

# The QTL analysis on maternal and endosperm genome and their environmental interactions for characters of cooking quality in rice (*Oryza sativa* L.)

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**Abstract** Investigations to identify quantitative trait loci (QTLs) governing cooking quality traits including amylose content, gel consistency and gelatinization temperature (expressed by the alkali spread value) were conducted using a set of 241 RIL populations derived from an elite hybrid cross of “Zhenshan 97” × “Minghui 63” and their reciprocal backcrosses BC<sub>1</sub>F<sub>1</sub> and BC<sub>2</sub>F<sub>1</sub> populations in two environments. QTLs and QTL × environment interactions were analyzed by using the genetic model with endosperm and maternal effects and environmental interaction effects on quantitative traits of seed in cereal crops. The results suggested that a total of seven QTLs were associated with cooking quality of rice, which were subsequently mapped to chromosomes 1, 4 and 6. Six of these QTLs were also found to have environmental interaction effects.

## Introduction

As a staple cereal crop in the world, rice feeds more than 50% of the world's population. The improvement of rice quality is one of few ways to meet the demands of a

growing population. The major components of rice quality are its appearance, cooking quality, eating quality and nutritional quality. Among these, cooking quality that includes amylose content (AC), gel consistency (GC) and gelatinization temperature (GT) is considered to be the most important trait.

Since the rice grain is a new generation and differs from its maternal plant that provides nutrition for seed development, the seed traits might be controlled by genes expressed in the genome of triploid endosperm and the maternal plant. The genetic analysis of rice had indicated that the inheritance of cooking quality traits are complex, which involved the genetic effects from endosperm genes and/or the maternal plant genes, being further partitioned into additive and dominance components, and the genetic parameters were also subject to the modification by genotype × environment interactions (Shi et al. 1997). The analysis of quantitative trait loci (QTLs) is an approach that unravels the gene activities. In the past decades, with the development of biotechnology and high-density marker linkage maps in rice, a series of studies for QTL mapping on the cooking quality of rice grain have been conducted (Aluko et al. 2004; Bao et al. 2004; He et al. 1999; Lanceras et al. 2000; Li et al. 2004; Liu et al. 2000; Rui et al. 2005; Tan et al. 1999). But the studies cited above were based on the assumption that the endosperm is a diploid tissue, without considering other potential factors such as maternal plant tissue. With regard to the specific gene expression in the triploid endosperm, several studies have been conducted to develop triploid models to identify the QTLs expressed in the endosperm (Wu et al. 2002; Xu et al. 2003; Kao 2004). Recently, more exquisite studies have been pursued successfully to distinguish the QTLs of the maternal and endosperm tissue (Cui and Wu 2005). Like the QTLs identified in phenotypes of maternal

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sporophyte that were occasionally affected by the environments, those of rice quality traits were also modified by the environment (He et al. 1999; Bao et al. 2004). Fan et al. (2005) reported six main-effect QTLs and two pairs of epistatic QTLs for three traits involved in QTL-by-environment interactions (QEs), which played important roles in controlling the traits. So far, the magnitude and prevalence of interactions between the QTLs of the triploid endosperm or diploid maternal genomes and environments for rice traits are still largely unknown.

This study aimed to track down the QTLs and QTL  $\times$  environment interactions underlying cooking quality traits, e.g., AC, GC and GT (expressed by the alkali spread value, ASV) in the endosperm and maternal plant. The QTL analysis was performed for a set of 241 RIL population derived from an elite hybrid cross of “Zhenshan 97”  $\times$  “Minghui 63”, and their reciprocal backcrosses BC<sub>1</sub>F<sub>1</sub> and BC<sub>2</sub>F<sub>1</sub> generations. The QTL genetic effects including the endosperm additive main effect, endosperm dominance main effect, maternal additive main effect and their environmental interactions were analyzed in the present experiment.

## Materials and methods

### Plant population and sample preparation

A set of 241 RILs population (F<sub>9</sub>) derived from an elite hybrid cross of “Zhenshan 97” (P<sub>1</sub>)  $\times$  “Minghui 63” (P<sub>2</sub>) by single-seed descend, provided by National Key Laboratory of Crop Genetic Improvement of Huazhong Agricultural University, was used in this study. All plants of the RILs and the two parental lines were planted in a randomized block design with two replications on the 19th of May in the year 1999 and 2000 at the experimental farm of Zhejiang University, Hangzhou, China, and transplanted to a paddy field 30 days later, with a single plant per hill spaced at 20 cm  $\times$  20 cm. These RILs were used as the female parents in a backcross program with the two original inbred parents as the male parents, in order to generate two backcross populations. The two backcrossing populations with RILs  $\times$  P<sub>1</sub> and RILs  $\times$  P<sub>2</sub>, each containing 241 lines, were harvested and dried to a moisture content of 13.0% with a range of 12.5–13.7% in rice grains. All the samples were dehusked in an electrical dehusser (Model B-76, China) and milled by sample miller (Model JB-20 Huangyan, China).

### Spectroscopic analysis

About 10 g of rice grains were ground on a cyclone sample mill (Udy corp., Fort Collins, Colo, USA) with a 0.5 mm

screen. The moisture content of all sample flours was balanced to about 12% with range of 11.7–12.4%. All the samples were scanned on NIRSystem model 5000 monochromator (NIRSystem, Silver spring, MD, USA) with a full cup and reflectance spectra (log 1/R) from 1,100 to 2,498 nm and recorded at 2 nm intervals. Each sample was scanned two times and the average spectrum was used for further analysis. To avoid irregular spectra due to measurement errors, the sample, for which the Mahalanobis distance (GH) from the mean value of the initial population was more than 3.0, was rescanned.

Reflectance spectra of calibration set were transformed by first derivative (1,4,4,1) and scatter correction with Detrend and standard normal variate (SNV). By using the modified partial least squares (MPLS), the calibration models for cooking traits including amylose content (AC, %), gel consistency (GC, mm), alkaline spread value (ASV, grade) were well developed (Wu and Shi 2007). The cooking traits of rice were analyzed with NIRS technology on platform WinISI II, version 1.04 (Infrasoft international inc., Port Matilda, PA, USA).

### Data analysis and QTL mapping

The linkage map used in this study was established by the National Key Laboratory of Crop Genetic Improvement of Huazhong Agricultural University. A total of 221 makers including 175 RFLPs, 45 SSRs and 1 Waxy covered all 12 rice chromosomes with a total genome size of 1,796.58 cM, and an average distance of 8.13 cM between pairs of markers. Recently, this linkage map has been used widely in the study of QTL mapping (Tan et al. 1999).

Descriptive statistics, including mean, standard deviation, minimum and maximum values and frequencies, were computed with the STATISTICA (version 5.5; Statsoft, Inc., USA) for the investigated traits. The QTL analysis was conducted based on the following mixed linear model for seed traits assuming the genotypes at all  $s$  QTL loci are observed,

$$y_{ij} = \mu + \sum_{k=1}^s (x_{ik}^{Am} a_k^m + x_{ik}^{Ae} a_k^e + x_{ik}^{De} d_k^e) + \sum_{k=1}^s (x_{ik}^{Am} ae_{kj}^m + x_{ik}^{Ae} ae_{kj}^e + x_{ik}^{De} de_{kj}^e) + e_j + \varepsilon_{ij}, \quad (1)$$

where  $y_{ij}$  is phenotypic value of subject  $i$  in environment  $j$ ;  $\mu$  is the population mean;  $a_k^m$ ,  $a_k^e$  and  $d_k^e$  are the maternal additive main effect, endosperm additive main effect and dominance main effect of the  $k$ th QTL, respectively;  $x_{ik}^{Am}$  (=1 for maternal genotype QQ or -1 for qq),  $x_{ik}^{Ae}$  (= 1.5, 0.5, -0.5 or -1.5 for endosperm

**Table 1** The cooking traits of rice including AC, GC and ASV of parents and the two backcross populations (BC<sub>1</sub>F<sub>1</sub> and BC<sub>2</sub>F<sub>1</sub>) of RILs in 1999 and 2000

Growth year	Traits	Parents		BC <sub>1</sub> F <sub>1</sub> (RILs × P <sub>1</sub> )				BC <sub>2</sub> F <sub>1</sub> (RILs × P <sub>2</sub> )			
		ZS 97	MH 63	Means	SD	Minimum	Maximum	Means	SD	Minimum	Maximum
1999	AC	28.05	14.07	21.64	3.80	13.02	30.60	17.20	5.90	7.21	27.29
	GC	45.23	81.11	47.63	10.76	22.25	78.35	59.98	16.82	21.73	86.70
	ASV	5.83	3.52	6.40	0.75	4.96	9.41	5.90	0.79	2.80	7.89
2000	AC	22.53	9.55	20.63	3.18	12.62	26.79	16.28	5.58	8.47	26.55
	GC	48.49	76.46	55.35	8.89	36.11	81.73	64.19	15.57	31.60	88.85
	ASV	6.74	4.16	5.41	0.53	3.63	7.11	5.16	0.64	3.30	7.15

genotype QQQ, QQq, Qqq or qqq, respectively), and  $x_{ik}^{\text{De}}$  (=1 for endosperm genotype QQq and Qqq or 0 for QQQ and qqq) are their corresponding coefficients the values of which depend on the genotypes at locus  $k$ , respectively;  $ae_{kj}^{\text{m}}(0, \sigma_{\text{AmE}_k}^2)$ ,  $ae_{kj}^{\text{e}}(0, \sigma_{\text{AcE}_k}^2)$ , and  $de_{kj}^{\text{e}}(0, \sigma_{\text{DeE}_k}^2)$  are the random interaction effects of maternal additive effect, endosperm additive effect and endosperm dominance effect with the environment for the  $k$ th QTL;  $e_j(0, \sigma_E^2)$  is the effect of environmental  $j$ ; and  $\varepsilon_{ij}(0, \sigma_e^2)$  is the random residual effect. In reality, QTL genotypes are unknown and the coefficients need to be inferred from the flanking marker genotypes (Jiang and Zeng 1997). Because of the restriction of the generations available, the first and the second dominance effects cannot be estimated separately. We re-parameterize them as an endosperm dominance effect. Such treatment will not influence the estimation of the total dominance effect and other effects of an individual.

QTL mapping for AC, GC and GT was implemented with the software package QTLNetwork-CL-2.0-Seed (Yang, et al 2007). Since the true number of QTLs and their positions are unknown a priori, as suggested by Yang et al. (2007), a two-stage mapping strategy was employed, i.e., screening significant marker intervals by the method proposed by Piepho and Gauch (2001) and scanning QTL with a step increment of 1 cM within each selected interval with inclusion of other significant paired marker effects, followed by parameter estimation with the full model (1), including all QTLs detected in the first stage. The empirical  $P$  value was determined by the permutation testing (Doerge and Churchill 1996). The genetic main effects of QTLs, the GE interaction effects, and corresponding  $P$  values were obtained by the Markov Chain Monte Carlo (MCMC) algorithm (Wang, et al. 1994) for Gaussian mixed linear model via Gibbs sampling. The discovered QTLs were named according to the standard nomenclature, as suggested (McCouch et al. 1997).

## Results

### Phenotypic performance of the cooking traits

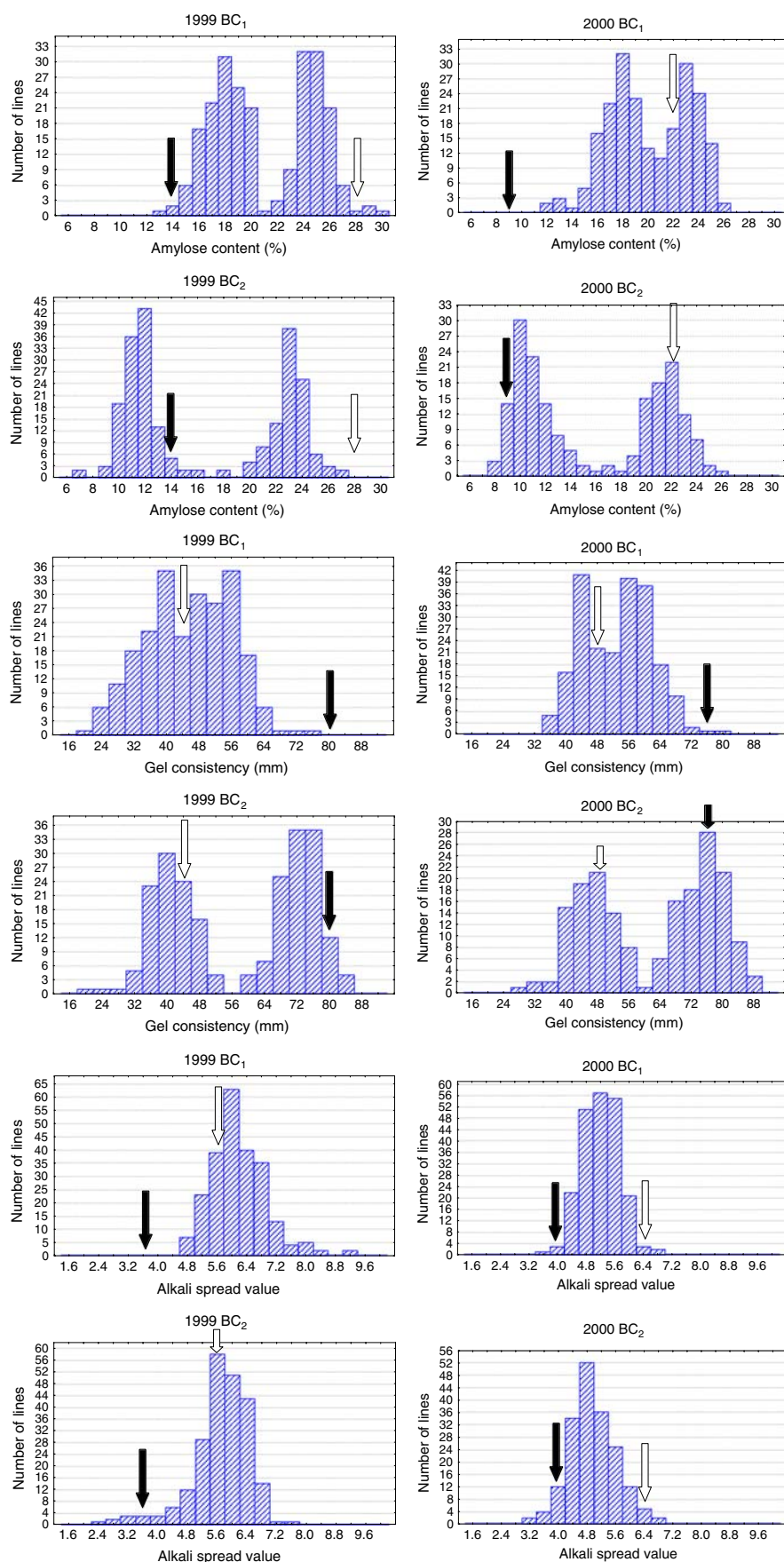
The cooking traits such as amylose content (AC), gel consistency (GC) and alkali spread value (ASV) of parent lines (Zhenshan 97 and Minghui 63) and their two backcross populations BC<sub>1</sub>F<sub>1</sub> (RILs × P<sub>1</sub>) and BC<sub>2</sub>F<sub>1</sub> (RILs × P<sub>2</sub>) are summarized in Table 1. Significant differences were found between the two parents for three traits. AC and ASV of rice for Zhenshan 97 were higher than those for Minghui 63, whereas GC for Zhenshan 97 was lower than that for Minghui 63 in both years. There were highly significant correlations among the three traits (Table 2). Such correlations might represent the real world because AC, GC and GT are the three most important traits related to the cooking quality of rice. The distributions of phenotypic values for AC, GC and ASV in BC<sub>1</sub>F<sub>1</sub> and BC<sub>2</sub>F<sub>1</sub> populations are presented in Fig. 1, respectively. AC and GC showed bimodal distributions, while ASV showed a normal distribution approximately. There were significant differences in distributions between BC<sub>1</sub>F<sub>1</sub> and BC<sub>2</sub>F<sub>1</sub> populations for all the phenotypes of cooking quality traits of rice. Both backcross populations also showed varying distributions in 1999 and 2000, implying that the cooking traits are subject to the modification by environments.

**Table 2** Correlation coefficients of the cooking traits in rice including AC, GC and ASV

Cooking traits	AC	GC
GC	−0.92**	
ASV	0.37**	−0.36**

\*\* Significant at the level of 1%

**Fig. 1** Frequency distributions of cooking quality traits for  $BC_1F_1$  ( $RILs \times P_1$ ) and  $BC_2F_1$  ( $RILs \times P_2$ ) in 1999 and 2000. *White and black arrows indicate the average values of the parents Zhenshan 97 and Minghui 63, respectively*



## QTL analysis for cooking quality traits of rice

QTL analysis identified a total of seven QTLs, associated with the cooking quality, which were subsequently mapped to chromosomes 1, 4 and 6 (Table 3, Fig. 2), respectively, namely *qAC-1-1*, *qAC-1-2*, *qAC-4-3* and *qAC-6-4* for AC, *qGC-1-1* and *qGC-6-2* for GC and *qASV-6-1* for ASV. Significant additive main effects ( $a^m$  and  $a^e$ ) of QTLs from diploid maternal plant and triploid endosperm were detected for all seven QTLs, and QTL  $\times$  environment interaction effects for six of these. The proportion of phenotypic variation attributable to the total genetic main effects and GE interaction of QTL were 0.800 and 0.009 for AC, 0.707 and 0.014 for GC, 0.113 and 0.007 for ASV, respectively. These results showed that the control for rice cooking quality was distributed over several chromosomes and the environmental interaction effects were also important for the performance of these quality traits.

## AC

The *qAC-4-3*, located between markers C56 and C820 on chromosome 4, had the largest maternal and endosperm additive main effects, and also an endosperm dominance main effect, although making a small contribution to the phenotypic variation. The *qAC-6-4* with the second largest effect was mapped to the interval between marker C952 and Waxy on chromosome 6, on which the *Wx* gene had already been located (Sano 1985). This QTL was found to have significant maternal interaction effects in 1999 and 2000, and its genetic main effect could explain phenotypic variation of 55.8%. The remaining two QTLs (*qAC-1-1* and *qAC-1-2*) were located between markers R753 and G359, and between C904 and R2632 on chromosome 1, respectively. The direction of additive main effect from *qAC-4-3* was positive in the maternal genome and negative in the endosperm one, whereas, the additive main effects from the other three QTLs was in the opposite direction, i.e., negative in the maternal genome and positive in the endosperm one. The significant dominance main effects for AC could be found from QTLs except for *qAC-1-1*. For GE interaction effects of QTLs, the results of the significant additive interaction effects from *qAC-6-4* and dominance interaction effects from *qAC-1-1* in both years, and additive interaction effect from *qAC-1-2* in 1999 as well as that found in the present experiment revealed that the effects from these QTLs varied in different environments.

## GC

Both QTLs (*qGC-1-1* and *qGC-6-2*) for GC were detected in the intervals between C904 and R2632 on chromosome

**Table 3** QTL locations and effects for AC, GC and ASV in BC<sub>1</sub>F<sub>1</sub> (RILs  $\times$  P<sub>1</sub>) and BC<sub>2</sub>F<sub>1</sub> (RILs  $\times$  P<sub>2</sub>) of RILs derived from the cross Zhenshan 97  $\times$  Minghui 63

QTLs	Chromosome	Mark interval	Position	Range	$a^m$	$a^e$	$d^e$	$ae_1^m$	$ae_1^e$	$de_1^e$	$ae_2^m$	$ae_2^e$	$de_2^e$
<i>qAC-1-1</i>	1	R753-G359	16.7	5.0–25.7	–11.05**	10.72**	–0.10	0.00	0.04	0.29*	0.00	–0.04	–0.29*
<i>qAC-1-2</i>	1	C904-R2632	102.5	100.9–104.5	–16.04**	15.59**	–0.18*	0.01	0.13*	0.00	–0.01	–0.13	0.00
<i>qAC-4-3</i>	4	C56-C820	0	0.0–3.0	41.77**	–41.48**	0.19*	0.00	–0.03	0.00	0.00	0.02	0.00
<i>qAC-6-4</i>	6	C952-Waxy	11.4	9.4–14.9	–23.50**	19.46**	–2.03**	–0.47**	0.00	0.00	0.45**	0.00	0.00
<i>qGC-1-1</i>	1	C904-R2632	103.5	100.9–107.7	5.02**	–3.78**	1.02**	1.11**	–1.75**	0.00	–1.12**	1.64**	0.00
<i>qGC-6-2</i>	6	C952-Waxy	11.4	10.4–12.4	17.20**	–6.37**	6.18**	1.43**	–0.14	0.55	–1.42**	0.13	–0.54
<i>qASV-6-1</i>	6	Waxy-C1496	14.9	12.9–16.6	–0.56**	0.39**	0.03	–0.12**	0.11**	0.00	0.11**	–0.11**	0.00

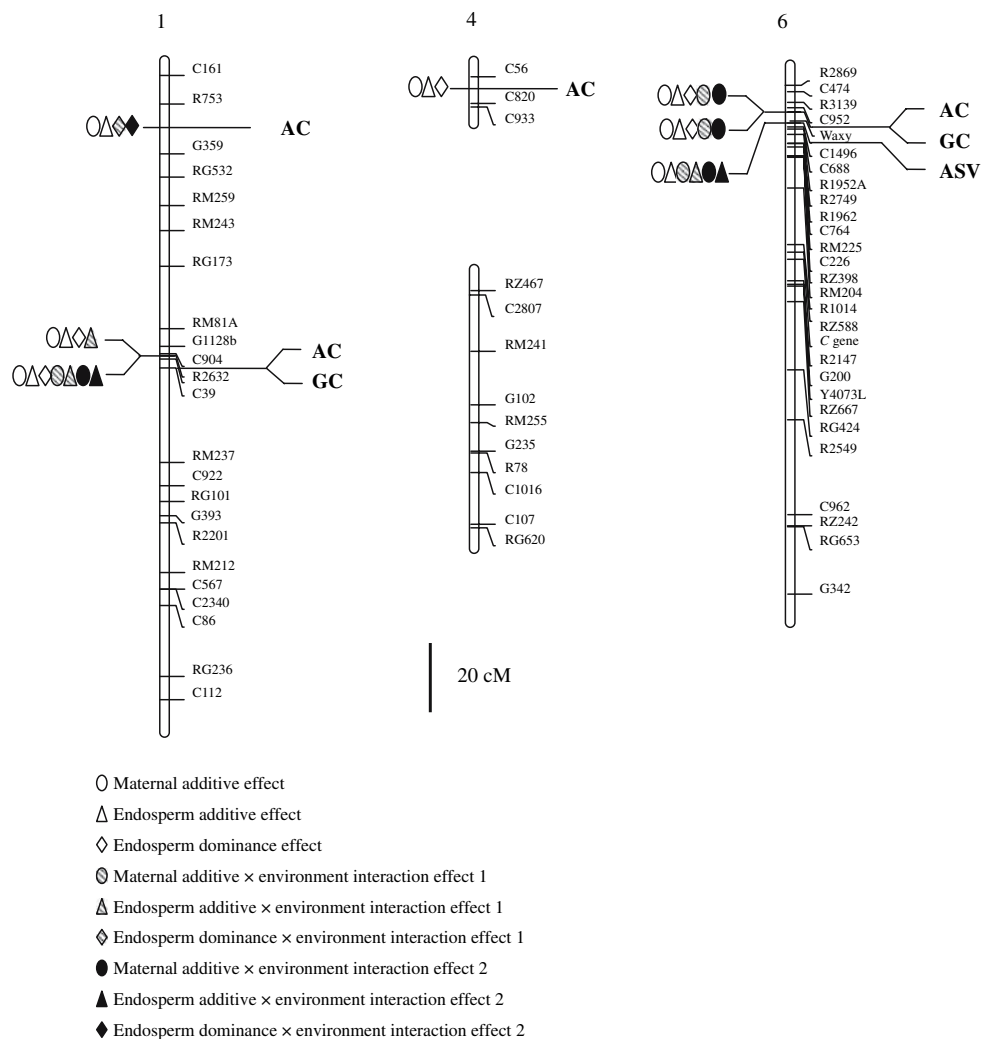
\* Significant at the level of 5%

\*\*\* Significant at the level of 1%

$a^m$  maternal additive effect,  $a^e$  endosperm additive effect,  $d^e$  endosperm dominance effect;  $ae_1^m$  maternal additive interaction effect in environment 1,  $ae_1^e$  endosperm additive interaction effect in environment 1,  $de_1^e$  endosperm dominance interaction effect in environment 1,  $ae_2^m$  maternal additive interaction effect in environment 2,  $ae_2^e$  endosperm additive interaction effect in environment 2, and  $de_2^e$  endosperm dominance interaction effect in environment 2



**Fig. 2** Mapping of the QTLs for controlling AC, GC and ASV using BC<sub>1</sub>F<sub>1</sub> (RILs × P<sub>1</sub>) and BC<sub>2</sub>F<sub>1</sub> (RILs × P<sub>2</sub>) of RILs derived from the cross Zhenshan 97 × Minghui 63



1, and between C952 and Waxy on chromosome 6. Maternal additive main effect, endosperm additive main effect and endosperm dominance main effect were found for both QTLs. Moreover, *qGC-1-1* also had significant maternal additive and endosperm additive interaction effects in both environments (1999 and 2000), whereas *qGC-6-2* only had significant maternal additive interaction effect in both environments. The proportion of phenotypic variation attributable to the genetic main effect of *qGC-6-2* was over 53%. These two QTLs showed the same direction of effect, positive in the maternal genome and negative in the endosperm one.

## ASV

Only one QTL (*qASV-6-1*) was detected for ASV, located between Waxy and C1496 on chromosome 6, and the genetic effects of *qASV-6-1* including the maternal additive and the endosperm additive main effects and their *GE*

interaction effects were significant in both environments. The genetic main effect of this QTL accounted for a relatively small proportion (11.3%) of phenotypic variation for ASV. This QTL showed negative effect in the maternal genome and positive effect in the endosperm one. Briefly, all QTLs detected showed the opposite directions of effect between the maternal genome and the endosperm one. According to the position and marker regions, the *qGC-1-1* might be tightly linked to the *qAC-1-2* and the *qGC-6-2* might be the same as *qAC-6-4*, which is more tightly linked to *qASV-6-1*.

## Discussion

Several studies have been conducted on cooking quality of rice with primary focus on amylose content (AC), gel consistency (GC) and gelatinization temperature (GT) to analyze the major and minor genes controlling grain quality. In these different experiments, different mapping

population have been used to identify QTLs controlling AC. Liu et al. (2000) reported two major QTLs controlling AC, located on chromosome 3 and 6, respectively, as well as five minor QTLs, using a population of 152 recombinant inbred lines (RILs) derived from a cross between CT9993 and Khaw Dawk Malil05. The major QTL on chromosome 6 was found to be close to *Wx* locus, and no interaction between the two major loci was detected. He et al. (1999) found a minor and a major gene for AC located on chromosomes 5 and 6, respectively, using a doubled-haploid (DH) population consisting of 132 lines. The major gene, which should be an allele of *Wx*, accounted for 91.9% of the total variation. Four QTLs for AC were detected on chromosomes 3, 4, 6 and 7 using a population of recombinant inbred lines (RIL) derived from cross KDML105 × CT9993 (Lanceras et al. 2000). On chromosomes 6 and 12, two QTLs were identified for amylose content, *ac6.1* and *ac12.1* (Li et al. 2004). Only one QTL for AC located on chromosome 6 and designated as *qAC-6*, was identified by Rui et al. (2005) using a DH population derived from the anther culture of an F<sub>1</sub> hybrid between WYJ2 and Zhenshan 97B. For GC, two QTLs were identified on chromosomes 2 and 7, respectively, using a DH population consisting of 132 pure lines (He et al. 1999). Two QTLs on chromosome 6 and one on chromosome 7 were detected for GC by using an RIL population derived from cross KDML105 × CT9993 (Lanceras et al. 2000). Three QTLs, designated as *qGC-1*, *qGC-2* and *qGC-6* were identified using a population consisting of 190 DH lines derived from an F<sub>1</sub> hybrid between WYJ 2 and Zhenshan 97B. Two QTLs for amylose content and gel consistency were detected and mapped on chromosomes 6, respectively, using 285 BC2F<sub>2</sub> families developed from an interspecific cross between cv IR64 and *Oryza rufipogon* (IRGC 105491; Septiningsih et al. 2003). The QTL with the largest effect (*qGC-6*) was located in the interval between RM190 and RM510 on chromosome 6 (Rui et al. 2005). Three QTLs for GT were detected on chromosome 2 and two on chromosome 6, using an RIL derived from a cross of KDML105 × CT9993 (Lanceras et al. 2000). Rui et al. (2005) detected one QTL for GT (*qGT-6*) using a DH population derived from the anther culture of an F<sub>1</sub> generation of the cross between WYJ2 and Zhenshan 97B. Most of these studies proved that the QTLs in the vicinity of *Waxy* locus were major contributors for the performance of AC, GC and GT. Therefore, all three traits are controlled either by the *Wx* locus or by a genomic region, which is tightly linked to this locus (Tan et al. 1999). Based on the present study (Table 3), tight linkage and/or pleiotropy might exist between the traits of AC and GC, due to one QTL (*qGC-1-1*) for GC being tightly linked to *qAC-1-2* and the other (*qGC-6-2*) being equal to *qAC-6-4*. Meanwhile, the pair of QTLs showed the opposite directions in both the diploid maternal and triploid endosperm

genomes, suggesting that these QTLs were responsible for most of the negative phenotypic correlation between the AC and GC (Table 2). For ASV, only one major QTL (*qASV-6-1*) was detected on chromosome 6 near the *Waxy* gene (*Waxy-C1496*) and tightly linked to *qAC-6-4* (*C952-Waxy*), and their effects showed the same directions in both the maternal and endosperm genomes. These indicated the cause of molecular basis to the positive phenotype relationship between AC and ASV, and to the negative between GC and ASV because of the significant positive or negative correlation coefficients, respectively (Table 2).

However, the cooking quality traits of rice were easily influenced by environmental conditions and the expression of quantitative genes from different genetic systems for cooking quality traits varied in different environments (Shi et al. 1997). Up to now, little information has been simultaneously found on the genetic main effects and the GE interaction effects of QTLs located on different chromosomes in different genetic systems. The results of the present study showed that the QTLs near the *Waxy* gene controlling AC, GC and GT were in good agreement with other studies, but the GE interaction effects of QTLs of diploid maternal plant and triploid endosperm were found for the first time. Among the QTLs for AC, the *qAC-4-3* on chromosome 4 without GE interaction effects played a stable role in controlling the performance of AC, overlapping with that found by Lanceras et al. (2000). The fourth QTL for AC (*qAC-6-4*) on chromosome 6, having visible maternal interaction effect in addition to the maternal and endosperm additive main effects, has not been reported in other studies and the environment of 1999 was good to reduce the AC, although its contribution was small. For the GC, while the QTL (*qGC-6-2*, equal to the *qAC-6-4*) had environmental interaction effect, the other QTL (*qGC-1-1*) was found to have notable maternal and endosperm additive interaction effects in the opposite direction in the present experiment. They might make a small contribution to the phenotypic variation due to their small effects. Likewise, the only one QTL controlling the ASV had a nearly equal value for two GE interaction effects and genetic main effects were quite strong, suggesting a gene expression stability. In general, the performance of cooking quality traits can be affected by the genetic effects of QTLs from different genetic systems including diploid maternal plant and triploid endosperm. In comparison with other genetic models, this model, which can distinguish the genetic effects expressed in the different chromosome ploidy genome, could be considered as a better tool to analyze the seed traits in the cereal crop.

The genetic effects of QTLs that control the seed quality of the cereal can be dissected into the diploid maternal and triploid endosperm genome, to allow people to know more about the genetic mechanism from the seed traits phenotype

to identification of genes. These will help breeders to adopt strategies for improving the quality traits more effectively. The QTLs may have three patterns in controlling the endosperm traits including having only maternal effect or endosperm effect, or having both maternal and endosperm effects. It is relatively easy to improve the quality traits of the former two kinds of QTLs using marker-assisted selection (MAS) if tight linkage molecular markers are available. In the latter kind of QTLs, it would be more challenging because the genetic effects of these QTLs might show different directions in the maternal and endosperm genome. The QTL having a higher genetic effect in the maternal genome than that in the endosperm can be more effectively used to improve the quality traits, because seed development depends on the maternal nutrient supplements. In this study, all the QTLs detected belong to the third pattern, in which QTLs controlling the performance of cooking quality traits of rice could be expressed in different genetic systems. The QTL (*qGC-6-2*) showing higher maternal additive effect than the endosperm additive effect could be introduced into the hybrid parents to get high GC value, i.e., increasing the tactility of the cooked rice. The AC, GC and ASV are the most important traits related to the cooking quality of rice and their close relationship was found in *indica* rice in the pervious study (Wang et al, 2005). The rice variety with a moderate AC, higher GC and ASV was more popularly accepted by the consumers. In this paper, high negative correlation between AC and GC is a good factor for improving the rice quality, while the positive correlation between AC and ASV is a negative aspect for improving the endosperm quality, and it is necessary to break down their linkage through genetic crossover and select target lines by using MAS technique.

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