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Analysis of digenic epistatic effects and *QE* interaction effects QTL controlling grain weight in rice*

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Abstract: Immortalized F_2 population of rice (*Oryza sativa* L.) was developed by randomly mating F_1 among recombinant inbred (RI) lines derived from (Zhenshan 97B × Minghui 63), which allowed replications within and across environments. QTL (quantitative trait loci) mapping analysis on kilo-grain weight of immortalized F_2 population was performed by using newly developed software for QTL mapping, QTLMapper 2.0. Eleven distinctly digenic epistatic loci included a total of 15 QTL were located on eight chromosomes. QTL main effects of additive, dominance, and additive × additive, additive × dominance, and dominance × dominance interactions were estimated. Interaction effects between QTL main effects and environments (*QE*) were predicted. Less than 40% of single effects, most of which were additive effects, for identified QTL were significant at 5% level. The directional difference for QTL main effects suggested that these QTL were distributed in parents in the repulsion phase. This should make it feasible to improve kilo-grain weight of both parents by selecting appropriate new recombinants. Only few of the *QE* interaction effects were significant. Application prospect for QTL mapping achievements in genetic breeding was discussed.

Key words: Immortalized F_2 population, Rice, Kilo-grain weight, QTL, Epistasis, QTL × environment
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INTRODUCTION

Kilo-grain weight, characteristically a complex trait, is an important component of yield in rice. QTL mapping for kilo-grain weight of rice was conducted using populations of F_2 (Lin *et al.*, 1996), doubled haploid lines (Lu *et al.*, 1997), recombinant inbred lines (Xiao *et al.*, 1996), backcross testcross (Xiao *et al.*, 1995; Li *et al.*, 1997) and ratooned F_2 (Li *et al.*, 2000). Considering the sensitivity of kilo-grain weight to environments, Lu *et al.*(1997) and Zhuang *et al.*(1997) compared the differential detection of QTL across environments to determine whether or not QTL × environment (*QE*) interaction existed. However, Jansen *et al.*(1995) argued that the differential QTL identification among different environments could not support the existence of *QE* interaction and vice versa, as the statistical power was low to detect these QTL simultaneously under various environments. After analyzing the interactions between markers using two-way ANOVA (analysis of variance) and multiple regressions, some investigators found epista-

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sis was a key part of the genetic basis of kilo-grain weight (Li *et al.*, 1997; Yu *et al.*, 1997).

However, the foregoing studies did not estimate epistatic effects between QTL, as well as predict *QE* interaction effects simultaneously. Wang *et al.*(1999) proposed a QTL mapping strategy that can estimate QTL epistatic effects of additive × additive and predict their interaction with environments. The methodology was used in a recent QTL mapping investigation (Liao *et al.*, 2000; Cao *et al.*, 2001a; 2001b; Li *et al.*, 2001; Luo *et al.*, 2001; Xing *et al.*, 2002). However, so far estimations of dominance, epistatic effects related to dominance and predictions of their interaction with environments are lacking. In the present study, an immortalized F_2 (IF_2) population was constructed according to the procedure described by Hua *et al.*(2002) for analyzing kilo-grain weight of rice by using the methods proposed by Gao and Zhu (2004) to estimate dominance, epistatic effects related to dominance and predict their interaction with environments.

MATERIALS AND METHODS

The RIL (recombined inbred line) population of rice derived from Zhenshan 97B × Minghui 63 was provided by Dr. Zhang Qifa of Huazhong Agricultural University. There are 241 individual lines in the RIL population with a genetic linkage map consisting of 221 markers which covered 1796.58 cM of the rice genome. We constructed an IF_2 population of rice with 240 F_1 hybrids obtained from random mating among the RIL lines.

The materials were evaluated in 1999 and 2000 at the experimental station of Zhejiang University. All hybrids and parental RILs were planted in the seedling nursery on May 19 and transplanted into field plots with three rows for the hybrids and five rows for RILs on June 15 in 1999 and on June 16 in 2000. The plots were arranged by a randomized complete block design with two replications. Each row within a plot consisted of 12 plants with a space of 17 cm between plants within the row and 26 cm between rows. Fertility and cultivation regimes were consistent with optimum rice production for the region. False hybrids were removed during the period of heading. At maturity, five representative plants from the middle of each row of a plot were sampled and dried under sunshine. Each sampled plant was evaluated for kilo-grain weight of the grains that were at least 67% plumping. The mean of five sampled plants from each plot was used in the data analysis.

QTL localization for kilo-grain weight, estimation for QTL main effects and prediction of *QE* interaction effects were conducted by QTL mapping software, QTLmapper 2.0 (Gao and Zhu, 2004). Significance level of genome scan was set at 0.05, the point-wise significance level of QTL mapping was 0.00018 with the corresponding threshold of likelihood ratio (LR) being 50.6 (Gao and Zhu, 2004).

We denoted QTL by the following rules: The first two letters (first one capitalized) represented abbreviation of the trait, followed by the number of chromosome the QTL occupied, then by ‘-’, the digit following the ‘-’ was the ordinal number of the QTL according to its position on the corresponding chromosome starting from the left end. The loci with distance below 5 cM were specified as the same QTL and considering the directional effects of concerned QTL.

RESULTS

Statistics of phenotypic variation and environmental effects

The statistical analysis showed that kilo-grain weight of Minghui 63 and Zhenshan 97 was not significantly different between the two years (Table 1). The mean performance of kilo-grain weight in IF_2 population of rice showed only a small fluctuation between two years, however, the range of kilo-grain weight in 2000 was about 4 grams larger than in 1999, which was also reflected in standard deviation. The skewness and kurtosis were near zero in these two years, indicating the phenotype value of kilo-grain weight was normally distributed.

Table 1 Summary of statistics of phenotype values of kilo-grain weight (g)

Year	Parents		Mean	Max.	Min.	SD	Skew	Kurt
	Minghui 63	Zhenshan 97						
1999	29.28	25.12	25.99	31.97	20.94	2.26	0.53	0.14
2000	29.15	22.55	25.83	34.08	18.24	2.62	0.08	0.15

QTL identification and location

LR values of 11 epistatic loci were beyond the significance threshold, suggesting that these loci might be QTL controlling kilo-grain weight in rice. The positions and designations for these QTLs are summarized in Table 2.

Following the foregoing rules, a total of 17 QTL among 11 epistatic loci were detected and distributed on eight chromosomes unevenly. However, these QTL need to be confirmed according to the significance test for their QTL main effects and *QE* interaction effects based on the null hypothesis for the genetic model of QTL mapping (Gao and Zhu, 2004).

Table 2 QTL controlling kilo-grain weight

QTL *i* [a]				QTL *j*			
Chrom.	Marker interval	Pos. [b]	QTL designation	Chrom.	Marker interval	Pos.	QTL designation
1	G359-RG532	0.040	Kw1-1	6	C952-Waxy	0.000	Kw6-1
1	C39-RM237	0.000	Kw1-2	2	C777-RZ386	0.000	Kw2-2
1	G393-R2201	0.000	Kw1-3	5	RG360-RM42	0.040	Kw5-1
1	R2201-RM212	0.000	Kw1-3	3	C1087-RZ403	0.020	Kw3-1
1	R2201-RM212	0.080	Kw1-4	5	RG360-RM42	0.040	Kw5-1
2	RM53-RZ599	0.100	Kw2-1	7	RG128-C1023	0.060	Kw7-1
3	C1087-RZ403	0.040	Kw3-1	11	Clone2-C405b	0.000	Kw11-1
3	C746-C944	0.040	Kw3-2	10	RM239-C1633	0.100	Kw10-1
5	RG360-RM42	0.040	Kw5-1	7	RG128-C1023	0.080	Kw7-1
6	Y4073L-RZ667	0.040	Kw6-2	6	RG653-G342	0.000	Kw6-3
7	C1023-R1440	0.000	Kw7-2	10	RM228-C371	0.000	Kw10-2

[a] QTL *i* and QTL *j* are a pair of QTL detected by two-dimensional searching; [b] Position here is the map distance of QTL from the left marker in the marker interval the QTL located, unit is M

Estimations of genetic main effects of QTL

Genetic main effects of QTL denote the components of genetic effects that are stable and do not change across environments. We list the significant main effects of QTL in Table 3.

The positive (negative) additive effects a_i (a_j) denoted that the Q_iQ_i (Q_jQ_j) of Minghui 63 could increase (decrease) kilo-grain weight, meanwhile q_iq_i (q_jq_j) of Zhengshan 97 could decrease (increase) the phenotype. The positive (negative) epistatic effects of additive × additive (aa_{ij}) suggested that the two epistatic loci with homozygous alleles from the same parent (Q_iQ_i Q_jQ_j or q_iq_i q_jq_j) could increase (decrease) the kilo-grain weight, otherwise Q_iQ_i q_jq_j or q_iq_i Q_jQ_j could decrease (increase) the phenotype. The positive (negative) additive × dominance (ad_{ij} or ad_{ji}) epistatic effects indicated that Q_iQ_i Q_jq_j or Q_iq_i Q_jQ_j could increase (decrease) the kilo-grain weight, otherwise (q_iq_i Q_jq_j or Q_iq_i q_iq_i) could decrease (increase) the phenotype.

Table 3 Estimation of genetic main effects of QTL for kilo-grain weight of rice

QTL i	QTL j	a_i^a	d_i	a_j	d_j	aa_{ij}	ad_{ij}	ad_{ji}	dd_{ij}
Kw1-1	Kw6-1	-0.79^{***}							
Kw1-2	Kw2-2	-0.44^{***}		0.34^{*}		0.63^{*}	0.49^{*}	-0.49^{*}	
Kw1-3	Kw5-1			-1.04^{***}					0.85^{*}
Kw1-3	Kw3-1			0.72^{**}	-0.40^{*}		0.73^{***}	0.86^{***}	
Kw1-4	Kw5-1			-1.04^{***}					
Kw2-1	Kw7-1			0.66^{**}	0.82^{*}	0.98^{*}		-0.97^{**}	
Kw3-1	Kw11-1	0.72^{**}	-0.40^{*}			-0.93^{***}			
Kw3-2	Kw10-1		-0.65^{*}				0.78^{*}	0.79^{**}	1.23^{*}
Kw5-1	Kw7-1	-1.04^{***}		0.66^{**}	0.82^{*}				
Kw6-2	Kw6-3	0.52^{***}		0.62^{***}	-0.58^{**}			-0.78^{***}	0.84^{***}
Kw7-2	Kw10-2	0.64^{***}		-0.33^{*}		-0.60^{***}	-0.63^{***}		

[a] a_i and d_i are the additive and dominance effects of QTL i, respectively; a_j and d_j are the additive and dominance effects of QTL j, respectively; aa_{ij}, ad_{ij} (ad_{ji}) and dd_{ij} are the epistatic effects of additive × additive, additive × dominance, and dominance × dominance between QTL i and QTL j, respectively;

*, ** and *** denote significance level at 0.05, 0.01 and 0.005, respectively

Among 88 QTL main effects of 11 pairs of epistatic loci, less than 40 percent were significantly different from zero, and most of these were additive effects. The additive effects of QTL with the genotype of Minghui 63 could be positive or negative, which implied that QTL controlling kilo-grain weight of rice occurred in the inbred parents in the repulsion phase. More negative dominance effects were found than positive; however, all significant dominance×dominance epistatic effects were positive.

Prediction of QTL × environment interaction effects

The advantage of QTL mapping approaches using mixed linear models is for simultaneously dealing QTL with complicated epistasis and *QE* interaction, so that it provides a powerful tool for geneticists and breeders to further analyze the interaction between QTL and environments. In the present study, Jackknife sampling techniques (Zhu, 1997) were used to test the significance of *QE* interaction effects for kilo-grain weight in IF_2 populations by removing one genotype at a time. Significant *QE* interaction effects are summarized in Table 4, excluding, for simplicity, epistatic locus pairs with no significant *QE* interaction effects. There are few QTL with significant *QE* interaction

Table 4 Prediction of *QE* interaction effects for kilo-grain weight of rice

Environment	QTL i	QTL j	$e_{A_iE_h}$ [a]	$e_{A_jE_h}$	$e_{AA_{ij}E_h}$	$e_{AD_{ij}E_h}$	$e_{AD_{ji}E_h}$	$e_{DD_{ij}E_h}$
1999 ($h = 1$)	Kw1-3	Kw5-1				0.63^{*}		
	Kw3-2	Kw10-1	-0.41^{*}					
	Kw5-1	Kw7-1						-1.35^{**}
	Kw6-2	Kw6-3		-0.38^{**}	0.57^{***}			
	Kw7-2	Kw10-2					-0.61^{**}	-0.62^{*}
2000 ($h = 2$)	Kw1-3	Kw5-1				-0.60^{*}		
	Kw3-2	Kw10-1	0.40^{*}					
	Kw5-1	Kw7-1						1.37^{**}
	Kw6-2	Kw6-3		0.36^{*}	-0.56^{***}			
	Kw7-2	Kw10-2					0.60^{**}	0.65^{*}

[a] $e_{A_iE_h}$ and $e_{A_jE_h}$ are additive interactions of QTL i or QTL j with environment h; $e_{AA_{ij}E_h}$, $e_{AD_{ij}E_h}$ ($e_{AD_{ji}E_h}$) and $e_{DD_{ij}E_h}$ are the interactions between AA_{ij}, AD_{ij} (AD_{ji}), DD_{ij} and environment h;

*, **, *** is significance level at 0.05, 0.01 and 0.005, respectively effects (Table 4), suggesting that kilo-grain weight might not be extremely sensitive to environments.

DISCUSSION

Table 5 presents comparisons of the QTL underlying grain weight detected in the present study with results from previous studies.

Among the 15 QTL identified in the present study (except Kw4-1 and Kw6-1), 11 could be detected at the exact marker interval or neighboring marker interval in at least one other investigation. The populations of those studies included RIL, F_2,

Table 5 Comparison of QTL underlying grain weight in rice with those detected in previous studies

QTL	Chrom.[a]	Mark. Int.[b]	Literature	Mark. Int.	Pop. [c]	Parent
Kw1-1	1	G359-RG532	Xing *et al.*, 2002	G359-RG532	RIL (I/I)	Zhenshan 97/Minghui 63
			Hua *et al.*, 2002	G359-RG532	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Zhuang *et al.*, 1997	RG532-RG173	F_2 (I/I)	Tesanai 2/CB
			Lin *et al.*, 1996	RG532-RG173	F_2 (I/I)	Tesanai 2/CB
Kw1-2	1	C39-RM237				
Kw1-3	1	G393-R2201				
Kw2-1	2	RM53-RZ599	Xing *et al.*, 2002	R1738-RM53 *	RIL (I/I)	Zhenshan 97/Minghui 63
			Luo *et al.*, 2001	RZ599-RZ476b *	RIL (J/I)	Lemont/Teqing
Kw2-2	2	C777-RZ386				
Kw3-1	3	C1087-RZ403	Xing *et al.*, 2002	C1087-RZ403	RIL (I/I)	Zhenshan 97/Minghui 63
			Hua *et al.*, 2002	C1087-RZ403	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Li *et al.*, 2000	R1966-C1087	RatooningF_2 (I/I)	Zhenshan 97/Minghui 63
			Luo *et al.*, 2001	RZ403b-RG482 *	RIL (J/I)	Lemont/Teqing
Kw3-2	3	C746-C944	Xing *et al.*, 2002	C944-R321	RIL (I/I)	Zhenshan 97/Minghui 63
			Yu *et al.*, 1997	C746-C944	$F_{2:3}$ (I/I)	Zhenshan 97/Minghui 63
Kw5-1	5	RG360-RM42	Xing *et al.*, 2002	R3166-RG360	RIL (I/I)	Zhenshan 97/Minghui 63
			Hua *et al.*, 2002	R3166-RG360	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Li *et al.*, 2000	R1674-RG360	RatooningF_2 (I/I)	Zhenshan 97/Minghui 63
			Yu *et al.*, 1997	RG360-C734	$F_{2:3}$ (I/I)	Zhenshan 97/Minghui 63
			Xiao *et al.*, 1995	RG360-RZ296	BC testcross (I/J)	9024/LH422
			Xiao *et al.*, 1996	RG360-RZ296	RIL (I/J)	9024/LH422
Kw6-2	6	Y4073L-RZ667	Hua *et al.*, 2002	C751A-RZ667	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Luo *et al.*, 2001	RZ667-C235a	RIL (J/I)	Lemont/Teqing
Kw6-3	6	RG653-G342	Luo *et al.*, 2001	RG653-RZ508	RIL (J/I)	Lemont/Teqing
Kw7-1	7	RG128-C1023	Hua *et al.*, 2002	RG128-C1023	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Li *et al.*, 2000	RG128-C1023	RatooningF_2 (I/I)	Zhenshan 97/Minghui 63
			Yu *et al.*, 1997	RG128-C1023	$F_{2:3}$ (I/I)	Zhenshan 97/Minghui 63
Kw7-2	7	C1023-R1440				
Kw10-1	10	RM239-C1633	Xing *et al.*, 2002	C148-RG239	RIL (I/I)	Zhenshan 97/Minghui 63
			Hua *et al.*, 2002	C1633-C677 *	IF_2 (I/I)	Zhenshan 97/Minghui 63
Kw10-2	10	RM228-C371	Xing *et al.*, 2002	R2625-RM228	RIL (I/I)	Zhenshan 97/Minghui 63
			Hua *et al.*, 2002	R2625-C371	IF_2 (I/I)	Zhenshan 97/Minghui 63
			Luo *et al.*, 2001	RG561-C223	BC testcross (J/I)	Lemont/Teqing
Kw11-1	11	Clone2-C405b	Xing *et al.*, 2002	C405b-RM254	RIL (I/I)	Zhenshan 97/Minghui 63

[a] Chrom. denotes chromosome; [b] Mark. Int. denotes marker interval; [c] Pop. denotes population type; I in the parentheses denotes *Indica*, J denotes *Japonica*; * denotes the marker interval is large

BC testcross, and IF_2 derived from the crosses of *Indica* × *Indica*, *Indica* × *Japonica*. All of these confirmed that the QTL controlling kilo-grain weight in rice found in the present study were reliable. The algorithm of QTL mapping proposed by Gao and Zhu (2004) had high power for detecting QTL.

The information of additive effects and epistasis related to additive effects will be helpful to traditional breeding. The present study revealed that positive and negative effects on additive and additive × additive epistasis were nearly half and half, which implied that QTL underlying kilo-grain weight were in the repulsion phase among the two parents. The repulsion distribution of QTL (genes) makes it feasible to pyramid favorable genes from different parents into a new variety via hybridization. The negative dominance effects of kilo-grain weight QTL implied that there exists the potential to increase yield of Shanyou 63 by increasing kilo-grain weight.

The favorable gene is a relative concept because of epistasis. A "favorable" gene with positive additive effects may become "unfavorable (deleterious)" following transfer into a new variety due to the large negative additive × additive effects in the new genetic background. In the present study, Kw3-1 had the largest positive additive effect (increasing 0.72 gram kilo-grain weight); at the same time, its additive × additive epistatic effect with Kw11-1 was –0.97, its additive×dominance and dominance × additive epistatic effects were 0.73 and 0.86 with Kw1-3, respectively. The "most deleterious" QTL may be Kw5-1 because of its largest negative additive effects (–1.04), but it had high positive dominance × dominance epistatic effect, showed high positive additive × additive epistatic effect (0.98) and large negative additive × with Kw5-1. The Kw7-1, with highest positive dominance effect (0.82) and large positive additive dominance epistatic effect (–0.97) with Kw2-1. Therefore pyramiding and manipulation of genes in selection programs should consider not only the additive effects of genes or QTL, but also the additive × additive epistatic effects among these genes and others.

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