

稻米粒形的 QTL 定位及上位性和 QE 互作分析

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摘 要: 利用 0 广陆矮 4 号^①× 10 佳辐占^②水稻重组自交系构建了 SSR 标记的遗传图谱. 联合 2007 年和 2008 年获得的两组稻米粒长 (GL)、粒宽 (GW)、长宽比 (L/W) 数据应用混合线性模型方法进行 QTL 定位, 并作加性效应、加性×加性上位互作效应以及加性 QTL、上位性 QTL 与环境的互作效应分析. 结果显示: (1) 在加性效应分析中两个群体共检测到 4 个控制粒长的 QTL, 4 个控制粒宽的 QTL, 5 个控制长宽比的 QTL, 贡献率分别为 13.81%、15.36% 和 16.29%. (2) 在上位互作效应分析中两个群体共检测到 2 对控制粒长的互作 QTL, 1 对控制粒宽的互作 QTL, 3 对控制长宽比的互作 QTL, 贡献率分别为 5.77%、2.59% 和 7.42%. (3) 环境互作检测中, 发现共有 13 个加性 QTL 和 4 对 QTL 的加性×加性上位性与环境产生了互作效应. 结果表明, 上位性效应和加性效应都影响稻米粒形遗传, QE 互作效应也对粒形有着显著的影响.

关键词: 水稻; 粒形; 数量性状座位; 上位效应; QE 互作效应

中图分类号: Q343.1+7 文献标识码: A

Mapping QTLs for Rice Grain Shape with QTL×Environment Interactions and Epistatic Effects Analysis

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Abstract: In this study, a recombinant inbred line (RIL) population derived from the indica-indica rice cross 10Guangluai 4^①× 10Jiafuzhan^② was used in mapping of Quantitative trait loci (QTLs). Based on mixed linear model QTLmapper1.6, mapping was carried out for grain shape such as grain length (GL), grain width (GW) and length-width ratio (L/W) in rice in 2007 and 2008. QTLs were determined at the one-locus and two-locus levels, and QTL-by-environment (QE) interactions were analyzed. Four, four and five QTLs were detected to have significant additive effects for GL, GW and L/W, and the contribution rate were 13.81%, 15.36% and 16.29%, respectively. Two, one and three pairs of epistatic QTLs with significant additive-by-additive (AA) interaction effects (epistatic effects) were identified for the three traits, and the contribution rate were 5.77%, 2.59% and 7.42%, respectively. Significant QE interactions were found for thirteen QTLs with additive effects and four pairs of epistatic QTLs. The results indicated that the epistatic and additive effects played an important role on the inheritance of grain shape, and the environmental factor had significant effects on the three traits.

Key words: rice (*Oryza sativa* L.); grain shape; QTLs; epistatic effects; QE interaction effects

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Grain shape including grain length (GL), grain width (GW) and length-width ratio (L/W) is a very important character of appearance quality and affects milling quality^[1], cooking quality^[2,3], nutritional quality^[4] and yield^[5]. Therefore, it is an important agronomic traits in rice breeding and directly related to market value of rice. It will be efficient for breeders to indirectly improve other grain quality by selecting proper grain shape directly. So many investigations have been focused on the inheritance of rice grain shape.

Most of the previous reports indicated that grain shape was controlled by multiple QTLs which mainly shown additive effects and influenced by maternal effects and QE interaction effects^[6-8]. Identification of QTLs has advanced rapidly for GL, GW and L/W^[9], and three genes have been cloned^[10,12], but few epistatic effects and QE interactions effects have been analyzed. In the present study, based on a mixed linear model^[13] and a recombinant inbred line (RIL) population, QTLs of grain shape were determined at the one-locus and two-locus levels, and the additive effects, epistatic effects and QE interactions were analyzed in detail. The results will be useful in detecting genetic networks for grain shape and molecular marker-assisted breeding.

1 Materials and methods

1.1 Plant materials

An indica-indica rice cross 10Guangluai 47 × 10Jiafuzhan was made in 2001. An RIL population (GJ-RIL) containing 435 lines derived from a single F₁ plant by single-seed descent was developed. In 2007 and 2008, 180 lines and their two parents were transplanted in paddy field of the Farm of Xiamen University, Xiamen, China, with one replication, in a randomized complete block design. Individual plot consisted of four rows, six plants per row with the planting density 20 cm × 20 cm. For each line, main panicles of eight plants were harvested.

1.2 Methods

1.2.1 Rice grain quality evaluation

Paddy rice

was de-husked and milled using a miller (manufactured by Taizhou Food and Oil Machinery Factory, Zhejiang, China) according to the National Standards NY 147-88. For evaluation of grain shape that consists of GL, GW, and L/W, ten unbroken milled rice grains from each line were randomly selected and lined up length-wise along a ruler to measure GL, then the grains were arranged breadth-wise to measure GW. The values were averaged and used as the measurements for GL and GW of the line. L/W of grains was calculated as grain length divided by width. All above parameters were measured with three replications for each sample of the RIL lines and their parents.

1.2.2 QTL analysis A genetic map of 149 SSR markers was constructed and the average distance between markers was 9.7 cM, which is lesser than the minimum required level for QTL mapping. QTLMapper 1.6 of the mixed linear model^[13] was employed to determine QTLs conditioning grain shape with the year as the environmental factor. By running the sub-menu of the Probabilities (The inclusion probability and the exclusion probability were 0.005. The threshold probability was 0.01), important markers and marker pairs were selected using stepwise regression analysis. The significance of the QTLs effects, including additive effect, additive-by-environment (AE) interaction effect, epistatic effect, and epistasis-by-environment (AAE) interaction effect, were further tested by running the sub-menu of the Bayesian test ($P < 0.005$). QTLs were designated as proposed by McCouch *et al.*^[14].

2 Results

2.1 Phenotypic variation

The mean values for the two parents and RIL in the years of 2007 and 2008 were listed in (Table 1). Significant differences were observed on all three grain shape parameters between the parents. The mean values of GL, GW and L/W all showed variations between two years, indicating that the environmental factor had effects on the three traits. The distributions of GL, GW and L/W of the RIL population were

Table 1 The phenotype for grain shape of the GJ-RIL and parents in different years

Year	Trait	Female parent	Male parent	Max	Min	Mean	Kurtosis	Skewness
2007	GL/mm	5.86	8.12	8.02	5.78	7.01	-0.778	0.063
	GW/mm	2.68	2.14	2.73	1.99	2.38	-0.579	-0.027
	L/W	2.19	3.79	3.77	2.20	2.96	-0.232	0.183
2008	GL/mm	6.00	8.01	8.00	5.77	6.97	-0.650	0.003
	GW/mm	2.66	2.06	2.79	1.94	2.39	0.116	-0.005
	L/W	2.26	3.89	3.82	2.13	2.93	0.097	0.176

Note: GL, Grain length; GW, Grain width; L/W, Length-width ratio; The same as below.

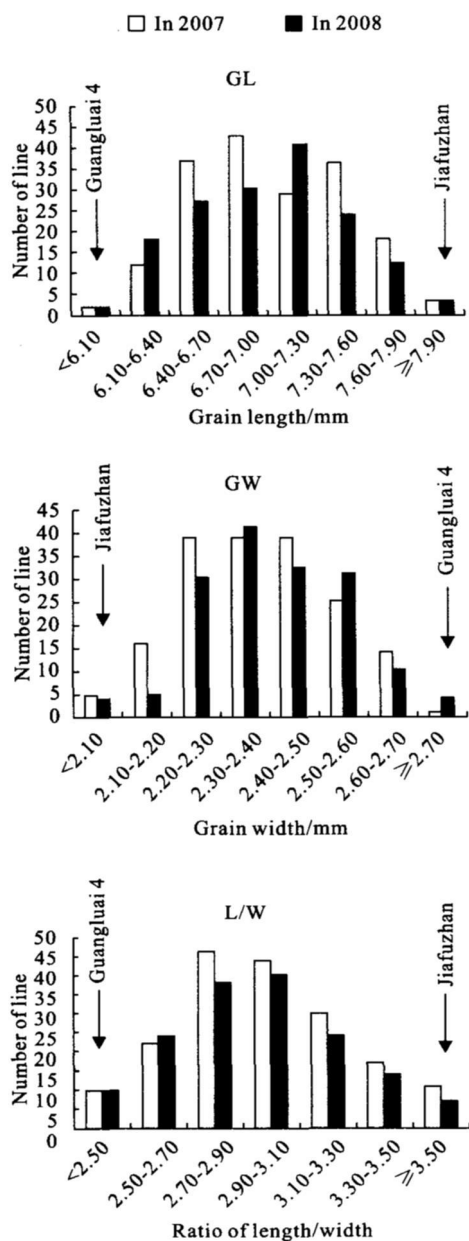


Fig. 1 Distributions of grain shape in GJ-RIL in different years

shown in histograms (Fig. 1). The distribution modes of the three traits showed unimodal, respectively. Transgressive segregations occurred in GW in two years. All the three traits in RIL exhibited continuous variations, showing quantitative inherited traits.

2.2 Significant additive QTLs and AE interactions

A total of thirteen QTLs were detected as having significant additive effects for the grain shape, including four for GL, four for GW and five for L/W (Table 2). All of these QTLs also exhibited AE interaction effects for the grain shape.

Four QTLs for GL were distributed on chromosomes 2, 3, 8 and 9. The phenotypic variation explained by individual QTL ranged from 1.67% ~ 7.01%, and all of them explained 13.81% of phenotypic variation (Table 2). Guangluai 4 alleles from *qGL-9* increased GL, while Jiafuzhan alleles from the other three QTLs increased GL. *qGL-3* on chromosome 3 showed the largest effect on the trait with a LOD score of 12.19 and explained 7.01% of the phenotypic variation. The phenotypic variation explained by individual AE interaction ranged from 0.58% ~ 14.56%, and all of them explained 29.41% of phenotypic variation. The AE interaction for *qGL-3* exhibited negative effect in 2007, while the others exhibited positive effects in 2007.

Four QTLs were distributed for GW on chromosomes 1, 3, 5 and 10. The phenotypic variation explained by individual QTL ranged from 2.08% ~ 4.96%, and all of them explained 15.36% of phenotypic variation (Table 2). *qGW-1* and *qGW-5* showed the largest effect on the trait and explained 4.96% of the phenotypic variation. Jiafuzhan at

les from *qGW-10* increased GW. 10Guangluai 4⑦ alleles from the other three QTLs increased GW. The phenotypic variation explained by individual AE interaction ranged from 3.55% ~ 11.09%, and all of them explained 25.53% of phenotypic variation. The AE interaction for *qGW-10* exhibited negative effect in 2007, while the AE interactions for the others exhibited positive effects in 2007.

Five QTLs for L/W were distributed on chromosomes 1, 2, 3 and 9. The phenotypic variation explained by individual QTL ranged from 1.48% ~ 7.92%, and all of them explained 16.29% of phenotypic variation (Table 2). 10Guangluai 4⑦ alleles from *qL/W-9* increased L/W, while 10Jiafuzhan⑦ alleles from the other four QTLs increased L/W. The phenotypic variation explained by individual AE interaction ranged from 4.02% ~ 10.41%, and all of them explained 36.04% of phenotypic variation. The AE interactions for *qL/W-1*, *qL/W-3-1* and *qL/W-3-2* exhibited negative effects in 2007, while the AE interactions for *qL/W-2* and *qL/W-9* exhibited positive effects in 2007.

2.3 Significant epistatic QTLs and AAE interactions

Six pairs of significant epistatic QTLs were detected for grain shape, of which two for GL, one for GW and three for L/W (Table 3). Four pairs of

these QTLs also exhibited AAE interaction effects for grain shape.

Two pairs of epistatic QTLs for GL were distributed on chromosomes 1 and 6. The phenotypic variation that was explained 3.10% and 2.67% (Table 3). The two-locus genotypes from the same parent appeared to increase GL for the pair of *qGL-1-2* and *qGL-6-2*, while recombinant two-locus combinations increased GL for the other pair. Significant AAE interactions were observed for the two pairs of epistatic QTLs. They explained 2.67% and 7.46% of the phenotypic variation. The AAE interaction for the pair of *qGL-1-2* and *qGL-6-2* exhibited negative effect in 2007, while the other pair exhibited positive effect in 2007.

One pair of epistatic QTLs for GW were distributed on chromosomes 2 and 7. The phenotypic variation was explained 2.59% (Table 3). The recombinant two-locus combinations increased GW for this pair. The AAE interaction exhibited positive effects in 2007.

Three pairs of epistatic QTLs for L/W were distributed on chromosomes 1, 5 and 7. They explained 7.42% of the phenotypic variation. The recombinant two-locus combinations appeared to increase GL for the pair of *qL/W-1-1* and *qL/W-1-2*, while two-locus genotypes from the same parent

Table 2 Additive QTLs and AE interactions for grain shape based on GJ-RIL

Trait	QTL	Interval	LOD	A ^{a)}	H ² (A)/%	AE ^{b)}	H ² (AE)/%
GL	<i>qGL-2</i>	RM322~ RM438	3.97	- 0.080 0	2.87	0.069	4.25
	<i>qGL-3</i>	RM16~ RM411	12.19	- 0.125 2	7.01	- 0.127	14.56
	<i>qGL-8</i>	RM152~ RM408	2.25	- 0.071 3	2.26	0.026	0.58
	<i>qGL-9</i>	RM242~ RM434	4.30	0.061 3	1.67	0.105	10.02
GW	<i>qGW-1</i>	RM462~ RM428	5.64	0.033 9	4.96	0.026	5.79
	<i>qGW-3</i>	RM503~ RM426	4.06	0.022 1	2.08	0.024	5.10
	<i>qGW-5</i>	RM598~ RM5140	8.63	0.034 0	4.96	0.036	11.09
	<i>qGW-10</i>	RM271~ RM311	3.46	- 0.028 0	3.36	- 0.021	3.55
L/W	<i>qL/W-1-1</i>	RM462~ RM428	3.82	- 0.049 3	2.46	- 0.047	4.59
	<i>qL/W-2</i>	RM322~ RM438	8.11	- 0.052 8	2.87	0.071	10.41
	<i>qL/W-3-1</i>	RM411~ RM504	10.72	- 0.088 2	7.92	- 0.073	9.53
	<i>qL/W-3-2</i>	RM347~ RM5475	2.64	- 0.039 2	1.56	- 0.045	4.02
	<i>qL/W-9</i>	RM242~ RM434	3.42	0.038 3	1.48	0.060	7.49

Note: a). Additive effects: Positive a value implies that the parent 10Guangluai 4⑦ takes positive effect value for the additive effect, while the parent 10Jiafuzhan⑦ takes the negative effect. Negative a value means that the parent 10Guangluai 4⑦ takes the opposite negative value for the additive effect, while the parent 10Jiafuzhan⑦ takes the positive; b). AE represented the effects of QTL × environment in 2007. The effects of QTL × environment in 2008 are the same as AE, but in reverse direction.

Table 3 Epistatic QTLs and AAE interactions for grain shape based on GJ-RIL

Trait	QTL	Interval i	QTL	interval j	LOD	AA ^{a)}	H ² (AA)/%	AAE ^{b)}	H ² (AAE)/%
GL	<i>qGL-1</i>	RM9~ RM488	<i>qGL-6-1</i>	RM 508~ RM469	3.85	- 0.083 2	3.10	0.054	2.67
	<i>qGL-1-2</i>	RM486~ RM265	<i>qGL-6-2</i>	RM 190~ RM197	4.04	0.077 4	2.67	- 0.090	7.46
GW	<i>qGW-2</i>	RM526~ RM106	<i>qGW-7</i>	RM 295~ RM481	4.01	- 0.024 8	2.59	0.023	4.07
	<i>qL/W-1-1*</i>	RM462~ RM428	<i>qL/W-1-2</i>	RM1~ RM 578	4.26	- 0.033 0	1.08		
L/W	<i>qL/W-5-1</i>	RM598~ RM 5140	<i>qL/W-5-2</i>	RM 289~ RM169	4.00	0.048 9	2.39		
	<i>qL/W-5-3</i>	RM480~ RM538	<i>qL/W-7</i>	RM 500~ RM445	4.55	0.059 6	3.59	- 0.054	5.78

Note: a). A positive AA value implies that the two-locus genotypes being the same as those in the parent Guangluai 4 or the parent Jiafuzhan take the positive effects, while the two-locus genotypes of recombination between the parent Guangluai 4 and the parent Jiafuzhan take the negative effects. The case of negative AA values is just the opposite; b). The AAE is the predicted interaction effects between the epistasis (between QTLs *i* and *j*) and environment in 2007. The interaction effect of between the epistasis (between QTLs *i* and *j*) and environment in 2008 is the same as AAE, but in reverse direction; *. The QTLs exhibit both additive and additive×additive epistatic effects.

increased GL for the others. Only one AAE interaction for the pair of *qL/W-5-3* and *qL/W-7* was observed, which explained 5.78% of the phenotypic variation. The AAE interaction exhibited negative effects in 2007.

3 Discussion

The important outcome of the present study is the characterization of the additive QTLs, epistatic QTLs and the QE interactions in controlling the expression of the three traits that are critical in determining the appearance quality.

A total of thirteen QTLs were detected and the *qGL-8*, *qGW10* were new QTLs for grain shape. There were nine loci detected in similar loci to those reported previously. RM16~ RM411 and RM411~ RM504 would be in a similar location as RZ403~ R19 and C1081~ RZ403, as reported by He *et al.*^[15] and Tan *et al.*^[16], respectively. RM322~ RM438 and RM438~ RM341, as reported by Rabiei *et al.*^[17], were likely in a similar locus. RM242~ RM434 would be in similar location to C472~ RM201, which was reported by Xing *et al.*^[18]. RM242~ RM434 would also be in similar location to RM242~ RM278, an epistatic QTL for L/W detected by Lei *et al.*^[19]. RM462~ RM428 would be in a similar location to C161~ R753 and C131~ RZ288, as reported by Tan *et al.*^[16] and Xu *et al.*^[5], respectively. RM598~ RM5140 would be in similar location to RG9~ RG182 and RM437~ RM289, as reported by Lin *et al.*^[20] and Rabiei *et al.*^[17], respectively. RM347~ RM5475 would be in

similar location to RM55, which was reported by Chen *et al.*^[21].

Six pairs of epistatic QTLs were detected, and one QTL of those, RM462~ RM428, was found in additive effect analysis. The epistatic QTL for GL, RM9~ RM488, would be in a similar location to the epistatic QTL for GL, RM104~ RZ14 that was detected by Lei *et al.*^[19]. The epistatic QTL for GW, RM526~ RM106, would be in similar location to the epistatic QTL for GL and L/W, OSR26~ RM208 detected by Lei *et al.*^[19], while the epistatic QTL for L/W, RM500~ RM445, would be in a similar location to the epistatic QTL for GL, G06080~ RM214 detected by Lei *et al.*^[19].

The importance of epistatic effects as the genetic basis for complex traits has been reported by previous quantitative genetic studies^[22,23]. To be compared with additive effects, epistasis also exhibited significant genetic effects in the present study. It is reported that all three types of epistasis were important factors that affected the genetic variation in populations^[24,26]: interactions between QTLs, interactions between QTLs and background (modifying) loci, and interactions between complementary loci^[25]. Liao *et al.* detected that the third type epistasis was perhaps the most important one^[25]. In the present study, the epistasis showed mainly the third type, and only one pair of AA interaction exhibited the second type. Some epistatic effects for paddy shape were detected involving additive QTLs^[27]. There was a hypothesis that additive QTLs and their epistatic QTLs are interchangeable

ble, depending on the genetic background and probably on the environment in which they were identified^[25,26]. And more epistatic QTLs were detected in the populations of parents with greater genotypic differences^[25].

In the present study, AE interactions had the largest effects on L/W, followed by GL and GW. Li *et al.*^[28] reported that all the QTLs detections for grain appearance quality were affected by QE interactions, and QTLs detections for GL and L/W may be more weakly affected. But Xing *et al.*^[18] suggested that most of the QTLs with larger genetic effects for paddy appearance quality didn't exhibit significant QE interaction effects. In the present study, AAE interactions were also detected. AAE interactions had the largest effects on GL, followed by L/W and GW. Analysis for paddy shape showed AAE interactions had the largest effects on GL in the studies of Tan *et al.*^[27].

In the present study, we detected different QTLs for corresponding traits in the same marker interval. For example, *qGL-2* and *qL/W-2* were detected in interval RM322~ RM438, and *qGL-9* and *qL/W-9* were

detected in interval RM242~ RM434, and *qGW-1* and *qL/W-1* were detected in interval RM462~ RM428. In addition, they all had AE interactions at the same time. Tan *et al.*^[16] suggested that the L/W almost completely controlled by the main-effect QTLs for GL and GW. Xing *et al.*^[18] reported that they detected a QTL for GL and a QTL for L/W both near the C1087 marker on chromosome 3, and they suggested that it may be one gene have one more effects on different traits. According to the genetic effects estimated for the genomic region containing the QE interaction effects detected in this study, the results should support the notion that GL was positively associated with L/W, but GW was negatively associated with L/W^[29].

Grain shape is an economically important character in rice planting. The studies of the genetic network of rice grain shape would be benefit to rice grain shape inheritance. The investigations of the genetic effects and QE interactions for grain shape in this study would also have great impact on the marker-assisted selection (MAS) for developing new varieties.

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