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Full Length Article

Study on Integration of Quantitative Trait Locus based on Meta-Analysis Related to the Resistance of Rice Sheath Blight

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Abstract

Rice sheath blight, caused by the soil-borne pathogen *Rhizoctonia solani*, is one of several important diseases which cause yield loss in rice (*Oryza sativa* L.) production. Resistance to disease is controlled by quantitative trait loci (QTLs), including a large number of results of mapping QTLs for rice sheath blight resistance have been reported. However, due to the large confidence interval, there were fewer QTLs that have already been mapped. Unfortunately, more closely linked molecular markers that could be used in breeding. The integration of QTL maps based on meta-analysis could be used to integrate consistent QTLs. A total of 303 QTLs related to disease-resistance in rice have not been yet available due to the large confidence intervals to achieve fine QTL linkage mapping. However, integration of multiple QTL linkage maps incorporating "consistent" QTLs which common to various maps would circumvent this problem. Here, 303 rice sheath blight resistance related QTLs collected from 30 linkage-mapped rice populations were collected. The consistent QTLs were calculated by the method of meta-analysis. The set of "consistent" markers was then integrated with the simple sequence repeat (SSR) reference map Cornell 2001 by BioMercator 2.1. Moreover, a consensus map of rice QTL conferring sheath blight was constructed. A total of 30 consistent resistance-associated QTLs and their linked markers that were localized to chromosomes 1, 2, 3, 5, 6, 7, 9 and 11 chromosomes. The map offered by this research will serve as a basis foundation of rice sheath blight resistance fine mapping, map-based cloning and marker-assisted breeding for rice sheath blight resistance. © 2019 Friends Science Publishers

Keywords: Meta-analysis; *Oryza sativa*; Quantitative trait locus (QTL) integration; Rice; Sheath blight

Introduction

Rice (*Oryza sativa* L.) is one of the most important food crops in the world and China plays a major role in global rice production (Li *et al.*, 2018). Rice sheath blight disease, caused by the soil-borne necrotrophic fungal pathogen *Rhizoctonia solani*, is one of the most destructive rice diseases. After initial disease manifestation occurs mainly in leaf sheaths and leaves, drying of leaves occurs that is followed by great reduction of seed setting rate and significant reduction of 1000-grain weight that frequently result in rice yield reductions of about 10% (Wang and Zheng, 2018). Rice fields severely infected by *R. solani* may even collapse and die across large areas, resulting in reduced yields of up to 50% (Wang and Zheng, 2018). Because no rice variety has yet been discovered that is highly resistant to sheath blight, progress toward breeding of disease resistant varieties has been slow. At present, rice sheath blight control largely relies on chemical treatment-based methods, with poor results and increased environmental pollution (Li *et al.*, 2017, 2018). Therefore, discovery of major disease resistance loci is urgently needed before breeding can efficiently generate disease-resistant rice varieties as a fundamental and effective strategy for ultimately controlling rice sheath blight.

Although a large number of QTLs controlling rice sheath blight resistance had been reported (Li *et al.*, 2018), published QTL maps have been fraught with many problems, such as large intervals between markers, low accuracy and large confidence intervals that have led to map differences among different studies (Tian and Wang, 2013). Because it has been difficult to find molecular markers

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closely linked to rice sheath blight resistance traits, few effective markers are currently available for marker-assisted breeding of resistant rice (Li *et al.*, 2018). Map integrationbased on meta-analysis can compensate for limited single mapping population results stemming from low molecular marker polymorphism. More specifically, by incorporating reliable and accurate "consistent" QTLs using meta-data analysis, high-density maps of molecular markers closely linked to useful marker-assisted breeding traits can be generated (Li *et al.*, 2014). In recent years, several studies demonstrating the successful application of meta-analysis for QTL mapping of wheat (*Triticum aestivum*) (Hu *et al.*, 2016), corn (*Zea mays*) (Wang *et al.*, 2011; Tian and Wang, 2013), soybean (*Glycine max*) (Zhang *et al.*, 2017) and rapeseed (*Brassica napus*) (Zhao *et al.*, 2017) have been reported.

In this study, the published QTLs and related data related to rice sheath blight resistance were collected and sorted. Meta-analysis was then used to generate a set of "consistent" rice QTLs that reliably correlate with sheath blight resistance. These QTLs and their closely linked molecular markers were then compiled to create an improved high-density linkage map to serve as a tool to improve molecular-assisted breeding efficiency toward development of new sheath blight-resistant rice varieties.

Materials and Methods

Collection and Management of QTLs Related to Rice Sheath Blight Resistance

The data of QTLs related to rice sheath blight resistance mainly including the name of the QTL, the chromosome, LOD, contribution rate, mapping population, mapping analysis method, the position in the map and adjacent markers were collected. The traits related to disease rating, relative lesion length, relative lesion height of rice sheath blight were collected (Li *et al.*, 2014). In this study, 303 QTLs related to rice sheath blight resistance were collected from 30 mapping populations (Table 1).

Mapping and Integration of QTLs Related to Rice Sheath Blight Resistance

The collected QTLs were proportionally projected to the reference map Cornell 2001 by tools-maps projection option of the software BioMercator 2.1. The QTLs and their common markers related to rice sheath blight resistance were integrated with the reference map, and a consensus map of rice QTL conferring sheath blight was constructed. The mapping method was detailed in Li *et al.* (2014) report.

Meta-analysis of QTLs Related to Rice Sheath Blight Resistance

Meta-analysis program in BioMercater 2.1 software was used for meta-analysis of rice sheath blight-related QTLs. For the same loci or overlapping loci on the same chromosome, a "consistent QTL" was calculated. The QTL gave five calculation models, among which the model with the smallest AIC (Akaiketype criteria values) was the optimal model. The analysis method was detailed in the report of Li *et al.* (2014).

Table 1: QTLs reported for rice sheath blight resistance

Ref. No.	QTL number	Population type	Analysis method	Reference
1	4	F_2	IM, CIM	Sharma *et al.* (2009)
2	5	F_2	SIM	Chen (2004)
3	12	RIL	CIM	Chen (2012)
4	12	BCF_5	SIM	Dang (2013)
5	10	F_2 RIL	CIM	Fu (2011)
6	4	F_2	SIM	Fu *et al.* (2012)
7	13	BCF_2	MIM	Eizenga *et al.* (2013)
8	10	RIL	CIM	Liu *et al.* (2009)
9	14	RIL	CIM	Liu *et al.* (2013)
10	7	DH	IM	Kunihiro *et al.* (2002)
11	4	RIL	IM	Han *et al.* (2002)
12	2	BC_1F_1	SIM	Hiroyuki *et al.* (2004)
13	4	DH	CIM, MIM	Hua (2007)
14	17	DH	MIM	Nelson *et al.* (2012)
15	8	F_2	IM	Zou *et al.* (2000)
16	4	F_2	SIM	Ji (2001)
17	3	CSSLs	SIM	Lin *et al.* (2013)
18	34	RIL	CIM	Liu (2010)
19	3	F_2	SIM	Lu *et al.* (2009)
20	3	F_2	IM	Pan *et al.* (1999)
21	15	RIL	SIM	Pinson *et al.* (2005)
22	12	RIL	CIM	Channamallikarjuna *et al.* (2010)
23	12	F_2	CIM	Wang (2013)
24	17	F_2	CIM	Wen (2014)
25	1	F_2	SIM	Xiang (2006)
26	5	DH	CIM	Xu *et al.* (2011)
27	7	F_2	IM	Yang (2003)
28	37	RIL	SIM	Liu *et al.* (2014)
29	18	RIL	CIM	Yu (2009)
30	6	F_4	SIM	Li *et al.* (1995)

Results

Distribution of QTLs Related to Rice Sheath Blight Resistance on the Cornell 2001 SSR Map

A total of 303 QTLs related to rice sheath blight from 30 mapping populations were integrated into the Cornell 2001 SSR reference map using BioMercator 2.1 to ultimately construct a distribution map of "consistent" rice sheath blight resistance-related QTLs (Fig. 1). The results showed that the QTLs of resistance to the rice sheath blight resistance QTLs were mainly distributed on chromosomes 1, 2, 3, 5, 6, 7, 9 and 11, with clustering of QTLs on chromosomes 1, 2, 3, 5 and 6 and fewer QTLs mapped to chromosomes 4, 8, 10 and 12. Notably, 43 QTLs were mapped to chromosome 1 of the Cornell 2001 SSR reference map (Fig. 1).

Results of Meta-analysis of QTLs Related to Rice Sheath Blight Resistance

In Table 2, meta-analysis of rice sheath blight resistance-

Table 2: Meta-analysis results of rice sheath blight resistance

Chromosome	AIC Value	Map Position	C.I. (from)	C.I. (to)	Map Distance	Left Marker	Coordinate	Right Marker	Coordinate
1	773.58	35.2	34.66	35.74	1.08	RM522	33.9	RM151	36.2
1	773.58	128.19	127.25	134.31	3.06	RM1297	127.2	RM1183	134.5
1	773.58	164.3	162.1	166.4	4.3	RM315	163.5	RM3602	167.6
1	773.58	241.66	227.8	247.2	19.4	RM3233	227.8	RM8134	247.2
2	966.58	8.63	6.9	10.37	3.47	OSR14	6.9	RM6842	13
2	966.58	66.73	66.17	67.29	1.12	RM27	66	RM29	68.9
2	966.58	85.45	84.68	86.22	1.54	RZ260	84	RM3858	87.2
2	966.58	161.53	160.36	162.71	2.35	C601	158.6	RM5472	162.7
3	1386.8	34.25	32.32	36.18	3.86	RG450	33	RG100	37.2
3	843.45	63.06	62.76	63.36	0.6	RM1350	62.5	RM7	64
3	843.45	181.88	179.13	184.63	5.5	RM15824	175	RM5924	187.1
3	843.45	369.52	359.03	380.01	20.98	RM3684	359.3	RM3585	378.3
5	665.42	60.05	59.53	60.58	1.05	RM516	59.6	RM5140	61.1
5	665.42	111.48	111.45	111.51	0.06	RM6545	111.4	RM7446	111.5
5	665.42	117.49	116.84	118.14	1.3	C246	117.3	RM26	118.8
5	665.42	132.4	131.9	132.89	0.99	RM1248	131.6	RM1182	133
6	92.61	4.8	2.2	7.4	5.2	RM170	2.2	RM190	7.4
6	92.61	33.32	30.26	36.38	6.12	RM217	27.6	RM253	37
6	92.61	68.55	63.22	74.24	11.02	RM3183	64.1	RM3	74.3
6	92.61	136.01	131.96	140.06	8.1	RM5509	129.6	RM412	142.4
7	970.94	34.42	33.63	35.2	1.57	RM5481	34.1	RM5793	35.6
7	970.94	69.89	68.61	71.17	2.56	RM455	65.75	RM3555	71.6
7	970.94	119.83	119.16	120.5	1.34	D760	118.6	RM248	120.8
7	970.94	484.75	453.08	516.41	63.33	RM17454	481.1	RM21078	603.4
9	126.93	30.3	28.16	32.43	4.27	RM296	27.7	RM1896	34
9	126.93	68.46	65.06	71.85	6.79	RM4107	64.4	RM242	73.3
9	126.93	105.27	103.01	107.53	4.52	MS-H	103	RG451	105.5
11	25.14	48.79	48.3	49.27	0.97	CT224	48.3	RM287	49.3
11	25.14	58.24	56.51	59.97	3.46	RM202	55.1	RM479	61.7
11	25.14	77.19	69.05	85.32	16.27	RM552	68.6	RM208	85.3

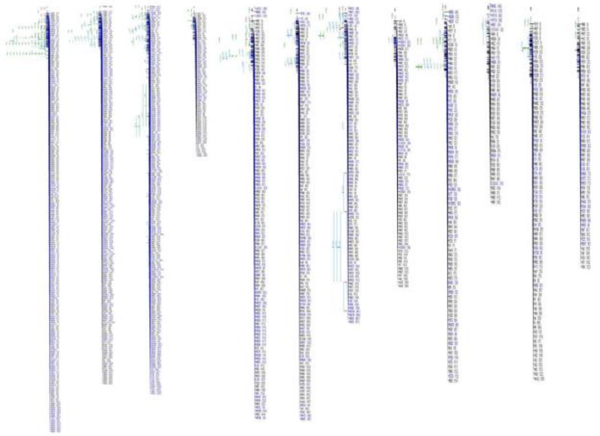

Fig. 1: Consensus map of QTL of rice sheath blight resistance

related QTLs generated 30 "consistent" QTLs mapped to 8 rice chromosomes. Resulting map distances between QTLs were smaller than those in the original reference map, with smallest and largest distances between QTLs observed of 0.06 cM and 63.33 cM, respectively. Moreover, "consistent" QTLs were discovered, of which 20 markers interval distances of less than 5 cM and 11 markers interval distances of less than 2 cM. "Consistent" QTLs localizing to chromosomes 2 and 5 were all separated by distances less than 5 cM.

At map position 111.48 cM on chromosome 5, the detected marker interval was RM6545-RM7446 and the confidence interval was 111.45-111.51 cM. The map distance of "consistent QTL" was only 0.06 cM; at map position 132.4 cM, the marker interval was RM1248-RM1182, and the confidence interval was 131.9-132.89 cM with a "consistent QTL" map distance of 0.99 cM. At map position 48.79 cM on chromosome 11, CT224-RM287 was detected as the marker interval, and the confidence interval (48.3-49.27 cM) was only 0.97 cM.

Discussion

The QTLs meta-analysis strategy proposed in recent years used the relevant information about the known QTLs, integrated and reanalyzed data, and then deduced the meta QTLs with higher reliability and more accurate location intervals. Zhang *et al.* (2017) integrated 48 QTLs about symbiotic nodule-related traits across 4 independent studies, and two meta-QTLs controlling nodule number, nodule size and nodule dry weight were proposed. Meta-QTL with confidence interval reduced to 3.9 cM. In this study, 303 QTLs related to the resistance of rice sheath blight from 30 mapping populations were collected and 30 "consistent QTLs" were identified. Zhou *et al.* (2014), Wang *et al.* (2011) and Tian and Wang (2013) integrated "consensus QTLs" related to the yield traits of maize by meta-analysis. Hu *et al.* (2016) integrated 168 QTLs controlling grain water-soluble carbohydrates content from different genetic mapping populations in wheat and 16 meta QTL and tightly linked markers were confirmed, with the minimum confidence interval of meta QTL reaching to 0.77 cM. In this study, 30 "consistent QTLs" related to rice sheath blight were integrated by meta-analysis, the average interval distance of these QTLs reduced to 9.09 cM, of which 20 has interval distances less than 5 cM, the smallest interval distance was only 0.06 cM, 11 of which were less than 2 cM.

Map integration based on meta-analysis was shown here to effectively short the QTL interval. For example, the previously reported rice sheath blight grade-associated QTL marker interval RM1216-RM14 on chromosome 1, which exhibited a peak marker contribution rate of 36.4% for RM1339 that accounted for 36.4% of the observed phenotypic variation (Sharma *et al.*, 2009). The QTL interval distance in original map was 52 cM, however, the "consistent QTL" interval distance in the integrated map was only 4.3 cM. There were 21 QTLs located on chromosome 5 from 15 mapping populations. These QTLs were projected into reference map Cornell 2001.

By meta-analysis, the intervals distance of QTLs from different populations and genetic backgrounds could be effectively reduced and the major QTLs could be accurately inferred. The rice sheath blight resistance QTL qSB-9 had been previously mapped to chromosome 9, with the resistance allele of rice variety Teqing designated qSB-9^{Tq}. The near-isogenic lines were used to fine-map and localize the QTL between RM242-Y92.5 (Yin *et al.*, 2009). In this study, the integrated "consistent QTL" was mapped to the position 68.46 cM on chromosome 9 within the RM4107-RM242 marker interval, which similar to that of major rice sheath blight resistance QTL qSB-9 obtained previously *via* fine-mapping. These results suggest that the integrated "consistent" QTL found here may indeed represent the major QTL associated with rice sheath blight.

As an important breeding strategy for the development of crops, molecular-assisted breeding can improve breeding efficiency and short breeding cycles. However, due to limited accuracy of major gene mapping, limited validity of molecular markers, difficult implementation of detection technologies and high economic costs, molecular-assisted breeding technology has not yet been widely applied to rice breeding (Zhou *et al.*, 2014).

Fortunately, integration of QTL maps based on meta-analysis, as done in this study, can discover QTLs and molecular markers closely associated with sheath blight resistance in rice, thereby facilitating molecular-assisted breeding.

In this study, Cornell 2001 was used as the reference map. The map was a high density genetic linkage map. There were a lot of common markers between the map and the original map, which facilitated the integration of the map and the QTL. The molecular marker closely linked to rice sheath blight QTL was SSR marker. The SSR marker detection technique was simple, reproducible and inexpensive, which could reduce breeding costs. Moreover, SSR molecular markers RM315, RM3602, RM6545, RM7446, RM1350, RM7, RM1248, RM1182 and RM287 were closely linked to the QTL of rice sheath blight resistance in this study, which could potentially be useful for molecular-assisted breeding of sheath blight-resistant rice. In addition, a clustered distribution of QTLs related to rice sheath blight was revealed by the integrated high-density QTL genetic map, providing a theoretical framework for future cloning of rice sheath blight resistance genes.

Conclusion

Rice sheath blight is one of several important diseases causing yield loss in rice production. Many QTL were mapped, but few of them could be used in molecular-assisted breeding. Meta-analysis map integration could effectively shorten the QTL interval distance by integrating "consistent QTL". In this study, meta-analysis of QTL mapping of rice sheath blight had been conducted by using BioMercator 2.1 software based on the reference map Cornell 2001, the data of 303 QTLs reported from 30 linkage-mapped rice populations were collected. A total of 30 "consistent QTLs" and linked markers were found from localized to chromosomes 1, 2, 3, 5, 6, 7, 9 and 11 chromosomes. These "consistent QTLs" and their closely linked markers could be used in molecular-assisted breeding of sheath blight-resistant rice in future.

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