

MOLECULAR DISSECTION OF QUANTITATIVE RESISTANCE OF SHEATH BLIGHT IN RICE (*Oryza sativa* L.)

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ABSTRACT

Using 266 Near Isogenic Introgression Lines with randomly introgressed Lemont segment of a cross between Lemont x Teqing, the genetic control of resistance to sheath blight of rice was also studied. Based on disease evaluation and a genetic map with 148 molecular makers, 15 M-QTLs detected for lesion height (LH) and actual lesion length (ALL) over assessment times were mapped on seven chromosomes (1, 2, 3, 4, 5, 9, and 12), explaining 35.8%-93.8% of the phenotypic variation. The QTLs with high additive effects for most resistance traits were found at the markers RM341 (on chromosome 2), RM156 (on chromosome 3), and RM280 (on chromosome 4). All the QTLs had the positive alleles from parent Teqing; Lemont did not contribute any alleles associated with higher disease resistance. Despite different assessment methods for host plant resistance, most QTLs controlling lesion height and actual lesion length in each assessment time were approximately mapped at the same chromosomal regions. Additive effects appeared to be more important than digenic interactions. Rice sheath blight resistance was found influenced by some morphological characters such as heading date but had no correlation with plant height. However, it can not be ascertained if the association between sheath blight resistance and morphological traits is due to pleiotrophic effect or to close linkage. Four QTLs, namely, QSbr1a, QSbr2a, QSbr4c, and QSbr9b that were found not associated with plant morphology or heading date are potentially useful in breeding programs for sheath blight resistance.

Key words: QTLs for resistance, rice, sheath blight.

INTRODUCTION

Rice sheath blight, caused by *Rhizoctonia solani* Kühn, is one of the major diseases of rice and severely impairs both rice yields and quality. Yield losses from 10 to 20% have been reported in farmers' fields (Teng et al 1990). Breeding and utilization of resistant varieties are still considered the most economic and effective ways for controlling rice sheath blight. Despite extensive screening for complete resistance or immunity, no complete sheath blight resistance has been identified to date and only moderate or partial resistance is available (Ou 1985; Dasgupta 1992; Rao 1995; Dath 1990). Nevertheless, there are several lines of evidence that partial resistance can offer adequate protection against the pathogen under field conditions (Rao 1995; Li et al. 1995b). Several genetic studies have been conducted using moderately

or partially resistant cultivars. However, the results on the genetic basis of the partial resistance to sheath blight were controversial. The quantitative trait loci (QTLs) mapping studies done so far identified six QTLs in Teqing and Lemont (Li et al. 1995b) and six QTLs in Jasmin 85 and Lemont (Zou et al. 2000) for partial resistance against sheath blight.

The objectives of this study were to identify quantitative trait loci for resistance to rice sheath blight and to explain the true relationship of sheath blight resistance with heading date and plant height.

MATERIALS AND METHODS

Plant materials

Two hundred and sixty six Teqing Near Isogenic Introgression Lines (NIILs) were

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developed by using Teqing as recurrent parent and Lemont as introgression parent.

The linkage map of Teqing NIL population was constructed by Xu and co-workers, Genome Mapping Laboratory, IRRI. A total of 148 markers involving 3 morphological markers, 11 RAPD, and 134 SSR markers were used to establish a linkage map using the software Map Manager QTX (Manly et al, 2001).

Field experiment.

The experiment was conducted in field plots at the Cuu Long Delta Rice Research Institute (CLRRI), Vietnam and was laid out in RCBD with 2 replications. Each of the NILs and parents were planted in a 5-row plot with 10 plants in each row, and spacing of 15x20 cm. The two parents as checks were transplanted after every 10 lines. Plots received 100-40-30 (N-P₂O₅-K₂O) kg ha⁻¹.

Inoculation and disease evaluation

The lines were inoculated 40 days after transplanting with 5g of inoculum placed in the base of each hill and between the tillers. Data based on lesion height (LH) and actual lesion length (ALL) were recorded at 7 days after inoculation and then at 7 day intervals until heading stage. The assessment of disease rating was based on a 0-9 scale, with 0 indicating no evidence of infection and 9 indicating that the plant was killed or collapsing. For instance, "5" indicated that about 50% of the height of the plants above the water line was diseased (Li et al. 1995b). Disease rating was only measured once, that is, 30 days after heading. Ratings of 0-3 were considered resistant (R) and 4-9 were grouped as susceptible (S). Morphological characters correlated with rice sheath blight resistance were also measured such as plant height and heading date. Culm angle and leaf angle mean was visually estimated on a row basis according to the standard procedure (INGER 1996).

Statistical analysis

The relationship between the characters was

determined by computing Pearson's correlation coefficients using SAS PROC CORR procedure (SAS Institute, 1996). The distribution of the morphological traits to the sheath blight disease was analyzed by using SAS PROC REG. The association between phenotype and marker genotype was investigated by single marker analysis using one-way ANOVA of SAS PROC GLM. The two-way ANOVA in SAS PROC GLM was used to identify digenic interaction between identified QTLs, as presented by the nearest marker loci. The P value ($P \leq 0.0005$) in the source of variance for m1*m2 (m1 and m2 are the nearest marker loci for QTL1 and QTL2, respectively) was used as the significant threshold to detect interaction between the two QTLs.

RESULTS AND DISCUSSION

Response of Parents and NILs to Sheath Blight Disease

Teqing had the lower lesion height (LH) and actual lesion plant (ALL) than those of Lemont at all assessment times. Mean scores taken at 30 days after heading were 9.0 and 7.0 for Lemont and Teqing, respectively (Table 1). The frequency distributions of LH, ALL, and disease ratings were continuous, typical of quantitative traits. The transgressive segregation was present mostly in the demonstration of progenies with disease values significantly larger than Lemont except for disease rating (Fig. 1).

Trait Correlation

Disease ratings were associated highly significantly ($P \leq 0.01$) with leaf angle, plant height, and heading date (respectively, $r = 0.21, -0.48, \text{ and } -0.44$) (Table 2). There was inconsistent correlation between LH and ALL and CA and LA over assessment times. Simple correlation analyses also showed that LH and ALL showed highly significant ($P \leq 0.01$) associations ($r = -0.20 \text{ to } -0.43$) with heading date but no correlation with plant height in this study.

Table 1. Means for the different sheath blight disease parameters of Teqing Near Isogenic Introgression Lines (NIILs) and parents.

Parameter*	NIILs				Parents	
	Mean	SD	Min.	Max.	Lemont	Teqing
LH(7DAI)	17.2	2.1	12.5	23.3	15.2	12.4
LH(14DAI)	23.6	3.7	15.3	36.5	19.6	16.9
LH(21DAI)	32.5	6.5	17.2	54.9	27.6	22.5
LH(28DAI)	42.0	8.0	21.8	68.2	37.5	32.5
ALL(7DAI)	10.3	2.3	5.2	18.9	7.7	7.3
ALL(14DAI)	14.7	3.1	8.3	25.6	13.5	10.0
ALL(21DAI)	19.5	4.8	10.2	39.1	15.5	11.8
ALL(28DAI)	25.1	7.0	12.7	54.6	20.3	14.8
SCORE(30DAH)	7.4	0.9	4.0	9.0	9.0	7.0

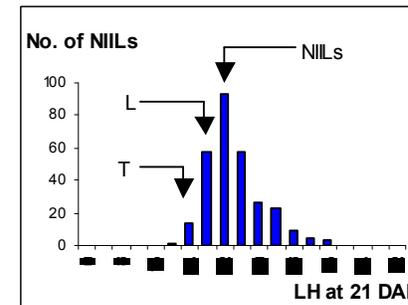
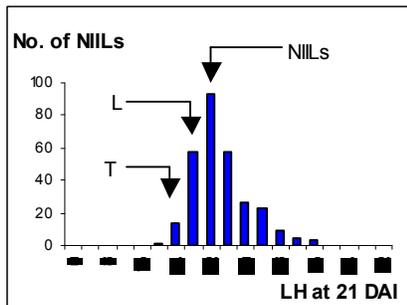
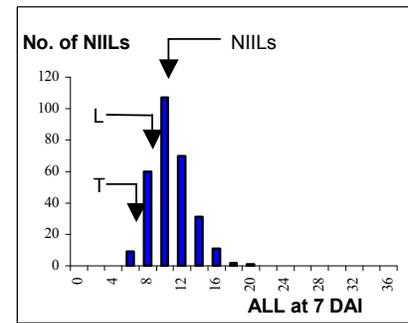
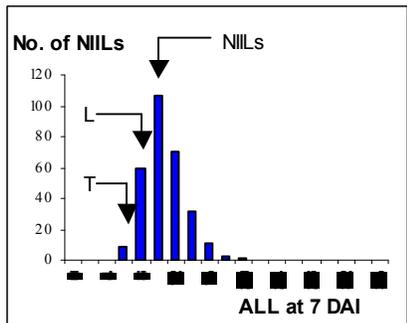
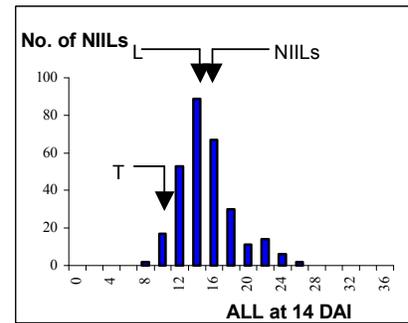
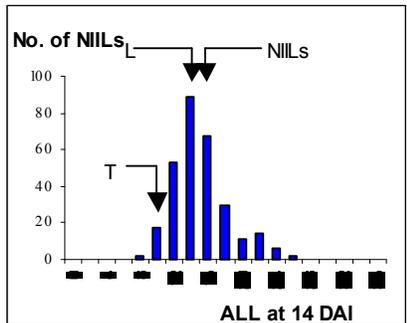
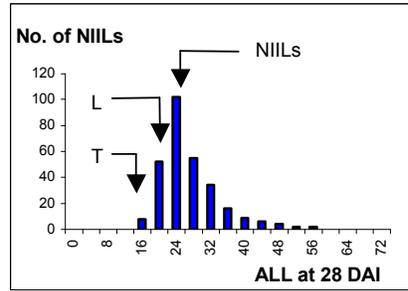
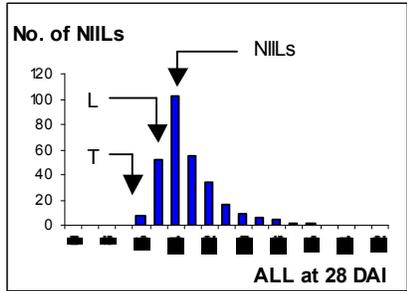
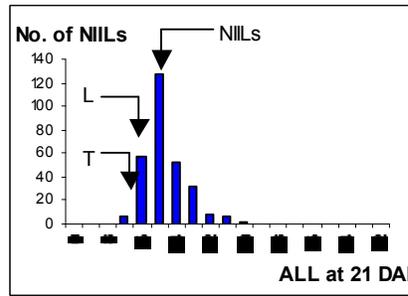
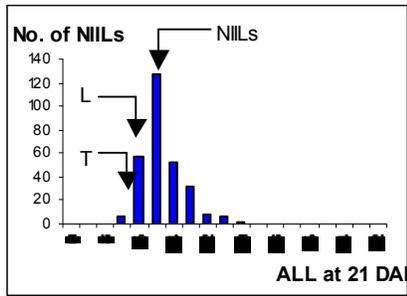
*LH: lesion height (cm), ALL: actual lesion length (cm), DAI: days after inoculation, DAH: days after heading.

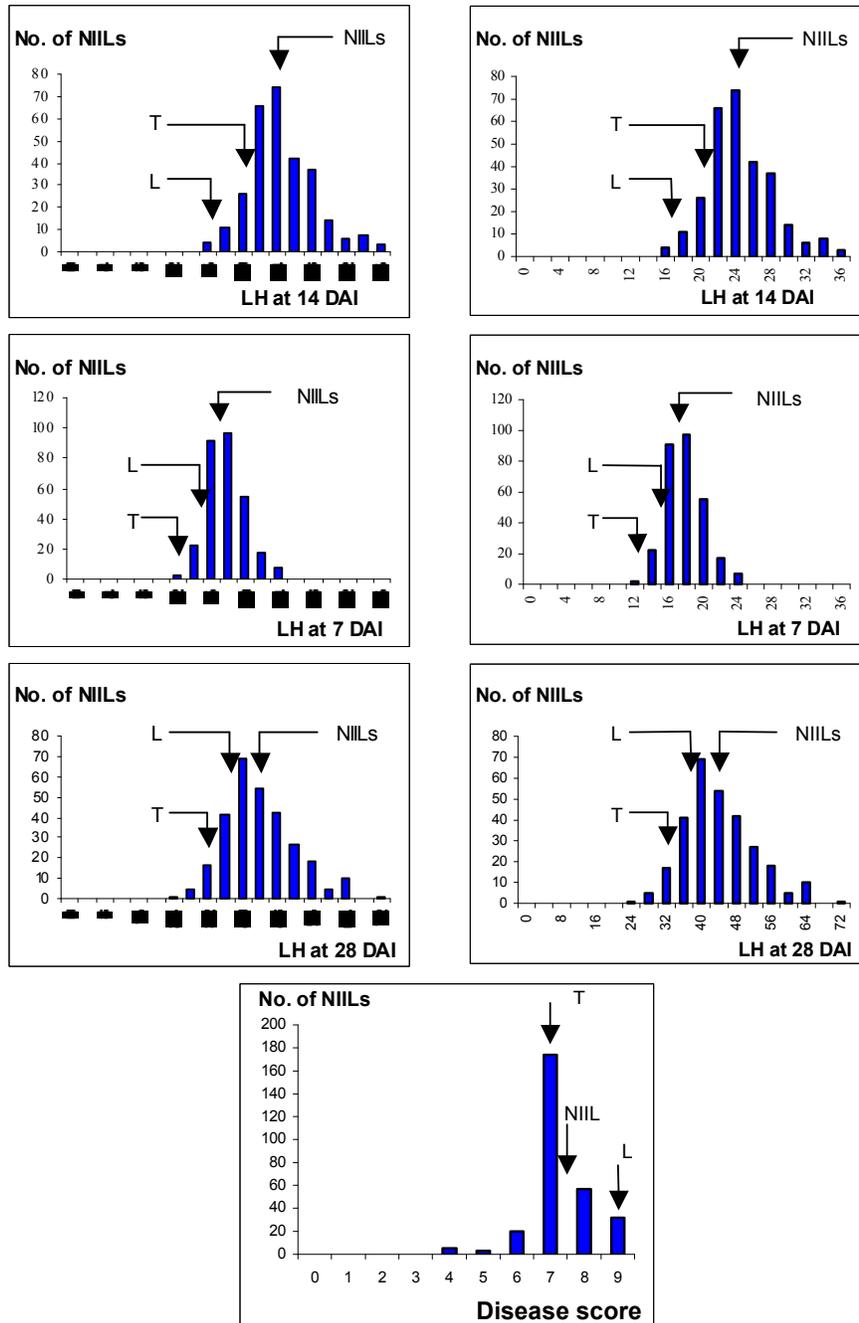
Table 2. Correlation between sheath blight resistance and four morphological traits in the Teqing NIILs population.

Traits [#]	SC	LH1	LH2	LH3	LH4	ALL1	ALL2	ALL3	ALL4	HD	PH	CA	LA
LA	0.21**	0.04	0.09	0.09	0.13*	-0.12*	0.03	0.08	0.10	0.12*	-0.28**	-0.02	1.00
CA	-0.09	-0.18**	-0.13*	-0.13*	-0.08	-0.09	-0.12*	-0.10	-0.10	-0.06	-0.01	1.00	
PH	-0.48**	0.25**	0.01	-0.06	-0.02	0.32**	0.11	0.01	-0.05	0.29**	1.00		
HD	-0.44**	-0.20**	-0.43**	-0.38**	-0.40**	-0.03	-0.28**	-0.32**	-0.39**	1.00			
ALL4	0.53**	0.50**	0.71**	0.80**	0.79**	0.48**	0.78**	0.90**	1.00				
ALL3	0.45**	0.53**	0.72**	0.78**	0.69**	0.60**	0.90**	1.00					
ALL2	0.36**	0.57**	0.73**	0.66**	0.58**	0.70**	1.00						
ALL1	0.04	0.67**	0.42**	0.36**	0.31**	1.00							
LH4	0.53**	0.47**	0.73**	0.86**	1.00								
LH3	0.53**	0.50**	0.84**	1.00									
LH2	0.45**	0.64**	1.00										
LH1	0.16**	1.00											
SC	1.00												

*, ** = significant at ≤ 0.05 and ≤ 0.01 , respectively

[#] SC: score, LH1: lesion height (7 days after inoculation), LH2: lesion height (14 days after inoculation), LH3: lesion height (21 days after inoculation), LH4: lesion height (28 days after inoculation), ALL1: actual lesion length (7 days after inoculation), ALL2: actual lesion length (14 days after inoculation), ALL3: actual lesion length (21 days after inoculation), ALL4: actual lesion length (28 days after inoculation), HD: heading date, PH: Plant height, CA: culm angle, LA: leaf angle.





Hình 1. Frequency distribution of lesion height (LH), actual lesion length (ALL) at 7, 14, 21, 28 days after inoculation (DAI) and disease score developed by inoculation with *Rhizoctonia solani*.

Contribution of Morphological Characters to Resistance

Multiple regression analyses indicated that morphological characters like leaf angle, culm

angle, plant height, and heading date collectively explained from 12-34%, of the total phenotypic variances in sheath blight disease parameters (Table 3). However, out of these traits, heading date contributed

considerably to the total phenotypic variation and plant height played an important role in the total phenotypic variation of disease rating with partial $R^2 = 22\%$. A small, but statistically significant contribution of culm angle to total phenotypic variation of all disease parameters was observed. Correlation and stepwise regression analyses indicated that the recorded resistance was somewhat affected by culm angle and highly affected by

heading date and plant height. The negative relationship between early maturity, short plant stature, and sheath blight disease rating must be considered when selecting plants for sheath blight resistance. However, for practical purposes, plants with early maturity and semidwarf stature are preferred in selection since late maturity and tall plant height are unacceptable characteristics in commercial rice production in the field.

Table 3. Contribution of morphological traits to phenotypic variation for *Rhizoctonia solani* resistance.

Trait [#]	Partial R ² (%)								
	Score	LH1	LH2	LH3	LH4	ALL1	ALL2	ALL3	ALL4
HD	9.89**	8.96**	19.17**	14.94**	16.58**	1.82*	8.09**	10.58**	15.53**
PH	22.45**	6.14**	1.98**	ns	ns	10.33*	3.90**	1.25*	ns
CA	1.51*	4.33**	2.83**	2.51**	1.36*	ns	2.02**	1.61*	1.72*
LA	ns	1.24*	ns	ns	1.20*	ns	ns	ns	ns
Cumulative R ²	33.85	20.67	23.98	17.45	19.14	12.15	14.01	13.44	17.25

*, ** = significant at ≤ 0.05 and ≤ 0.01 , respectively, ns = not significant.

[#] LH1: lesion height (7 days after inoculation), LH2: lesion height (14 days after inoculation), LH3: lesion height (21 days after inoculation), LH4: lesion height (28 days after inoculation), ALL1: actual lesion length (7 days after inoculation), ALL2: actual lesion length (14 days after inoculation), ALL3: actual lesion length (21 days after inoculation), ALL4: actual lesion length (28 days after inoculation), HD: heading date, PH: Plant height, CA: culm angle, LA: leaf angle.

QTLs for Sheath Blight Resistance

The number and locations of significant QTLs detected for LH and ALL did not vary strongly among the assessment times. No QTLs were detected for LH and ALL at 7 DAI. Six QTLs for LH at 14 DAI, eight QTLs for LH at 21 DAI, seven QTLs for LH at 28 DAI, four QTLs for ALL at 14 DAI, five QTLs for ALL at 21 DAI, and eight QTLs for ALL at 28 DAI were mapped on chromosomes 1, 2, 3, 4, 5, 9, and 12, explaining 66.0%, 87.3%, 64.5%, 35.8%, 54.6%, and 93.8% of the phenotypic variation, respectively (Table 4). The percentage of phenotypic variation (R^2) explained by a single QTL ranged from 6.7% to 17.4% for LH and 6.5% to 18.9% for ALL. QTLs *Qsbr2a* and *Qsbr4c* explained most of the phenotypic variation in each assessment time.

In the above chromosomal regions, the alleles of Teqing reduced both LH and ALL, Lemont parent did not contribute any alleles associated with sheath blight resistance. Li et al (1995b) identified six QTLs for disease score in the F₄ population of Lemont/Teqing, but one allele on chromosome 8 for resistance contributed by Lemont could not be identified in the present study. On the other hand, the main QTL (*Qsbr4c*) controlling LH and ALL associated with RM280, on chromosome 4, was located near the chromosomal region of resistance QTL detected by Li et al and *Qsbr2a* controlling LH and ALL associated with RM341, on chromosome 2, was approximately mapped on the same chromosomal region of *qSB2* identified by Zou et al (2000).

Table 4. QTLs detected for Sheath blight resistance based on single marker analysis using ANOVA in a backcross population of a cross between Lemont and Teqing.

QTL	Chr.	Marker interval ^a	Traits ^b	A ^c	R ² (%) ^d	P
<i>QSbr1a</i>	1	<u>RM259-RM23</u>	LH3	1.25	9.20	0.0001
			LH4	2.73	6.70	0.0001
			ALL2	1.14	6.50	0.0001
			ALL3	1.60	8.70	0.0001
			ALL4	2.39	7.30	0.0001
<i>QSbr1b</i>	1	RM212-OSR3	LH2	1.25	9.20	0.0001
<i>QSbr2a</i>	2	RM29-RM341	LH2	1.83	13.80	0.0001
			LH3	3.16	14.50	0.0001
			LH4	3.85	11.60	0.0001
			ALL2	1.59	12.00	0.0001
			ALL3	2.49	14.80	0.0001
			ALL4	3.95	17.30	0.0001
<i>QSbr2b</i>	2	RM250-RM48	Score	0.55	12.00	0.0001
<i>QSbr3</i>	3	<u>RM156-RM16</u>	LH2	2.03	9.30	0.0001
			LH3	3.75	10.00	0.0001
			LH4	3.50	6.70	0.0001
			ALL2	1.66	7.20	0.0001
			ALL3	2.94	11.10	0.0001
			ALL4	4.35	11.20	0.0001
			Score	0.60	10.40	0.0001
<i>QSbr4a</i>	4	<u>RM261-RM142b</u>	LH2	1.11	7.60	0.0001
			LH3	2.70	8.30	0.0001
			LH4	2.95	6.70	0.0001
			Score	0.46	8.30	0.0001
<i>QSbr4b</i>	4	RM303-RM255	ALL4	5.01	12.30	0.0001
<i>QSbr4c</i>	4	<u>A17130-RM280</u>	LH2	1.99	17.30	0.0001
			LH3	3.46	17.40	0.0001
			LH4	4.56	15.80	0.0001
			ALL2	1.24	10.10	0.0001
			ALL3	2.10	12.70	0.0001
			ALL4	3.65	18.90	0.0001
			Score	0.45	11.70	0.0001
<i>QSbr5a</i>	5	OSR35-RM13	LH3	2.60	8.10	0.0001
			LH4	3.48	6.80	0.0001
<i>QSbr5b</i>	5	RM13-gl.1	ALL3	2.63	7.30	0.0001
			ALL4	4.12	8.30	0.0001
<i>QSbr9a</i>	9	<u>RM215-OSR12</u>	Score	0.49	10.40	0.0001
<i>QSbr9b</i>	9	<u>OSR12-RM205</u>	LH2	1.63	8.80	0.0001
			LH3	3.96	11.40	0.0001
			LH4	4.35	10.20	0.0001
			ALL4	3.36	7.90	0.0001
<i>QSbr12a</i>	12	OSR20-RM277	LH3	2.56	8.50	0.0001
<i>QSbr12b</i>	12	RM277-RM260	Score	0.48	7.70	0.0001
<i>QSbr12c</i>	12	<u>RM270-RM235</u>	ALL4	2.79	10.60	0.0001

^b LH2, LH3, LH4: lesion height at 14, 21, 28 DAI; ALL2, ALL3, ALL4: actual lesion length at 14, 21, 28 DAI.

^c A: additive effect, positive value indicates the resistance allele coming from Teqing recurrent parent.

^d R²: percent phenotypic variation explained.

^a The underlined markers are associated with the detected digenic interaction QTLs affecting sheath blight resistance.

Additive effect increased over evaluation times. The QTLs with high additive effects for most resistance traits were found at markers RM341 (on chromosome 2), RM156 (on chromosome 3), and RM280 (on chromosome 4).

Although there were different QTLs involved in the expression of ALL at 14, 21, 28 DAI, the coincidence of QTLs for LH and ALL was observed on five chromosomes 1, 2, 3, 4, and 9 (Table 4, Fig. 2); 61.2%, 48.0%, and 79.2% of the phenotypic variation of LH could be explained by ALL at 14, 21, and 28 DAI, respectively. Since more than half of QTLs for LH coincided with QTLs for ALL, the association of LH with ALL is more likely due to pleiotrophic effect than close linkage of LH and ALL on seven different chromosomes. This effect was also supported by the highly significant correlation between two characters (Table 2). Interestingly, *QSbr3* and *QSbr9* were mapped on the same chromosomal regions of bacterial blight main-effect QTLs (M-QTLs) *QBb3a* and *QBb9b*, respectively (Zhong et al, 2002) (Fig. 2). Also, *QSbr1a*, *QSbr2a*, and *QSbr3* were located near the chromosomal regions of bacterial blight M-QTLs *QBbr1a*, *QBbr2b* (Zhong et al, 2002), and blast M-QTLs *QBr2a*, *QBr3* (Loan, 2002).

Six QTLs for disease rating were identified and found to all together contribute 60.5% of the phenotypic variation (Table 4, Fig. 2). Additive effects ranged from 0.48-0.60. QTLs *QSbr4c*, *QSbr9a*, and *QSbr12b* had

independent effects on heading date and plant height. The QTL *QSbr2b* was approximately mapped on the same location as previously detected QTL (Li et al, 1995b).

Interaction between QTLs for Sheath Blight Resistance

Out of 15 possible digenic interactions for disease score, 15 for LH2, 28 for LH3, 21 for LH4, 6 for ALL2, 10 for ALL3, and 28 for ALL4, only one digenic interaction for score (6.7%), 3 for LH3 (10.7%), and 1 for ALL4 (3.6%) were significant ($P \leq 0.0003$) (Table 5). Most digenic interactions were negative, indicating that the parental types of alleles at the interacting loci resulted in increased resistance while the recombinant types were associated with reduced resistance. The percentages of these interactions were small. However, most previous QTL mapping experiments have revealed very limited or no interactions among QTLs (Paterson et al, 1988; Stuber et al, 1992; Lin et al, 2002), whereas a few others have suggested the importance of epistatic interaction (Li et al, 1997; Yu et al, 2002). Of these digenic interactions, there were the interactions between putative QTL alleles with high additive effects such as RM156 and RM205, RM280 and RM205. The usual estimates of main effects can be confounded by interaction (Li et al, 1997). For breeding purposes using MAS, QTLs that do not require epistatic interactions are more desirable.

Table 5. Additive x additive interactions (AA_{IJ}) between QTLs for resistance to *Rhizoctonia solani* in the backcross population of a cross between Lemont and Teqing.

Trait*	Chr.	Marker interval I	Chr.	Marker interval J	AA_{IJ}	R^2 (%)	F	P
LH3	3	RM156-RM16	9	OSR12-RM205	-3.12	23.11	27.65	0.0001
	4	RM261-RM142b	4	A17130-RM280	-2.13	21.51	23.41	0.0001
	4	A17130-RM280	9	OSR12-RM205	-1.88	21.74	13.87	0.0002
ALL4	1	RM259-RM23	12	RM270-RM235	2.50	10.01	13.47	0.0003
SCORE	3	RM156-RM16	9	RM215-OSR12	-0.33	18.98	15.69	0.0001

* LH3: lesion height at 21 DAI, ALL4: actual lesion length at 28 DAI.

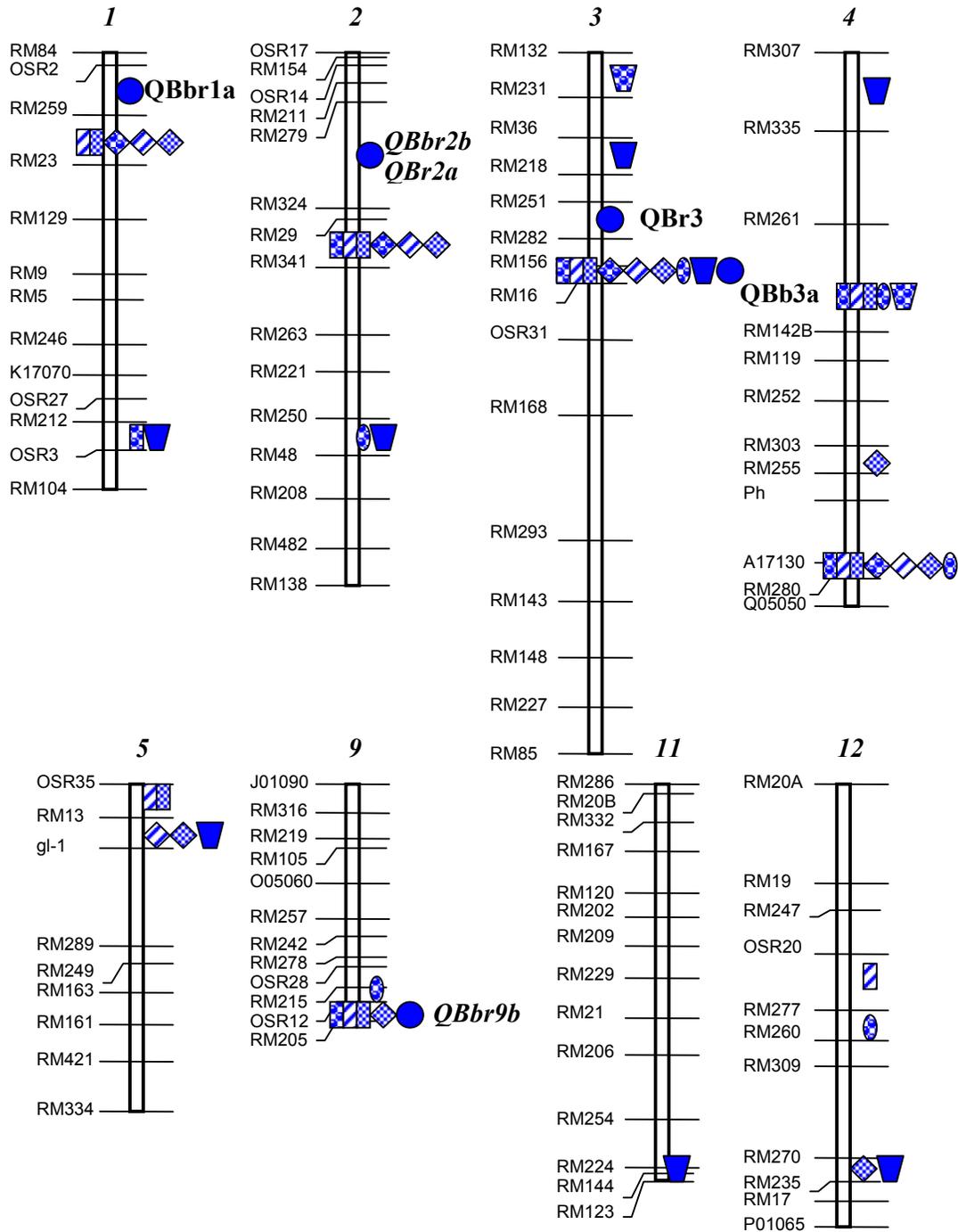


Fig. 2. Chromosomal locations of putative QTLs contribution to resistance to *Rhizoctonia solani* at different growth stages in a backcross population of a cross between Lemont and Teqing.

-  Putative QTLs contributing to reduced lesion height at 14, 21, and 28 DAI, respectively.
-  Putative QTLs contributing to reduced actual lesion length at 14, 21, and 28 DAI, respectively.
-  Putative QTLs contributing to reduced disease score and controlling heading date and plant height, respectively.
-  QTLs for resistance to bacterial blight and blast identified in the same population, *QBbr* for resistance to bacterial blight, *QBr* for resistance to blast.

QTLs for Heading Date and Plant Height

In order to explain the true relationship between sheath blight resistance and heading date and plant height, QTLs for these two characters were also mapped in the same population. Two QTLs (*QHd3* and *QHd4*) controlling heading date were associated with RM132 and RM261 on chromosome 3 and 4, respectively. Eight QTLs (*QPh1*, *QPh2*, *QPh3a*, *QPh3b*, *QPh4*, *QPh5*, *QPh11* and *QPh12*) controlling plant height (Fig. 2) were also detected in seven chromosomes (1, 2, 3, 4, 5, 11, and 12). There was only one case for resistance QTLs (*QSbr4a*) and heading date (*QHd4*) mapped at the same chromosomal region on chromosome 4. Heading date had negative correlation with disease resistance (Table 2).

Li et al (1995a) detected 3 QTLs for heading date and 4 QTLs for plant height in the resistance loci interval, except in one resistance QTL mapped on chromosome 4. Zou et al (2000) showed that most detected resistance loci were not linked to the locus for heading date or plant height. Nevertheless, in the present study, as shown in Fig. 2, *QPh3b*, *QPh5*, *QPh12* and most of QTLs controlling sheath blight resistance were approximately located in the same interval on chromosomes 3, 5 and 12, respectively. However, there was no significant correlation between plant height and LH, and ALL at all assessment times except between LH and ALL at 7 DAI but no QTLs were detected at this time. Neither heading date loci nor plant height was identified near or in the same interval with QTLs controlling sheath blight resistance located on chromosomes 1, 2, 4 and 9. This suggests that resistance QTL (*QSbr4c*) located on the same chromosomal region and linked to RM280 on chromosome 4 is meaningful and useful in the transfer of resistance alleles

from Teqing into breeding materials.

Generally, the results showed that sheath blight resistance was associated with later-maturing varieties and had no correlation with plant height. However, it can not be ascertained if the association between sheath blight and morphological traits is due to pleiotrophic effect or close linkage. Some of the potential reasons for this association are: 1) short statured varieties tend to be early season varieties that develop when environmental conditions most favor the disease development and with their thick canopy create a hot, highly humid environment in which the disease develops and spreads; 2) there is a short distance from the water line to the panicle in short plants, so the same amount of disease causes more damage (score) on short plants than on tall plants; and 3) hybrid breakdown is commonly seen in crosses between indica and japonica (Oka, 1988), thus some plants (shorter plants) may show weakness. In spite of difficulties in current breeding directions toward shorter, early-maturing, and sheath blight resistant varieties, among the identified resistance QTLs, *QSbr1a*, *QSbr2a*, *QSbr4c*, and *QSbr9b* that were not associated with plant morphology or heading date are potential and useful in breeding programs for sheath blight resistance.

In this study, the effect of culm angle and leaf angle on sheath blight resistance was not mentioned because of the inconsistent correlation between the two characters and resistance.

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SUMMARY IN VIETNAMESE**Tính kháng số lượng đối với bệnh đốm vằn trên cây lúa**

Dựa trên bản đồ liên kết và phản ứng đối với bệnh đốm vằn của 266 dòng đẳng gen có nguồn gốc từ cặp lai giữa Lemont và Teqing, 15 QTLs có tính cộng (main-effect QTLs) điều khiển chiều cao vết bệnh và chiều dài vết bệnh đã được định vị trên bảy nhiễm sắc thể (1, 2, 3, 4, 5, 9 và 12). QTLs có tính cộng ảnh hưởng đến tính kháng ở tất cả các thời điểm đánh giá liên kết với dấu phân tử RM341 (trên nhiễm sắc thể 2), RM156 (trên nhiễm sắc thể 3) và RM280 (trên nhiễm sắc thể 4). Tất cả các alen cho hiệu quả giảm chiều cao vết bệnh và chiều dài vết bệnh đều có nguồn gốc từ Teqing. Hầu hết các QTLs ảnh hưởng đến chiều cao vết bệnh và chiều dài vết bệnh ở mỗi thời điểm đánh giá đều được định vị ở cùng một vị trí trên nhiễm sắc thể. Ảnh hưởng của tính cộng đối với tính kháng bệnh đốm vằn quan trọng hơn tính tương tác. Ngày trở tương quan nghịch với tính kháng bệnh nhưng chiều cao cây lại không tương quan với tính kháng. Bốn QTLs - QSbr1a, QSbr2a, QSbr4c, và QSbr9b - không liên kết với ngày trở cho ta một triển vọng trong chương trình chọn tạo giống kháng bệnh đốm vằn.
