, the major ShB-QTL *qShB9-2* previously identified using the microchamber and mist-chamber assays under greenhouse conditions was confirmed by field evaluations at three locations in the present study. The markers RM215 and RM245 were closely linked to *qShB9-2* and can be used as reliable markers for improving ShB resistance in rice breeding programs

Table 2. Summary of quantitative trait loci (QTL) for resistance to rice sheath blight (ShB) disease at each of the inoculated fields at Arkansas (AR), Texas (TX), and Louisiana (LA) using composite interval mapping (CIM), 2008 to 2009

ShB-QTL	Chr. ^w	Marker interval	Nearest marker locus	Distance to QTL (cM) ^x	LOD value ^y	Phenotypic variation (%)	Additive effect ^z	Location
<i>qSB2.1-AR</i>	2	RM279–RM71	RM555	4.0	3.7	6.82	0.37	Stuttgart, AR
<i>qSB2.2-AR</i>	2	RM221–RM112	RM221	5.1	3.6	6.50	0.36	Stuttgart, AR
<i>qSB2.1-TX</i>	2	RM424–RM341	RM561	8.6	4.6	8.64	0.40	Beaumont, TX
<i>qSB2.2-TX</i>	2	RM221–RM250	RM530	1.5	4.1	6.64	0.33	Beaumont, TX
<i>qSB2-LA</i>	2	RM221–RM112	RM530	3.4	3.3	5.70	0.17	Crowley, LA
<i>qSB3-AR</i>	3	RM5626–RM55	RM55	1.7	3.7	5.82	0.37	Stuttgart, AR
<i>qSB3-TX</i>	3	RM5626–RM55	RM55	3.9	3.3	5.62	0.33	Beaumont, TX
<i>qSB7-AR</i>	7	RM5711–RM2	RM125	4.1	4.0	7.41	0.42	Stuttgart, AR
<i>qSB7-LA</i>	7	RM5711–RM2	RM125	4.0	6.0	11.54	0.27	Crowley, LA
<i>qSB9-AR</i>	9	RM215–RM245	RM245	1.4	5.4	8.55	0.45	Stuttgart, AR
<i>qSB9-TX</i>	9	RM215–RM245	RM245	3.4	6.5	11.72	0.45	Beaumont, TX
<i>qSB9-LA</i>	9	RM215–RM245	RM245	3.4	2.6	4.56	0.15	Crowley, LA
<i>qSB11.1-TX</i>	11	RM7203–RM536	RM202	0	3.2	4.79	–0.29	Beaumont, TX
<i>qSB11.2-TX</i>	11	RM536–RM229	RM287	0.8	3.3	5.29	–0.31	Beaumont, TX

^w Chromosome.

^x Genetic distance in centimorgans (cM).

^y ShB-QTLs were declared using the log of the odds likelihood ratio (LOD) value of 2.4.

^z The additive effect is the effect associated with substitution of a Jasmine 85 allele by its corresponding Lemont allele.

Table 3. Haplotype analysis of the sheath blight (ShB)-resistant Lemont × Jasmine 85 recombinant inbred lines (LJRILs) at ShB quantitative trait loci (QTLs) identified with composite interval mapping using field data in Stuttgart, AR, Beaumont, TX, and Crowley, LA

Haplotype	LJRIL	Disease ratings (0-to-9 scale) ¹				Alleles at ShB-QTLs ¹¹			
		AR	TX	LA	Average	<i>qShB2</i> ^y	<i>qShB3</i> ^w	<i>qShB7</i> ^x	<i>qShB9</i> ^y
1	51	3.6	2.5	4.7	3.6	J	J	J	J
1	101	4.8	3.3	5.5	4.5	J	J	J	J
1	186 ²	3.8	3.5	6.5	4.6	J	J	J	J
1	221	5.7	6.5	7.3	6.5	J	J	J	J
2	103 ²	4.8	4.0	6.0	4.9	L	J	J	J
2	142	5.0	3.8	6.0	4.9	L	J	J	J
2	158 ²	5.4	4.3	6.8	5.5	L	J	J	J
3	46	3.4	5.3	1.8	3.5	J	L	J	J
3	220 ²	4.3	4.5	5.8	4.9	J	L	J	J
4	80	3.5	5.3	2.8	3.9	h	J	J	J
5	251	5.0	5.8	4.3	5.0	J	J	h	J

¹ Average of the field disease ratings in Arkansas, Texas, and Louisiana.

¹¹ Parents Lemont (L) and Jasmine 85 (J) and heterozygous alleles (h).

^w Chromosome 2, resistant allele origination from Jasmine 85, nearest simple-sequence repeat (SSR) marker = RM530.

^x Chromosome 3, resistant allele origination from Jasmine 85, nearest SSR marker = RM55.

^y Chromosome 7, resistant allele origination from Jasmine 85, nearest SSR marker = RM125.

^z Chromosome 9, resistant allele origination from Jasmine 85, nearest SSR marker = RM245.

² These lines were released as germplasm.

using marker-assisted selection, for fine mapping, and for positional cloning. In comparison with field ShB evaluations, the microchamber and mist-chamber assays were simple, effective, and reliable assay methods in tagging genetic resistance to *R. solani* that was also manifested under field conditions (6,12).

Acknowledgments

This work was supported, in part, by the United States Department of Agriculture–Cooperative State Research, Education and Extension Service (USDA-CREES) National Research Initiative Applied Plant Genomics Program, entitled “RiceCAP: A coordinated research, education, and extension project for the application of genomic discoveries to improve rice in the United States” (USDA/CSREES grant 2004-35317-14867). We thank M. Jia for assistance in genotyping; S. Belmar and D. Groth for assistance in the preparation for sheath blight inoculum; and T. Beaty, L. Simpson, and P. Roberts for assistance in field evaluation of sheath blight disease.

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