

Detection of Main-effect QTLs, Epistatic QTLs and QE Interactions for Grain Appearance of Brown Rice (*Oryza sativa* L.)

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Abstract

The objective of this study is to identify main-effect QTLs, epistatic QTLs, and the interactions between QTL and the environment associated with grain appearances of brown rice. A genetic linkage map was created with 172 DNA markers spanning 12 rice chromosomes based on 120 DH lines, which derived from a cross between 'Samgang' (*Tongil*) and 'Nagdong' (*Japonica*). One thousand-grain weight, length, width, length-to-width ratio, and thickness were evaluated regarding the DH population. Twenty independent QTLs and fourteen epistatic QTLs were identified in using CIM by two programs, known as WinQTLcart2.5 and QTLMAPPER. The QTLs of qgw9.1 in an interval of RM434-RM242 on chromosome 9 and qgw11.1 at a peak marker of RM287 on chromosome 11 for one thousand-grain weight, qgwi2.2 for grain width at a peak marker of RM450, qlw2.1 for length-to-width ratio flanked by RM492 and RM324, and qgt2.1 for thickness flanked by 2009 and RM492 on chromosome 2 were detected over two years, which can be considered as stable QTLs. The epistatic effect might be an important component for genetic basis of one thousand-grain weight and width. The main-effect QTLs of grain width and length to width ratio were easily influenced by environments.

Key words: Grain appearance, main-effect QTLs, epistatic QTLs, QE interactions

Introduction

Grain appearance, consisting of one thousand-grain weight, length, width, shape and thickness plays an important role in international marketing for consumers and sellers. Since the characteristics related to rice grain appearance are quantitatively inherited, it is difficult for breeders to efficiently achieve improvement by using conventional selection methods. The development of DNA markers and linkage maps has provided new opportunities for the genetic improvement of rice grain quality. Thus, it should be particularly helpful in enhancing breeding efficiency to use markers closely linked to genes for grain quality in order to screen target genotypes directly in early generations. Recently, the QTLs related to yield potential and grain quality have been detected by using the genetic linkage maps. Many QTLs, with respect to traits of grain appearance, have been reported (Aluko et al. 2004; Jiang et al. 2005; Rabiei et al. 2004; Wan et al. 2005). The identification

of QTLs for grain appearance and the elucidation of their genetic control are necessary for the development of MAS strategies aimed at improving breeding efficiency.

The expression stability of a QTL is critical in determining its usefulness in molecular breeding by using DNA markers linked to the QTLs. In order to establish an effective MAS system for quality improvement, the stability of QTLs related to grain quality must be determined by the analysis of QE interactions and epistatic effects. To date, knowledge is still lacking as to the extent of studies on the epistatic effects of QTLs and their environmental interactions with regard to the development of grain appearance. Moreover, the growing magnitude of QTLs with expression stability is required in order to improve the selection efficiency of a MAS system and advance the improvement of grain quality in rice.

The objectives of this study are: 1) QTL identification for grain appearance by using a genetic linkage map including 172 DNA markers based on 120 DH lines from a cross between 'Samgang' and 'Nagdong' and 2) The epistatic effects and QE interactions of rice qualities in multi-environments were implemented in order to further understand the relationships between

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gene and gene or environment and to provide useful information for target putative QTLs and MAS.

Materials and Methods

Plant materials and field trial

One hundred and twenty DH lines, developed by anther culture of the F₁ from a cross between 'Samgang' and 'Nagdong', were used as the mapping population. 'Samgang' is a *Tongil* variety with long and slender grains. 'Nagdong' is a *japonica* variety with short, rounded grains.

The current study was conducted during the rice-growing season on experimental fields at Kyungpook National University and Gunwie, Korea from 2005 to 2006. Using a spacing pattern of 15 cm between plants and 30 cm between rows, approximately 30-day-old seedlings from each DH line consisting of three rows with 20 plants per row were grown, with parent plants placed between every ten DH lines as the control. Fertilizer was applied at the rate of 110 kg N ha⁻¹, 45 kg P₂O₅ ha⁻¹, and 57 kg K₂O ha⁻¹.

Trait evaluation

The harvested rice grains were collected from the second row of each DH line or parent, dried naturally, and then stored at room temperature for at least three months before analysis. A instrument designed to measure moisture, GMK-303, was applied in surveying the water content of the brown rice. The moisture level of 12-13% was controlled. Damaged grains, red grains, green grains, and broken grains were removed from the brown rice before testing. One thousand per replicate of grain weight were measured three times. Grain length, width, ratio of length to width, and grain thickness of 30 grains for each line, respectively, were determined by using a vernier caliper.

Map construction and QTL analysis

A total of 172 DNA markers consisting of 56 SSR and 116 STS markers were used to create a genetic linkage map spanning the 12 rice chromosomes by using Map Manage QTX b20 (Manly 1999). The WinQTLcart 2.5 program was used for main-effect QTL detection in this study. QTL parameters of all putative QTLs were estimated using CIM and the restricted maximum likelihood estimation method with all significant markers identified in the first step fixed in the model to control the background genetic variation. One thousand permutations were used to obtain thresholds, change this sentence into "and the LOD of 2.46 at 0.05 significant level." was used for claiming significant QTL in this study (Zeng 1994). Epistatic QTLs and the QE interaction were identified by using a QTLMAPPER version 1.6 program (Wang et al. 1999). Maximum-likelihood estimation and best linear unbiased prediction (BLUP) were used to calculate QTL effects including additive and epistatic QTLs effects, and QE interaction including additive × environment interaction and epistatic QTLs × environment interaction, respectively, with a threshold of the P ≤ 0.005.

Data analysis and QTLs nomenclature

Marker and trait statistics were used in order to estimate the basic genetic parameters and test for marker distorted segregation. The correlation coefficient, t-test, and one-way ANOVA for quality traits in the DH population in two or three years were calculated by using the SAS 9.1 program. In addition, QTL nomenclature was followed in the sequence as outlined: Start each qtl with a lowercase "q". Use a two-three letter name in small letters to designate the trait actually being measured. Add a dot (.) and a number of the end of the chromosome to designate the numerical identifier of QTL for the same trait which is identified on the same chromosome.

Results

Phenotypic variation

Phenotypic distributions of grain appearance are shown in Fig.

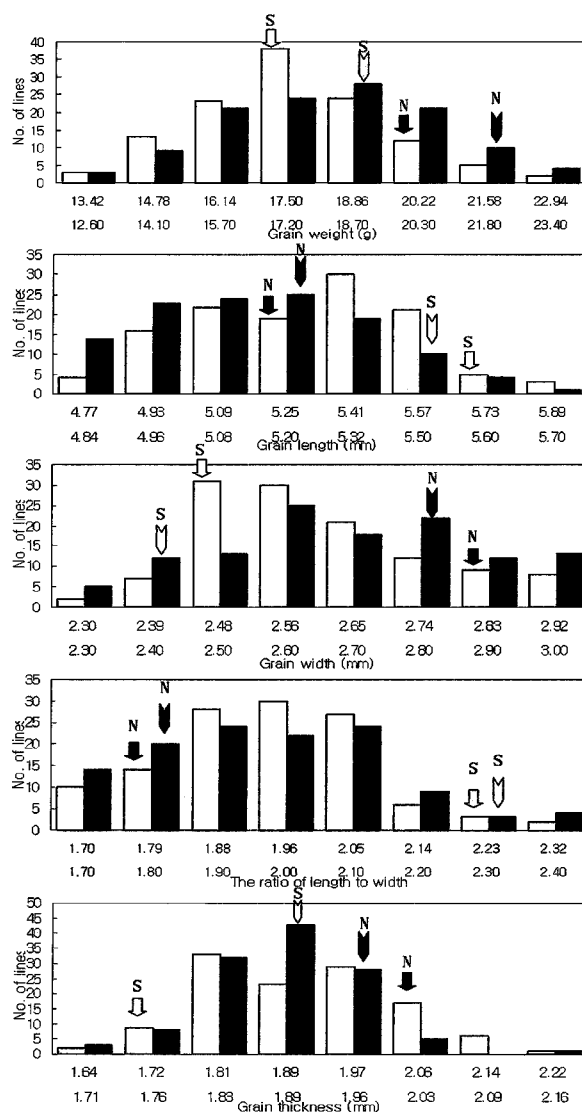


Fig. 1. Frequency distributions of five traits associated with grain appearance in DH population from a cross 'Samgang/Nagdong'. 'N' with ↓ and 'S' with ↘ indicate mean values of 'Nagdong' and 'Samgang' in 2005 and 2006, respectively.

Main-effect QTLs, Epistatic QTLs and QE Interactions Regarding Grain Appearance

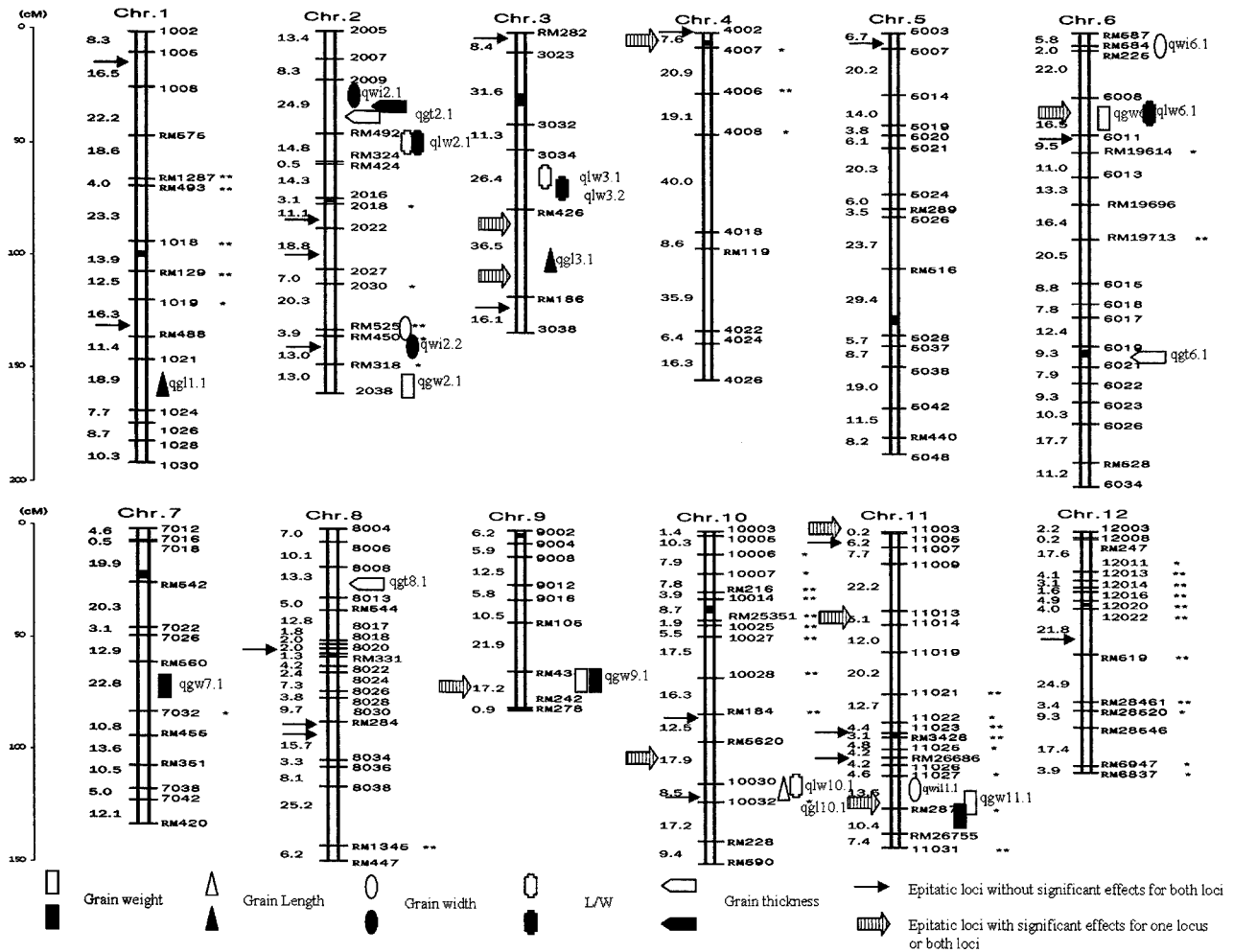


Fig. 2. Chromosomal locations of QTLs and epistatic QTLs for grain appearance. Unfilled symbols indicate the individual properties of 2005; filled symbols indicate the individual properties of 2006. The left side of chromosomes indicates the interval distance between markers using cM (centiMorgan) as the unit; the right side of chromosomes indicates DNA markers. The centromeres were signed by black bar. * and ** indicate that the markers are distorted segregation at $P < 0.05$ and $P < 0.01$ level of Chi-square test.

1. Continuous and approximately normal phenotypic distributions were observed, indicating quantitative inheritance of all characteristics studied. The t-test showed significant differences regarding five traits between two parents over two years. In comparison with ‘Samgang’, ‘Nagdong’ was associated with a higher one thousand-grain weight, a shorter grain length, a wider grain width, a lower ratio of grain length to width and a greater thickness (Table 1). Significant variances over two years were observed on all appearance traits by one-way ANOVA ($P < 0.01$), indicating significant interactions between genotype and environment.

QTL mapping

In total, 20 QTLs were mapped on ten chromosomes, with the exception of chromosomes 4 and 5, regarding five characteristics of grain appearance in brown rice with LOD values of 2.50-10.16 (Table 2 and Fig. 2). Among them, five QTLs were located on the same chromosome regions across two years. The ‘Samgang’ parent contributed nine QTLs for grain length and the ratio of length to width, and one QTL for grain weight on chromosome 7, whereas the remaining QTLs were contributed by ‘Nagdong’ alleles in regards to one thousand-grain weight, width, and thickness.

QTLs for one thousand-grain weight

Five QTLs influencing one thousand-grain weight (GW) were identified and located on chromosomes 2, 6, 7, 9, and 11, respectively. The qgw2.1 in the region RM318-2038 on chromosome 2 with a LOD value of 3.73 showed an additive effect of 0.79 on the trait which explained 11% of the total phenotype variation. The qgw6.1 were detected on chromosome 6 with flanking mark-

Table 1. Mean values of five traits related to grain appearance of parents and DH population.

Traits	Year	Parents			Mean±SD	DH Lines
		Samgang	Nagdong	<i>t</i> -value		
GW (g)	2005	17.73±0.15	20.77±0.57	8.92**	19.25±1.70	18.05±2.29
	2006	17.67±0.33	20.44±0.41	19.75**	19.06±1.46	18.95±2.23
GL (mm)	2005	5.64±0.10	5.20±0.01	7.41*	5.42±0.25	5.28±0.24
	2006	5.50±0.07	5.05±0.04	21.45**	5.28±0.24	5.26±0.26
GWi (mm)	2005	2.50±0.02	2.94±0.05	5.25**	2.72±0.24	2.68±0.19
	2006	2.42±0.03	2.79±0.04	30.55**	2.62±0.20	2.68±0.17
L/W	2005	2.25±0.02	1.77±0.03	22.9**	2.01±0.27	1.97±0.15
	2006	2.27±0.04	1.79±0.03	39.2**	2.03±0.25	1.97±0.16
GT (mm)	2005	1.83±0.02	2.03±0.01	7.19**	1.93±0.11	1.95±0.09
	2006	1.83±0.04	2.00±0.04	13.52**	1.91±0.09	1.92±0.09

Note: SD, GW, GL, GWi, L/W, and GT mean standard deviation, one thousand-grain weight, grain length, grain width, length to width ratio, and grain thickness, respectively. * means significant at 0.05 level, ** mean significant at 0.01 level.

ers of 6008 and 6011, and accounted for 12% phenotype variation with a LOD value of 4.34. A genomic region with an interval of RM560-7032 was located on chromosome 7, which described as qgw7.1. It accounted for 5% phenotype variation at a LOD value of 2.98. The qgw9.1, located in the RM434-RM242 interval on chromosome 9, and a QTL of qgw11.1, located on chromosome 11 at the peak of RM287 across two years, accounted for 12 and 11% of the average variations with mean LOD values of 3.98 and 3.89, respectively (Fig. 2).

QTLs for grain length

Three QTLs of qgl1.1, qgl3.1, and qgl10.1 regarding grain length were identified at the regions 1021-1024 on chromosome 1, RM426-RM186 on chromosome 3, and 10030-10032 on chromosome 10, respectively.

QTL for grain width

Four QTLs of qwi2.1, qwi2.2, qwi6.1, and qwi11.1 were detected on chromosomes 2, 6, and 11, respectively. The qwi2.2 was repeatedly detected over two years with a LOD of 5.85 at the peak marker of RM450, explaining 22% of phenotype variations. The qwi2.1 was mapped on chromosome 2 with flanking markers of 2009 and RM492 at a LOD value of 4.76, accounting for 19%

Table 2. QTL locations and biometrical parameters for rice grain appearance in two years.

Traits	Year	QTLs	Chr.	Interval markers	LOD	R ² (%)	Add.	Chr.		
GW	2005	qgw 2.1	2	RM318-2038	3.73	11	-0.79	Nagdong		
		qgw 6.1	6	6008-6011	4.34	12	-1.05	Nagdong		
		qgw 9.1	9	RM434-RM242	2.50	6	-0.55	Nagdong		
		qgw 11.1	11	11027-RM287	3.87	9	-0.77	Nagdong		
	2006	qgw 7.1	7	RM560-7032	2.98	5	0.52	Samgang		
		qgw 9.1	9	RM434-RM242	5.45	18	-0.96	Nagdong		
		qgw 11.1	11	RM287-RM26755	3.91	12	-0.82	Nagdong		
		GL	2005	qgl 10.1	10	10030-10032	3.58	15	0.09	Samgang
			2006	qgl 1.1	1	1021-1024	3.35	12	0.10	Samgang
qgl 3.1	3	RM426-RM186		3.34	21	0.13	Samgang			
GWi	2005	qwi 2.2	2	RM525-RM450	9.05	31	-0.11	Nagdong		
		qwi 6.1	6	RM587-RM584	2.46	6	-0.04	Nagdong		
		qwi 11.1	11	11027-RM287	5.70	15	-0.07	Nagdong		
	2006	qwi 2.1	2	2009-RM492	4.76	19	-0.06	Nagdong		
		qwi 2.2	2	RM450-RM318	2.64	13	-0.06	Nagdong		
		LW	2005	qlw 2.1	2	RM492-RM324	6.18	13	0.05	Samgang
qlw 3.1	3			3034-RM426	3.88	12	0.05	Samgang		
qlw 10.1	10			10030-10032	10.16	25	0.08	Samgang		
2006	qlw 2.1		2	RM492-RM324	7.46	21	0.07	Samgang		
	qlw 3.2		3	RM426-RM186	3.12	13	0.06	Samgang		
	qlw 6.1		6	6008-6011	6.31	22	0.08	Samgang		
GT	2005	qgt 2.1	2	2009-RM492	3.68	9	-0.03	Nagdong		
		qgt 6.1	6	6019-6021	5.27	10	-0.04	Nagdong		
	2006	qgt 8.1	8	8008-8013	5.86	9	-0.03	Nagdong		
		qgt 2.1	2	2009-RM492	2.88	14	-0.04	Nagdong		

Note: Chr. means chromosomes; R² means percentage of phenotypic variation explained; Add. means additive effect. The makers underline mean significant relatively.

Table 3. The contributions of phenotypic variations explained by digenic epistatic QTLs and QE interactions.

Grain quality traits	A R ² (%)	AA R ² (%)	AE R ² (%)	AAE R ² (%)	MR ² (%)
One thousand-grain weight (GW)	22.19	54.37	4.35	1.88	30-38
Grain length (GL)	36.90	55.97	4.21	9.30	15-33
Grain width (GWi)	27.85	41.71	15.30	16.26	32-52
Ratio of Length to Width (LW)	54.46	34.43	12.10	12.34	50-56
Grain thickness (GT)	28.47	13.44	5.07	9.20	14-28

Note: A R² indicates the phenotype variations totally explained by additive effect on single locus of epistatic combinations; AA R², AE R² and AAE R² indicate the phenotype variations totally explained by additive × additive interactions, additive and environment interactions, and interactions between additive × additive and environments, respectively. MR² indicates the phenotype variations totally explained by the main-effect QTLs.

of phenotype variation. The qwi6.1 and qwi11.1 were detected at intervals RM587-RM584 and 11027-RM287 on chromosome 6 and 11 with a LOD score of 2.46 and 5.70 in 2005, which accounted for 6 and 15% of phenotype variations, respectively.

QTLs for the ratio of length to width

Five QTLs of qlw2.1, qlw3.1, qlw3.2, qlw6.1, and qlw10.1 controlling the ratio of length to width of brown rice were detected in chromosomes 2, 3, 6, and 10, respectively. The qlw2.1, with additive effect of 6% on the trait and mean LOD score of 6.82, was located on chromosome 2, flanked by RM492 and RM324, which explained 17% of the total phenotype variation. The qlw3.1 and qlw10.1, with LOD values of 3.88 and 10.16, were detected in intervals 3034-RM426 and 10030-10032, which explained 12 and 25% of phenotype variations in 2005, respectively. The QTLs of qlw3.2 and qlw6.1, with LOD values of 3.12 and 6.31, explained 13 and 22% of total phenotype variations, respectively.

QTLs for grain thickness

Three QTLs were detected for grain thickness, consisting of one QTL identified over both years and two QTLs in 2005. A QTL of qgt2.1 was located on chromosome 2 with flanking markers 2009 and RM492 at an average LOD value of 3.28, where a QTL for grain width was also detected, further illustrating a significantly positive correlation between two traits ($r = 0.63^{**}$, $r = 0.74^{**}$). This accounted for 9 and 14% of phenotype variations, respectively. The qgt6.1 and qgt8.1 were mapped in the intervals of 6019-6021 and 8008-8013 on chromosomes 6 and 8 with LOD scores of 5.27 and 5.86, which explained 10 and 9% of total phenotype variations, respectively.

Epistatic QTLs and QE interactions

Significant QE interactions were detected on three main-effect QTLs, consisting of qwi2.2 and qwi11.1 for grain width, and qlw10.1 for the ratio of length to width. Moreover, the contributions of phenotype variations explained by additive-by-environment interactions on the three noted QTLs were 5.68, 9.55, and 10.66%, respectively. QTL and environment interactions totally explained 6.94, 6.73, 16.38, 16.68, and 10.03%, respectively, regarding phenotype variations.

Two kinds of epistatic QTLs could be classified, which include that one is no significant effects on traits detected for both loci, and

significant effects detected on traits for one locus or both loci (including main-effect QTLs). No interaction was detected between QTLs. Fourteen pairs of epistatic loci were detected in regards to five grain appearance traits, but six pairs of loci involved an independent main-effect QTL. As well, six of 14 epistatic QTLs involved both loci without significant effects on traits (Fig. 2.). For the combinations of RM434-RM242 (main-effect QTL) and 11013-11014 on grain weight, a positive additive-by-additive effect of 0.776 g from the parental two-locus genotypes was calculated with the highest likelihood of 14.58, even though the opposite behaviors on the additive effect of each locus were detected. Three pairs of epistatic QTLs on the ratio of length to width showed negative additive-by-additive effects indicated that the recombinants of two loci had negative effects on the improvement of the trait.

In total, the single loci of epistatic QTLs accounted for 22.19-54.46% of phenotype variations, whereas the additive effect and environment interaction accounted for 4.21-15.30% of phenotype variations on five traits, respectively (Table 3). The additive \times additive effects accounted for 13.44 to 55.97% of phenotype variations, but the interactions between additive \times additive effect and environment explained 1.88 to 16.26% of phenotype variations on five traits, respectively. Results indicated that additive \times additive effects occupied a considerable proportion of the contribution of phenotype variation for five grain appearance traits. In the same way, the main-effect QTLs and epistatic QTLs of grain width showed a tendency to be easily affected by environments. Furthermore, in comparison with the contribution explained in phenotypic variation by additive and epistatic effects, additive effects have more important roles regarding grain length, the ratio of length to width and thickness than epistatic effects, whereas epistatic effects play a greater role on one thousand-grain weight and width than additive effects.

Discussion

Five QTLs were mapped for one thousand-grain weight, of which qgw7.1, qgw9.1, and qgw11.1 were reported on previous studies. The qgw7.1 flanked by RM560 and 7032, had been reported to be at the same location by Brondani et al. (2002) with a peak marker of RM11 using 96 BC₂F₂ lines from an interspecific cross RS-16 (*O. glumaepatula*) / BG90-2 (*O. sativa*), and Xu et al (2004) with flanking markers of RM336 and RD7.2 using 292 F₁₃ RI lines from a cross 'Lemont/Teqing' (*indica/japonica*). Moreover, qgw9.1, with a significant marker of RM242, was mapped by Xing et al. (2002) and Marri et al. (2005) using 240 RI lines from cross 'Zhenshan 97/Minghui 63' (*indica/japonica*) and 251 BC₂ testcross lines, respectively. In this study, the chromosomal region with an interval of RG570-RG667 identified by Ge et al. (2005) was considered to be same QTL to the qgw9.1, the same result as RZ422 detected individually by Xiao (1998). A QTL with interval markers G257-G44 was identified on the long arm of chromosome 11 by Ge et al. (2005). As well, qgw11.1 was also detected in that region in this study. The qgw2.1 was detected on the region near to the Qkw2a with interval markers of Pall-RZ58, which was reported by Li et al. (1997).

The qgw6.1, with an interval of 6008-6011 on the short arm of

chromosome 6, was a novel QTL which reported firstly in this study, but QTLs controlling one thousand-grain weight were detected on the same chromosome by Li et al. (1997) and Hittalmani et al. (2003) with intervals of RG424-RG179 and RG433-cat_1, respectively. Most of increasing effects of QTLs on chromosomes 9 and 11 for one thousand-grain weight derived from alleles of *indica* or *wild* rice varieties among previous reported studies, whereas those of QTLs on two chromosomes detected in the present study were from 'Nagdong', *japonica* alleles.

Rabiei (2004) reported a QTL of gl2 flanked by RM434 and RM341, in which qgl2.1 was also mapped in the interval of RM492-RM324 in the present study. The qgl10.1 was also located by Jiang (2005) on the same location with interval markers of RM304-RM147. This is the first report regarding the QTLs of qgl1.1, qgl2.1, and qgl3.1, despite the fact that Li (2004), Wan (2005), and Xu (2004) had released some QTLs on chromosomes 1 to 3. With respect to qwi2.1 and qwi2.2, Rabiei (2004) and Xu (2004) had identified the same chromosomal regions on each map, named gb2 and QGw2 with the intervals RM279-RM555 and CDO718-RM263, respectively. The qwi2.2, averaging 22% of phenotype variations detected across environments, was regarded as the major QTL, which could be useful in MAS programs. Zhang (2004) presented two QTLs, qGW-2a and qGW-2b in the intervals of GA120-G357 and CT565-RG171. It is difficult to confirm the two QTLs located on the same position with qwi2.1 and qwi2.2. Otherwise, the QTLs of qwi6.1 and qwi11.1 were new loci that were associated with grain width found in the present study.

Wan et al. (2005) reported that a QTL associated with the length to width ratio and regarded as a stable QTL was located on chromosome 3 with flanking markers of R19 and C1677 using 66 chromosome segment substitute lines across eight environments. We found the qlw3.1 to be located in this same chromosomal region. The QTL of lwr6, with flanking markers of RM253 and RM162 released by Aluko et al. (2004), were confirmed to be located on the same position as qlw6.1. There were no QTLs for length to width ratio which were reported on the chromosome regions close to qlw2.1 and qlw3.2 by previous studies.

Qgt8, with flanking markers of RM38 and RM25 on the short arm of chromosome 8, was identified by Zheng et al. (2007). As well, the QTL of qgt8.1 was confirmed on a similar position to chromosome 8 with flanking markers of 8008 and 8013 in this study. Jiang et al. (2005) reported two QTLs on chromosomes 6 and 8 for grain thickness, flanked by RM121-RM136 and RM210-RM80, respectively. Both QTLs were absolutely differentiated from qgt6.1 and qgt8.1. Furthermore, a chromosomal region of qgt2.1 was detected over two years in this study, while a QTL with a peak marker of W131132 was reported on the near side by Yoshida et al. (2002).

Three loci with pleiotropic effects were observed. The locus within the genomic region 2009-RM492 on chromosome 2 simultaneously influenced grain width, thickness, and the ratio of length to width. Moreover, this locus had a simultaneous effect on panicle length, for which a QTL of qPAL2 was detected by Kim (2006) in the same population. But there were no significantly phenotypic correlations between panicle length and grain width, or grain thickness, or the ratio of length to width. The chromosome regions controlling

one-thousand weight and grain thickness on chromosomes 7 and 8 were located on different genomic positions of same linkage groups to those controlling days to heading, qHD7 and qHD8, respectively (Kim 2006), which implied there might be some relationships between heading date and grain weight, or grain thickness.

The epistatic effects and QE interactions were detected to further understand what the relationship between loci and how to manipulate these relations so that they can serve more useful for quality breeding on the gene level. In addition, how to apply for the epistatic QTLs with increasing or decreasing effects for grain qualities on MAS system, however, the vast amount of data are the best approach to getting out the reality. The QTLs of qgw11.1, qgw6.1, and qgw9.1 regarding one thousand-grain weight, and qgl3.2 and qgl10.1 with respect to grain length were involved in epistatic effects, but the increasing inter-effects observed on all loci mentioned above indicated that epistatic effects might be useful factors in promoting gene expression of QTLs in any complex backgrounds. Also, the epistatic interaction between qlw3.2 and a modifying factor in the interval 5003-5007 was detected with a negative effect, therefore indicating a disadvantage to breeding. Overall, attention should be paid in removing deleterious alleles near the influential QTLs by MAS. According to the results of this study, the introgression of favorable allele related to quality traits, such as one thousand-grain weight on chromosome 11, from parents will be carried out in the future study.

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