Australian Journal of Crop Science AJCS
AJCS 7(13):2036-2047 (2013) ISSN:1835-2707

QTL analysis of eating quality and cooking process of rice using a new RIL population derived from a cross between Minghui 63 and Khao Dawk Mali105

Nassirou Tondi Yacouba[1, 2], Bo Yu[1, 2], Guangjun Gao[1], Qinglu Zhang[1], Caiguo Xu[1], Jinhua Xiao[1] and Yuqing He[1]*

[1]National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuhan 430070, China
[2]These authors contributed equally to this work.

*** Corresponding author: yqhe@mail.hzau.edu.cn**

Abstract

The cooking and eating quality of the rice grain is one of the most serious problems in many rice producing areas of the world. In this study, QTL analysis was performed for rice cooking and eating quality using a new recombinant inbred line (RIL) population derived from a cross between Minghui 63 (MH63), the Chinese best male sterility restorer in the hybrid rice programs, and Khao Dawk Mali105 (KDML105), the Thai jasmine rice, known as the best quality rice. The traits analyzed included amylose content (AC), gel consistency (GC), alkali spreading value (ASV), and 13 parameters from the viscosity profile. Comparison of the QTLs identified revealed 11 QTL clusters for these traits distributed on six chromosomes. The QTLs for the traits in the same class often clustered into the same chromosomal regions. A total of 29 QTLs were identified for 16 traits (or parameters) in the two years at P≤0.01 level. Our results clearly showed that the QTL cluster (six QTLs) corresponding to the *Wx* locus controlled six of the viscosity parameters such as BAtime-time needed from initial viscosity increase to peak viscosity (PKV), hot paste viscosity (HPV), final viscosity (FV), setback viscosity (SB) and consistency viscosity (CS), and had no effect on AC, GC, and ASV. The QTL cluster (13 QTLs) corresponding to the *Alk* locus played a role in ASV, GC, AC and all of the viscosity parameters except for PKV, FV and CS. In this study both AC and GC were not influenced by the *Wx* gene region. Our study investigated QTL analysis for the seven parameters of the viscosity profile, namely, Atemp, Atime, Btemp, Btime, BAtime, V95, and FV. Most of the QTLs previously found for these parameters on chromosome 6 in the *Wx* and *Alk* loci and on chromosome 5 and chromosome 7 were confirmed in the present study. Furthermore, new minor and major QTLs were also mapped on the chromosomes 5, 6, 7, 8, 11 and 12 for these parameters. However, we noted the instability of some of these QTLs across the environments and their small phenotypic variation value. Further investigation of these new QTLs or locus could bring more specific and comprehensive and probably complete information about them.

Keywords: QTL, Recombinant inbred line, Rice quality, SSR markers, Viscosity profile.
Abbreviations: AC-amylose content; Add-additive effect; *Alk*-alkali gene locus; Atemp-pasting temperature; Atime-pasting time; BAtime-time needed from initial viscosity increase to PKV; BD-breakdown viscosity; Btemp-peak temperature; Btime-peak time; Chrs-chromosome; CPV-cool paste viscosity; CS-consistency viscosity; FV-final viscosity at 40°C; GC-gel consistency; GT-gelatinization temperature; HPV-hot paste viscosity; KDML105-Kkao Dawk Mali105; MH63-Minghui 63; PKV-peak viscosity ; QTL-quantitative trait loci; RIL-recombinant inbred lines; RVA-rapid visco analyzer; SB-setback viscosity; SD-standard deviation; SSR-simple sequence repeats; V95-viscosity at 95°C; Var%-phenotypic variation percentage; *Wx*-waxy gene locus.

Introduction

Rice is the most important food crop in the world because nearly half of the world population depends on rice for survival. Although yield is the most valuable characteristic for farmers, but when the milled rice reaches the market, quality becomes the key determinant of its sale ability. Thus breeders are mandated to develop germplasm of high quality that suits the particular needs of the market being targeted. Improving varieties with good grain quality having been an important objective of improvement programs today, and its relevance is much greater (Pingali et al., 1997). Hence, knowledge about the genetic mechanism of rice grain quality will be of benefit to rice breeders (He et al., 1999). There are several defined classes of rice, based on the physical appearance of the milled rice, the cooking properties and the aroma of the rice. The significance of grain quality varies from region to region, depending on the requisites established by the international market, ethnic customs, uses, etc. For example, the preferences and tastes of Asian communities differ from those of Latin America (Martínez Racines et al., 1989). The appearance quality is often judged in China by the percentage of grain with a white core and a square of white core (He et al., 1999). The cooking quality is judged by the amylose content, alkali spreading score and gel consistency. Plant breeders have made crosses between varieties that differ markedly in their grain characteristics, making selection for quality that are less predictable and more difficult (Pingali et al., 1997). Rice quality comes from a polygenic group of traits affected by environmental factors, crop management and the resulting interactions among these (Wrigley and Morris, 1996). Many studies had been conducted on the inheritance of rice grain quality (McKenzie & Rutger, 1983; Sano et al., 1986; Pooni et al., 1992; Zhu &

Weir, 1994; Mo, 1995). Pooni et al. (1992) showed that quality improvement through conventional breeding was difficult due to the quantitative inheritance. However, the development of DNA marker technology facilitates understanding of complex quantitative traits. The investigations on the inheritance of rice grain quality in the past decades indicated that rice eating quality was directly related to three physico-chemical properties, AC (Juliano, 1985), GC (Cagampang et al., 1973) and gelatinization temperature (GT) (Little et al., 1958), and it was found that these traits were controlled by the *waxy* locus and/or tightly linked genomic region on chromosome 6. So far, many major and/or minor quantitative trait loci (QTLs) had been detected in rice for cooking and eating era. The results from molecular marker based quantitative trait locus (QTL) analyses of AC, GC and GT revealed that AC was mainly controlled by the *waxy* gene locus (*Wx*) on chromosome 6 (He et al., 1999; Tan et al., 1999; Bao et al., 2000; Lanceras et al., 2000; Septiningsih et al., 2003; Aluko et al., 2004), which encoded granule-bound starch synthase (Wang et al., 1995). Lanceras et al. (2000) found 4 QTLs for AC on chromosomes 3, 4, 6 and 7. These QTLs accounted for 80% of the phenotypic variation observed in AC. Two QTLs on chromosome 6 and one on chromosome 7 were detected for GC, which accounted for 57% of phenotypic variation. Umemoto et al. (2002) confirmed these findings and demonstrated that the *alk* locus encoded the enzyme soluble starch synthase IIa. Bao et al. (2002) and Lanceras et al. (2000) found the effect of the *wx* region on GC. However, He et al. (1999) and Bao et al. (2002) showed that GC was controlled by two QTLs with minor effects. Zhou et al. (2003) improved the eating and cooking quality of rice cultivar Zhenshan 97 by introgressing the *waxy* gene region from Minghui 63 (*wx*-MH), a restorer line that had medium AC, soft GC and high GT. Li et al. (2004) identified 4 QTLs for AC, 3 for GT and 5 for GC using backcross-inbred lines. Tian et al. (2005) found that the *Alk* locus predominantly controlled the ASV, and the *Wx* locus was the major QTL specifying AC and a minor one for GC, but no effect on ASV. Fan et al. (2005) reported similar results. In this study, a new RIL population derived from a cross between MH63 and KDML105 was used to map QTLs involving in eating and cooking quality related traits in rice including AC, GT, GC, and 13 viscosity parameters. The results thus obtained may provide enhanced understanding to the breeding of high quality rice varieties.

Results

Linkage map

In this current study, 1450 primer pairs (RM series only) were used to screen the two parents for polymorphism, only 208 SSR markers was polymorphic and among them 113 were useful to construct the linkage map. The total markers covered all chromosomes except chromosome 10. The length of map was 2339.8 cM, and average was 17.46 cM between two markers. The gaps in this map could be explain by the fact that the parents used in this study were *indica* rice with low amylose content, therefore it was difficult to find polymorphic markers. Indeed, many SSR markers, e.g., some closely linked to the *waxy* gene on the chromosome 6, were polymorphic between the two parents. But segregation analysis confirmed that their region was not associated with variation for the trait which probably suggested that it was not segregating in this population in this locus.

Parents and population phenotypic variations

The mean values for the two parents and RILs in the year 2009 and 2010 are listed in Table 1. No Significant phenotypic differences were detected between the parents for AC and GC and significant phenotypic differences for ASV using a *t* test ($P < 0.01$), in which MH63 showed low AC, soft GC and low ASV and comparatively KDML105 had low AC, medium GC and high ASV. However, small difference were detected for the population mean in AC and the parents value, the same for GC and all the viscosity traits except V95, HPV and CS, but significant differences in ASV were observed between the two parents and the population mean value. For each trait, the population data showed approximately normal distributions in both two years. The RIL population mean showed low AC, high-intermediary ASV and medium to soft GC.

Correlations of traits and parameters

The principal component analysis was used to analyze (Table 2) the correlation between all traits, and it was obvious to find that the principal components analysis results are not consistent in two years repeat. In the year of 2009, all traits could be divided into two groups; the first group contained ASV, Atime, Atemp, Btime, Btemp, BAtime, PKV, SB, BD and V95. Traits, HPV, CPV, and FV were in the second group. The same in the year 2010, all the traits could be also divided into two groups, ASV, Atime, Atemp, BAtime, HPV, CPV, FV were in the same group, while PKV and SB were in another group. When comparing the results of the two years, it was found that ASV, Atime, Atemp and BAtime were always in the same group, the same PKV and SB were always together, but they belonged to the first group and the second group, respectively in 2009 and 2010. Another notable result was that HPV, CPV and FV belonged to the first group in 2009 and to the second group in 2010. These results suggested that those traits were probably influenced by environment. However, the coefficient of pairwise correlation analysis showed (Table 3) that all the viscosity parameters were significantly correlated (positively or negatively) except FV and peak time and peak temperature (Btime-Btemp), and also SB and V95. GC also correlated significantly with all the RVA profiles. AC and ASV correlated significantly with most of the RVA profiles, positively or negatively at least for one year.

QTLs analysis by interval mapping method

QTLs for Amylose content (AC)

Two QTLs were found responsible for AC, one in 2009 and another one in 2010. The QTL in 2010 was detected in the interval of RM402-RM5963 on the chromosome 6 (Table 4, Fig. 2) which corresponds to the *Alk* locus. This QTL accounted for 8.6% of the total phenotypic variation and its increasing effect came from KDML105 alleles (Table 3). For the one detected on Chr 8 in 2009, the phenotypic variation value was about 5.7% and was increased by the allele of MH63.

QTLs for Gel consistency (GC)

Three QTLs were detected for GC in the two years. One QTL was mapped in RM402-RM5963 (Chr 6), coincided with the *Alk* locus in both two years (Table 4, Fig. 2); the phenotypic variation value explained was 26.3% and 25.8%, respectively

Table1. Descriptive statistics of the rice cooking and eating quality traits (parameters) in parents and mapping population observed in 2009 (upper) and 2010 (lower).

	Population		Parents	
Traits	Mean ± SD	Variation range	MH63	KDML105
Atime	6.32±0.66	5.08-7.25	6.72±0.046	5.64±0.052
	6.55±0.86	5.00-767	6.83±0.085	5.58±0.085
Atemp	78.00±4.09	68.90-84.10	81.8±0.458	74±0.61
	78.45±5.54	67.40-86.40	82.53±0.058	74.73±0.93
Btime	8.03±0.20	7.25-8.75	8.08±0.085	8.08±0.55
	7.73±0.17	6.92-8.00	8.20±0.046	8.08±0.63
Btemp	89.30±1.59	84.00-95.90	89.5±0.17	89.67±0.25
	87.17±1.12	81.80-88.90	89.57±0.40	89.67±0.26
BAtime	1.71±0.76	0.66-3.33	1.36±0.095	2.44±0.052
	1.17±0.81	0-2.75	1.36±0.098	2.50±0.085
PKV	364.24±34.15	286-502	324±8.89	353.67±5.69
	392.32±30.32	178-455	313±3.21	343±6
V95	309.72±18.22	262-427	282.33±0.58	326.3±6.43
	274.22±18.50	220-317	284.33±3.51	317.67±1.15
HPV	208.97±23.09	149-326	177.67±4.93	248.067±1.15
	157.74±14.16	122-188	181.33±4.04	241.33±7.02
CPV	310.06±19.49	247-438	290.33±1.53	311.67±2.52
	235.41±18.14	183-275	292±2.64	306.33±3.05
FV	290.86±19.29	236-453	267.67±1.53	285.33±3.05
	234.12±16.75	186-274	268.67±4.62	279.67±6.33
BD	155.27±40.53	50-290	146.33±13.80	105±6.08
	236.01±21.86	178-290	132.00±1.00	101.67±1.15
SB	-54.19±37.79	-237	-33.67±9.87	-42±3.46
	158.63±22.89	115-217	-21.33±1.15	-36.67±3.05
CS	101.09±14.08	59-157	112.67±4.04	63±2.65
	77.38±8.21	46-96	110.67±1.53	65±4
AC	14.46±2.23	7.70-32.66	15.29±0.015	13.24±0.036
	11.18±2.24	6.86-27.92	15.47±0.03	13.74±0.015
GC	52.94±8.10	25.00-86.50	76.67±1.53	58±0.5
	62.83±6.31	43.50-80.50	77±1.8	60.5±1
ASV	3.00±2.01	1.00-7.00	1.83±0.17	5.89±0.09
	2.80±1.72	1-6.6	1.78±0.09	5.94±0.1

SD, standard deviation.

in 2009 and 2010 and in the two years the increasing allele came from MH63. This QTL had been described as *gc6b* (near marker RM402) in a previous study (Fan et al. 2005). Two other QTLs were found in the interval RM481-RM18 (Chr 7) and RM122-RM413 (Chr 5), respectively. These two QTLs accounted for 9.82% and 9.10% of phenotypic variations and the increasing allele came from the allele of KDML105.

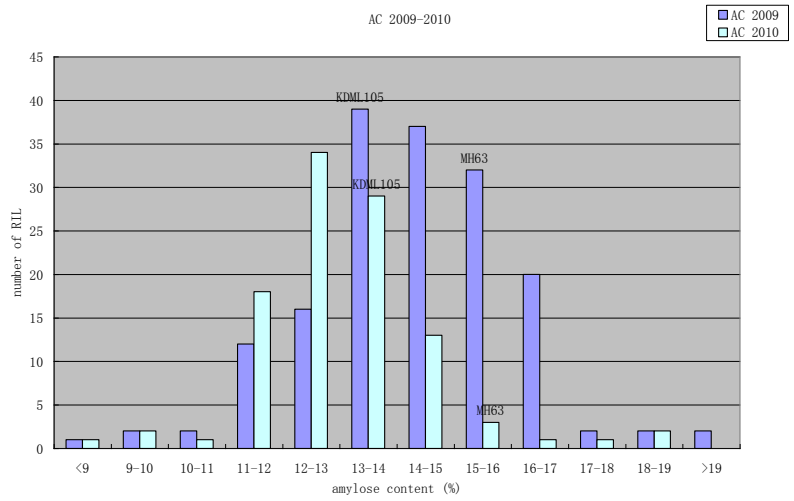
QTLs for Alkali spreading value (ASV)

A total of two QTLs were found responsible for ASV over the two years all located on the Chr 6 (Table 4, Fig. 2), in which one was detected in both years at the same interval RM402-RM5963, and counted for 59.8% and 55.8%, respectively in 2009 and 2010 of the total phenotypic variation value. This QTL coincided with the *Alk* locus. The other one was mapped in the interval RM136-RM3, accounting for 41.9% of the total phenotypic variation. All the QTLs had their increasing effects from the KDML105 allele (Table 4).

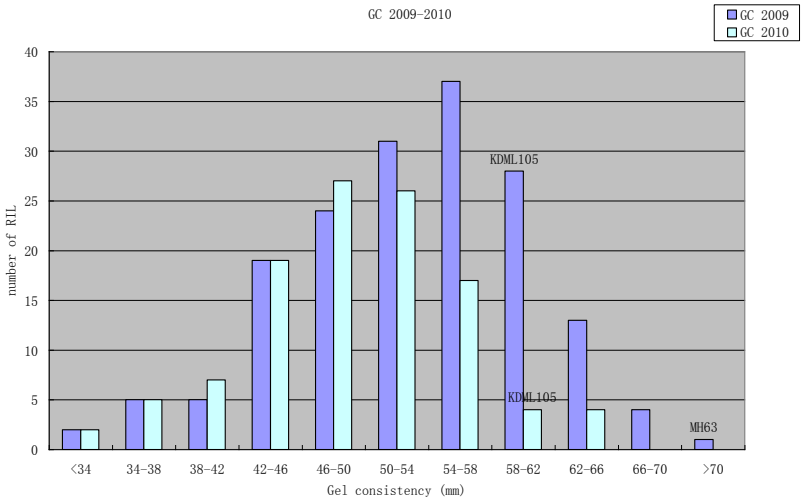
QTLs for Viscosity profile parameters

QTLs for pasting temperature (Atemp) and Pasting time (Atime)

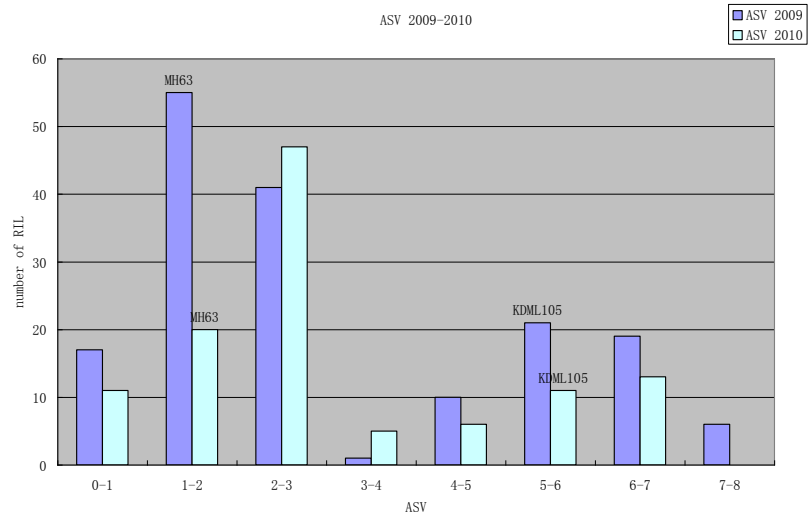
A total of three QTLs were detected for Atime (Table 4, Fig. 2). Of them, one was found in the same interval in the both years in RM402-RM5963 on the chromosome 6, which coincided with the *Alk* locus, accounting for 68.4 and 68.45% of the total phenotypic variation value. On the chromosome 6, another QTL was found in RM584-RM402 in 2009, accounting for 28.5% of the total phenotypic variation value. The last QTL was located on chromosome 5 (RM18452-RM18614) in 2010, their phenotypic variation value counted for 5%. For all the QTLs, the increasing effects came from MH63 allele (Table 4). Two QTLs were detected for Atemp in 2009 and 2010 (Table 4, Fig. 2). Of them, one was located in RM402-RM5963 in the both years, which coincided with the *Alk* locus, accounting for 66.2% and 67.1% of the total phenotypic variation, respectively in 2009 and 2010. Their increasing effect came from MH63.



(a)



(b)



(c)

Fig 1. Distribution of (a) amylose content (AC), (b) gel consistency (GC) and (c) alkali spreading value (ASV) traits in a new RIL population derived from a cross between MH63 and KDML105 in two years, bimodal distributions were observed. The AC values of MH63 were 15.27% and 15.44% and those of for KDML105 were 13.2% and 13.72%, respectively in 2009 and 2010. The GC values were 75mm and 75.5mm for MH63 and 57.5mm and 59.5mm for KDML105, respectively in 2009 and 2010. The ASV values were 2.0 and 1.8 for MH63 and 5.1 and 6.0 for KDML105, respectively in 2009 and 2010.

In 2010 another QTL was detected in RM3394-RM20916 (Chr 7), accounting for 6.0 % of the phenotypic variation value and the increasing effect also came from MH63 allele.

QTLs for Peak temperature (Btemp), peak time (Btime) and time needed from point A to point B (BAtime)

Four QTLs were found to be responsible for Btime in the two years. Of them, one QTL was detected in both years and coincided with the *Alk* locus on the Chr 6, accounting for 15.1 and 7.8% of the total phenotypic variation value, respectively in 2009 and 2010 (Table 4, Fig. 2). Their increasing allele came from KDML105 and MH63 respectively one for each year. Three more were detected in RM413-RM17896 (Chr 5), M445-RM11 (Chr 7) and RM547-RM310 (Chr 8), accounting for 4.6%, 6.6% and 8.3% of the total phenotypic variation, respectively. The increasing effects came from the MH63 allele for all of them. For Btemp, three QTLs were found to be responsible for the trait in the two years. Of these QTLs, one coincided with the *Alk* locus in both years, accounting for 13.7% and 8.7% of the total phenotypic variation value, respectively in 2009 and 2010 (Table 4, Fig.2), the increasing effect came from KDML105 and MH63 respectively. One more QTL was found in RM413-RM17896 (Chr 5) with 4.8 % as contribution for the total phenotypic variation value. Another QTL detected in 2009 was near the *Wx* locus (RM469-RM508), accounting for 7.8% of the total phenotypic variation. The increasing effect of these last two came from MH63 allele. For the trait BAtime analysis, a total of four QTLs were found responsible in the two years (Table 4, Fig. 2). Two QTLs were constantly detected in both years, in which one coincided with *Wx* locus (RM133-RM584), accounting for 7.5% and 30.1% of the total phenotypic variation value, respectively in 2009 and 2010. And the other one in RM402-RM5963, the *Alk* locus, explained 70% and 61.4% of the total phenotypic variation respectively in 2009 and 2010. Two QTLs were mapped on the chromosome 5 in RM18614-RM164 and chromosome 11 in RM26643-RM7120, accounting for 5.07% and 4.05% of the phenotypic variation value respectively in 2010. The increasing effects came from the KDML105 allele for all the QTLs in the *Wx* locus and those from the *Alk* locus came from MH63 allele, the same as the one on Chr 11.

QTLs for Peak viscosity (PKV), viscosity at starting of 95°C (V95) and hot paste viscosity (HPV)

A total of five QTLs were identified responsible for PKV in 2009 and 2010. In which, four were mapped in 2009 on the chromosome 2 and 5 with one each, and two on the chromosome 6, one of these two coincided with the *Wx* locus interval RM133-RM584, explaining 7.2% of the total phenotypic variation. The only one QTL found in 2010 was on the chromosome 3, accounting for 10.1% of the phenotypic variation (Table 4, Fig. 2). Two QTLs were found responsible for V95, one each year. The one mapped in RM402-RM5963 (Chr 6) in 2010 coincided with the *Alk* locus and account for 18.99% of the phenotypic variation. The increasing effect came from MH63 allele for that QTL, comparatively the one found in 2009 on the chromosome 2, the increasing effect came from KDML105, accounting for 6.0% of the total phenotypic variation (Table 4, Fig. 2).For the HPV, five QTLs were identified within the two years, three and two respectively in 2009 and 2010. The QTL detected in 2009 on the chromosome 6 corresponded to the *Wx* locus (RM133-RM584), accounting for 8.0% of the phenotypic variation, the increasing effect came from KDML105. One QTL was mapped in RM402-RM5963 which coincided with *Alk* locus, and accounts for 24.1% of the phenotypic variation. The other QTLs were found on the chromosomes 3, 11 and 12, collectively explaining 9.9, 5.6, and 6.2% of the total phenotypic variation respectively (Table 4, Fig. 2).

QTLs for Cool paste viscosity (CPV) and final viscosity at 40°C (FV)

Five QTLs were detected to be involved in controlling CPV. Of them, only one was detected in 2010 on the chromosome 6 and had the largest value 22.1% of the total phenotypic variation and coincided with *Alk* locus. The other four QTLs in 2009 were mapped on the chromosomes 5, 6, 8 and 12, collectively explaining 10.0, 5.7, 12.3 and 6.2% of the phenotypic variation. The increasing effects came from MH63 allele for all except the one on the chromosome 6 in 2009 which came from KDML105 allele (Table 4, Fig. 2). Four QTLs were identified for FV, three and one in 2009 and 2010 respectively. The one found in 2010 coincided with the *Wx* locus, explaining 21.9% of the total phenotypic variation; MH63 allele increased the effect (Table 4, Fig. 2). The three other QTLs were identified on the chromosomes 5, 8, and 12, accounting for 8.4, 10.0 and 5.5% of the phenotypic variation respectively; also the increasing effects came from the MH63 allele.

QTLs for Breakdown (BD), Consistency (CS) and Setback (SB)

Five QTLs were found to be involved in controlling BD in the two years, three in 2009 and two in 2010. The two QTLs found in 2010 were on the chromosome 6 and one of them corresponded to the *Alk* locus in the interval RM402-RM5963, explaining 16.0% of the phenotypic variation. In those mapped in 2009, one coincided with *Wx* locus with 7.9% of phenotypic variation. The other QTLs were detected on the chromosome 6 and 7, collectively explaining 10.6, 9.3 and 7.2% of the total phenotypic variation. MH63 increased the QTL effect in the *Wx* locus and KMDL105 did the same in the *Alk* locus (Table 4, Fig. 2). Nine QTLs were found to be responsible for SB, four and five in 2009 and 2010, respectively. Three of them were located on the chromosome 7, collectively explaining 6.5, 11.8 and 14.3% of the phenotypic variation (Table 4, Fig. 2). The increasing effects came from MH63. Two each year were mapped on the chromosome 6, in which one in the *Wx* locus and another in the *Alk* locus, accounting for 10.0 and 25.8% of the total phenotypic variation. KDML105 increased the QTL effect in the *Wx* locus and MH63 increased it in the *Alk* locus (Table 4). The two more QTLs on the chromosome 6 collectively explained 10.63% and 19.78% of the total phenotypic variation. Three and two QTLs were detected for CS in 2009 and 2010, respectively (Table 4, Fig. 2). One of them was mapped on the chromosome 6 in 2010, which coincided with the *Wx* locus in the interval RM133-RM584, explaining 29.2% of the total phenotypic variation. Within the other more QTLs, two were located on the chromosome 4, one on the chromosome 8 and one on the chromosome 11, respectively explaining 7.3, 8.5, 9.5, 7.6 and 6.5% of the total phenotypic variation.

Comparison of the QTLs and their co-localization

Comparison of the QTLs identified above revealed 11 QTL clusters for these traits that are distributed on 6 chromosomes (Fig. 2). The QTL for the traits in the same class often

Table 2. Principal component of analysis of eating and cooking traits of rice grain in a new RIL population derived from a cross between MH63 and KDML105, with standardized loadings (The absolute values of marked loadings > 0.7).

Traits	Principal Components of 2009				Principal Components of 2010			
	1	2	3	4	1	2	3	4
AC	-0.19	0.60	0.03	0.59	-0.36	-0.07	0.52	-0.17
ASV	-0.75 *	-0.21	0.50	0.12	-0.84*	0.15	0.30	-0.21
GC	0.57	0.03	-0.14	-0.21	0.53	-0.35	-0.20	0.34
Atime	0.71 *	0.23	-0.60	-0.18	0.90 *	-0.33	-0.15	0.17
Atemp	0.74*	0.22	-0.59	-0.08	0.88*	-0.35	-0.18	0.14
Btime	-0.87*	-0.06	-0.37	-0.13	0.42	-0.51	0.67	0.13
Btemp	-0.85 *	0.00	-0.29	-0.17	0.39	-0.48	0.66	0.23
BAtime	-0.85 *	-0.22	0.42	0.12	-0.88*	0.25	0.31	-0.15
PKV	0.72 *	0.40	0.55	-0.05	0.30	0.92*	0.12	0.21
V95	0.03	0.80*	0.43	-0.32	0.67	0.61	0.38	0.09
HPV	-0.45	0.80*	0.05	-0.39	0.78 *	0.48	0.32	-0.09
CPV	-0.30	0.91*	-0.11	0.17	0.82 *	0.51	0.14	-0.21
FV	-0.13	0.93 *	0.04	0.24	0.78 *	0.56	0.12	-0.25
SB	0.73*	-0.12	0.54	-0.18	-0.32	0.82*	-0.13	0.38
CS	0.32	-0.04	-0.23	0.87	-0.52	0.66	0.00	0.53
BD	0.86 *	-0.12	0.44	0.18	0.60	0.36	-0.36	-0.44
% of Variance	39.80	23.18	15.20	10.46	43.43	26.28	11.72	7.00
Total Proportion	6.37	3.71	2.43	1.67	6.95	4.21	1.88	1.12

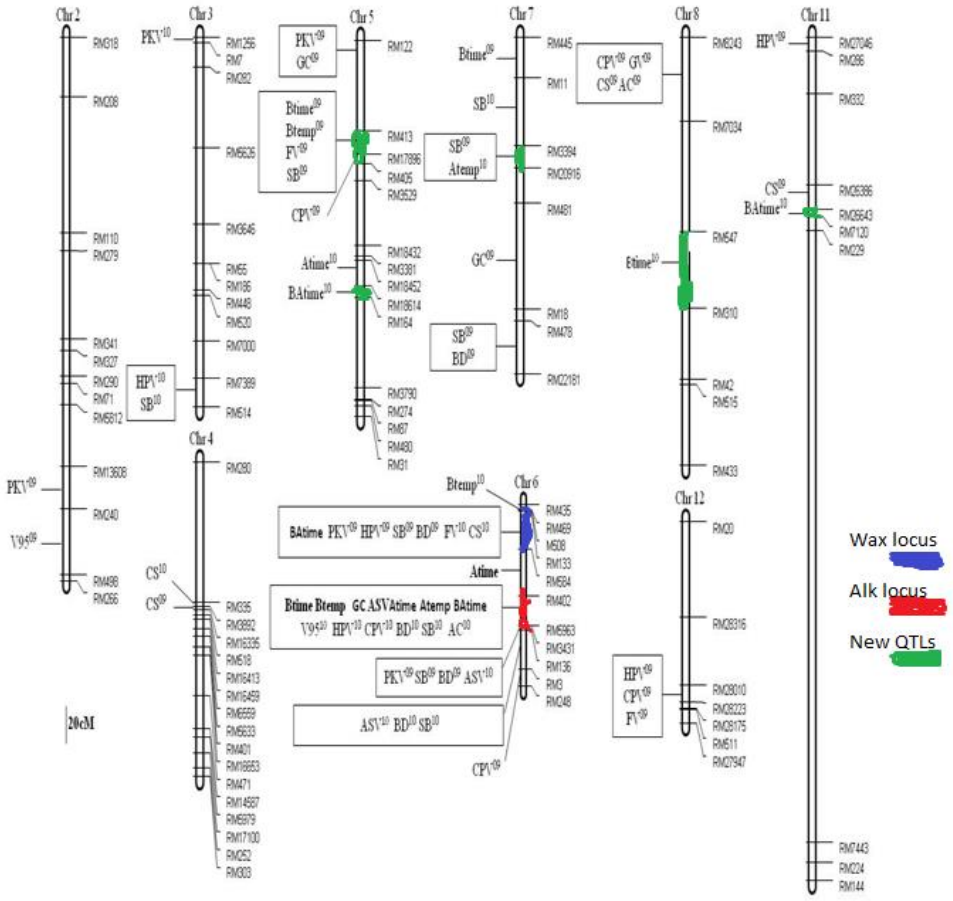


Fig 2. Distribution of QTLs of eating and cooking traits of rice grain in a new RIL population derived from a cross between MH63 and KDML105 in the linkage map. The marker name is shown on the right of the chromosome. The superscript 09 or 10 indicates the year (2009 or 2010) in which the QTL was detected; the letters in bold face indicate that the QTLs were detected in both years. The blue color segment shows the *waxy* locus cluster; the red color segment shows the *Alk* locus cluster and the green color segments show the new QTL about the seven parameters of the viscosity profile, namely, Atemp, Atime, Btemp, Btime, BAtime, V95, and FV.

clustered into same chromosomal regions. The QTL clusters corresponding to the *Wx* locus and *Alk* locus were detected for most of the traits. The QTL clusters corresponding to *Wx* locus simultaneously controlled most of viscosity parameters, but had no effect on AC, GC, Atime, Btime, V95 and CPV, while the QTL corresponding to *Alk* locus played a role in AC, ASV, GC, and all the viscosity parameters except for PKV, FV and CS. The positive effects of the cluster corresponding to the *Alk* locus came from MH63 for almost all the traits, except AC, ASV, BAtime, Btime, Btemp and BD. In the present study, co-localization of the QTLs not only found in these two major loci, but also in other loci such as those on chromosomes 3, 5, 6, 7, 8 and 12.

Discussion

In the present study, the genetic basis of the cooking process and eating quality traits of the rice grains reflected by AC, GC, ASV, and the parameters of viscosity profile, was dissected simultaneously with a new RIL population developed using two parents with contrast phenotypes. A total of 29 distinct QTLs were identified for 16 traits (or parameters) in the two years at $P \leq 0.01$ level. According to Kharabian-Masouleh et al., (2012) six genes, granule bound starch synthases (GBSSII), starch synthases (SSI, SSIIIa, SSIIIb, SSIVa) and branching enzymes (BE), had low to medium effects on variation in starch traits. SNPs in these genes had association with a number of characters with low to medium R2 values. Our results clearly showed that the QTL corresponding to the *Wx* locus controlled only six viscosity parameters, and had no effect on AC, ASV and GC. The QTL corresponding to the *Alk* locus played a role in ASV, GC, AC and all of the viscosity parameters except for PKV, FV and CS. It was known that AC is a key factor in determining rice cooking quality and market class (He et al., 1999), and known to be associated with variation at the *waxy* (*Wx*) locus on chromosome 6 and several modifiers have also been reported in the same region (Wu & Tanksley, 1993; Li et al., 1994; Tanksley et al., 1995; He et al., 1999). However, in this study, no QTL was identified at the *Wx* locus for AC.. Besides the *Wax* locus, some loci regulating AC were identified and mapped to chromosomes 2, 4, 5, 6, 7 and 9 (Kaushik & Khush, 1991; He et al., 1999; Yano et al., 2000). Moreover, in this study we found one QTL for AC on chromosome 6 in the *Alk* locus in the interval RM402-RM5963, this QTL was reported before in many studies near this interval or inside it (Tan et al., 1999; Aluko et al., 2004; Fan et al., 2005; Wang et al., 2007). The second QTL for AC was detected on the chromosome 8, it has been reported before by Sabouri (2009). In this study AC and GC had no significant differences between the two parents and, both AC and GC were not influenced by the *Waxy* gene region; this could be explained by the fact that *waxy* gene is allelic in MH63 and KDML105 and AC/GC were not segregated in the RILs population. It is important to choose parents with suitable characteristics in QTL mapping. However, GT is controlled by a major QTL on chromosome 6, independent of the *waxy* gene, at a location coinciding with the *Alk* locus (Umemoto et al. 2002). It was concluded that this QTL is an allele of the *Alk* gene encoding soluble starch synthase IIa. Our results did not differ from those of Tan et al. (1999), but were in agreement with those of He et al. (1999), Lanceras et al. (2000), and Umemoto et al. (2002) who concluded that GT was primarily controlled by the *Alk* gene region. However, we can not be in agreement with those of Lanceras et al. (2000), and Tan et al. (1999), who also mapped a major QTL for GC in the *waxy* gene region. The major QTLs identified in our study for ASV (GT) were mapped in the interval, RM402-RM5963, and RM136-RM3 of which the first one correspond to the *Alk* locus. Our result might support the theory of Li et al. (2003) which said that AC might affect ASV and concluded that AC changes ASV at this locus, although the effect may be minor. The results from Wang et al. (2007) clearly supported the result of Fan et al. (2005) as they detected the all related QTL at two loci at P=0.01 level and particular we also detected a QTL for GC at *Alk* locus, we support this theory as we detected a QTL for GC; we mapped a major QTL in both two years on the chromosome 6 corresponding to the *Alk* locus, which was also located by Wang et al. 2007 but the probable discrepancy between their results and ours may be attributed to the differences in the genetic materials used and experiential locations. However the parent used in our study showed no large differences for GC. We also found two more QTLs on chromosome 5 mapped by (Sabouri, 2009), and on chromosome 7, reported by some previous studies (Tan et al. 1999; He et al. 1999; Lanceras et. 2000; Bao et al. 2002 and Li et al. 1999), these QTLs collectively explained a small phenotypic variation value. Since we found major QTL for GC in the same interval we found major QTLs for ASV in the *Alk* locus, Li et al. (2003) suggested that GC could be modified by ASV. A decade ago, study conducted by Gravois and Webb (1997) revealed that the paste viscosity appeared to be controlled by one major gene with additive effects, and now through Q'I'L mapping for each RVA profile parameter, studies conclude that this gene is *Wx* gene on chromosome 6 which encodes the granule-bound starch synthase. This *Wx* gene was detected for six viscosity parameters in our study, namely BAtime, PKV, SB, FV, HPV and CS, though they were also affected by other QTLs. A recent association study in glutinous rice has shown strong relationships between pullulanase and RVA profile parameters. The differing observations are most likely due to the structure of each population, Kharabian-Masouleh et al., (2012). Minor genes are very population-specific and the analysis of Yan et al. (2010) was undertaken within a glutinous population composed of rice varieties which have very low amylase content and this would have revealed the role of pullulanse in this genetic background. However, RVA parameters such as starch paste viscosity and other starch quality traits may be controlled by a complex genetic system involving many starch-related genes. Allahgholipour et al. (2006) showed that the pasting properties of rice flour have a direct relationship with the GT and GC, and Yan et al. (2005) studied the relationship between AC and the RVA pasting properties and they showed that varieties with similar AC have different pasting characteristics and were also different in eating and cooking quality and also demonstrated that a strong relationship does exist between the AC (%) and RVA pasting properties, as observed in a large germplasm collection. In the same order of idea, Wang et al. (2007) also reported this relationship more specifically saying that among the secondary paste viscosity parameters, previous studies indicated that BD and SB are highly correlated with eating quality (Shu et al., 1998; Larkin & Park, 2003), such that rice varieties with relatively good eating quality have higher BD but lower SB (Shu et al., 1998). Our results showed that BD and SB are two main members in the first group in 2009, as indicated by principal component analysis (Table 2) and BD and SB had positive value. The Debranching enzymes (ISA) genes contribute to the degree of setback on glutinous rice cultivars, Kharabian-Masouleh et al., (2012); we believe that our major QTLs for RVA profile parameters are influenced by that locus. In this study we investigate QTL analysis about

Table 3. Coefficients of pairwise correlations of eating and cooking traits of rice grain in a new RIL population derived from a cross between MH63 and KDML105.

	GC	ASV	AC	Atime	Atemp	Btime	Btemp	BAtime	PKV	V95	HPV	CPV	FV	SB	CS
ASV	-0.48**														
	-0.52**														
AC	0.03	-0.07													
	0.37**	-0.23**													
Atime	-0.88**	0.44**	-0.12												
	-0.90**	0.59**	-0.34**												
Atemp	-0.87**	0.47**	-0.09	0.96**											
	-0.90**	0.59**	-0.35**	0.99**											
Btime	0.48**	-0.46**	0.01	-0.36**	-0.41**										
	-0.19	0.21*	0.12	0.42**	0.39**										
Btemp	0.48**	-0.44**	0.03	-0.38**	-0.42**	0.95**									
	-0.23**	0.19	0.14	0.39**	0.37**	0.87**									
BAtime	0.89**	-0.51**	0.11	-0.97**	-0.95**	0.58**	0.59**								
	0.93**	-0.59**	0.39**	-0.98**	-0.98**	-0.24**	-0.24**								
PKV	-0.35**	0.30**	0.07	0.28**	0.30**	-0.81**	-0.72**	-0.47**							
	-0.13	-0.11	-0.13	-0.004	-0.03	-0.24**	-0.19	-0.05							
V95	-0.01	0.03	0.27**	0.0005	-0.03	-0.18	-0.1	-0.05	0.6						
	-0.36**	0.11	-0.16	0.35**	0.32**	0.23**	0.21*	-0.32**	0.81**						
HPV	0.14	-0.14	0.34**	-0.1	-0.16	0.34**	0.41**	0.18	0.04	0.73**					
	-0.46**	0.19	-0.19	0.47**	0.45**	0.24**	0.20*	-0.45**	0.69**	0.94**					
CPV	0.01	-0.13	0.64**	0.02	0.03	0.22**	0.27**	0.04	0.09	0.61**	0.79**				
	-0.52**	0.19	-0.24**	0.52**	0.50**	0.13	0.1	-0.53**	0.68**	0.88**	0.96**				
FV	-0.03	-0.15	0.62**	0.06	0.07	0.02	0.07	-0.04	0.3	0.67**	0.69**	0.93**			
	-0.48**	0.15	-0.23**	0.47**	0.45**	0.08	0.04	-0.48**	0.69**	0.87**	0.94**	0.99**			
SB	-0.27**	0.3	-0.3	0.21*	0.22**	-0.74**	-0.62**	-0.38**	0.82**	0.19	-0.33**	-- 0.40**	-0.20*		
	0.41**	-0.36**	0.1	-0.58**	-0.6**	-0.47**	-0.36**	0.53**	0.57**	0.09	-0.15	-0.22**	-0.19		
CS	-0.22**	0.04	0.32**	0.19	0.3**	-0.26**	-0.29**	-0.24**	0.06	-0.36**	-0.54**	0.08	0.15	-0.01	
	-0.46**	0.12	-0.26**	0.43**	0.43**	-0.18	-0.2	-0.5	0.36**	0.40**	0.47**	0.70**	0.72**	- 0.30**	
BD	-0.37**	0.33**	-0.14	0.29**	0.34**	-0.88**	-0.84**	-0.49**	0.82**	0.09	-0.54**	-0.38**	-0.14	0.87**	0.36**
	0.26**	-0.33**	0.01	-0.45**	-0.47**	-0.56**	-0.45**	0.36**	0.73**	0.24**	0.02	0.03	0.07	0.93**	0.06

***** and****** for significance at $p < 0.05$ and $p < 0.01$, respectively. #RIL population observed in 2009 (upper) and 2010 (lower).

the seven parameters of the viscosity profile, namely, Atemp, Atime, Btemp, Btime, BAtime, V95, and FV, most were the parameters which belong to the heating period of viscosity analysis previously reported by Wang et al. (2007) for the first time. We located most of the QTLs already found by that previous study on chromosome 6 in the *Waxy* and *Alk* loci, on chromosome 5 and chromosome 7. Furthermore, we also mapped some new QTLs that never reported before on the chromosomes 5, 6, 7, 8, 11 and 12. Indeed, for pasting time (Atime), we found a new QTL in interval RM18452-RM18614 accounting for 5% of the total phenotypic variation value. The analysis of the trait peak temperature (Btemp), our investigation find out a QTL in the *Alk* locus (RM402-RM5963) in both years, accounting for 13.7% and 8.7% of the total phenotypic variation respectively in 2009 and 2010. The trait peak time (Btime) showed also a QTL in the *Alk* locus in both years accounting for 15.1% and 7.8% as phenotypic variation respectively in year 2009 and year 2010. Additionally we found two more new QTLs only in one year each, on the chromosome 7 in RM445-RM11 in 2009 and on the chromosome 8 in RM547-RM310 accounting for 6.6% and 8.3% of the total phenotypic variation respectively. The time needed from point A to point B (BAtime) also showed a new QTL on the chromosome 11 found only in one year in the interval RM26643-RM7120. Final viscosity at 40°C (FV) analysis showed three QTLs all in 2009 only, on the chromosome 5 (RM413-RM17896), chromosome 8 (RM8243-RM7034) and chromosome 12 (RM28010-RM28223) accounting for 8.4%, 10% and 5.5% of the total phenotypic variation. Under all the foregoing, we can say that a further deep investigation of these new QTLs locus could bring more specific and comprehensive and probably complete information about them. However, we noted the instability of some of these QTLs across the environment and their small phenotypic variation.

Materials and Methods

Plant materials

The mapping population consists of 186 recombinant inbred lines (RILs) developed from a cross between MH63 and KDML105. MH63 is the Chinese best male sterility restorer variety in the hybrid rice programs and has an acceptable eating and cooking quality, such as medium AC, soft GC, high GT and translucent endosperm. KDML105 is the Thai jasmine Rice, best known for its aroma and its good cooking and eating quality. It is soft-tender and fluffy when cooked and has low AC, low GT, medium GC with good potential in producing good quality rice. The field experiment was conducted during the rice-growing seasons of 2009 and 2010 on the experimental farm at Huazhong Agricultural University, Wuhan, China.

Traits measurement

In order to measure the quality related traits, seeds were harvested from the plants grown in 2009 and 2010 growing seasons. All the seeds were stored at room temperature for a period of at least 3 months after harvesting, before the quality analysis. Head rice and flour was prepared following the methods described by Tan et al. (1999). The milled rice was ground into powder with an Udy Cyclone sample Mill (Udy Corporation, Fort Collins, CO, USA), and was then sieved through a 100-mesh sieve. Samples were refrigerated until analysis. The measurement of the traits was done according to the practical notes from Wang et al. (2007).

Alkali spreading value (ASV)

Gelatinization temperature (GT) was evaluated as the alkali spreading value (ASV). Samples containing six milled rice kernels each were put into plastic boxes, and 10 mL of 1.7% *w*/*v* KOH solution was added to each box. The boxes were stored at temperatures of 30 ± 2 ℃ for 23 h. The degree of disintegration and the transparency of paste dissolved out of the kernels were evaluated using a 7-point scale as described by Little et al. (1958) and Bhattacharya (1979).

Gel consistency (GC)

GC analysis followed the methods described by Cagampang et al. (1973).

Amylose content (AC)

AC was measured as described by Tan et al. (1999) and Tian et al. (2005), where the Automatic Recording Titrator (ART-3, Hirama Laboratories, Kanagawa, Japan) was used to analyze AC by the iodine titration method.

Viscosity properties

Viscosity profile was determined with a Micro Viscoamylograph (Ident No. 803201, Brabender, Germany), mainly according to the instruction manual, with reference to the American association of cereal chemists (2000) standard method AACC 61-01 and 61-02.

Linkage map construction and QTL analysis

Markers and techniques used in this study for PCR, polyacrylamide gel electrophoresis (PAGE), and silver staining of SSR markers were as described by Chen et al. (1997) and Temnykh et al. (2000). The genetic map was constructed using 113 SSR markers which over almost all the chromosomes of the rice SSR maps constructed by McCouch et al. (2002) using the Mapmakers Exp3. The whole genome was scanned for QTLs using MAPMAKER/QTL 1.0 (Lincoln, 1992) with a LOD threshold of 2.0.

Statistical analysis

The *t*-test, correlation analysis and principal factor analysis were carried out using the statistical package Statistica (StatSoft 1991).

Conclusions

In view of all the foregoing, it is concluded that our results could have significant implications in rice quality improvement programs. It is obvious that in addition to the major genes, attention should be also directed to the effects of minor QTLs and epistatic QTLs. The information obtained should be useful for manipulating the QTLs for these traits by molecular marker-assisted selection. Moreover, marker-assisted selection will be particularly useful for breaking the unfavorable linkage of the genes, such as in the case of the major QTLs for GT on chromosome 6 detected in this study. This would enable all of the favorable alleles to be combined in a single individual, which would be impossible to attain using conventional methods. However, it is difficult to determine whether QTLs are in the same locus or are tightly linked. We also note the instability of some of these QTLs

Table 4. QTL identified for the rice eating and cooking quality traits in new RIL population derived from a cross between MH63 and KDML105.

Traits	QTL	Chrs	Interval	LOD	Add	Var%
09 AC	*qAC-8*	8	RM8243-RM7034	2.34	0.56	5.7
10 AC	*qAC-6*	6	RM402-RM5963	2.46	-0.68	8.6
09 GC	*qGC-5*	5	RM122-RM413	2.41	-2.48	9.1
	qGC-6	6	RM402-RM5963	11.08	4.36	26.3
	qGC-7	7	RM481-RM18	2.30	-2.56	9.8
10 GC	*qGC-6*	6	RM402-RM5963	6.12	4.19	25.9
09 ASV	*qASV-6-1*	6	RM402-RM5963	39.64	-1.94	59.8
10 ASV	*qASV-6-1*	6	RM402-RM5963	21.39	-1.55	55.8
	qASV-6-2	6	RM136-RM3	8.07	-1.59	41.9
09 Atime	*qAti-6-1*	6	RM584-RM402	18.97	0.62	28.5
	qAti-6-2	6	RM402-RM5963	61.31	0.65	68.4
10 Atime	*qAti-5*	5	RM18452-RM18614	2.28	0.19	5.0
	qAti-6-2	6	RM402-RM5963	41.36	0.80	68.4
09 Atemp	*qAte-6*	6	RM402-RM5963	50.40	3.98	66.2
10 Atemp	*qAte-6*	6	RM402-RM5963	41.37	5.18	67.1
	qAte-7	7	RM3394-RM20916	2.56	1.45	6.0
09 Btime	*qBti-5*	5	RM413-RM17896	2.14	0.05	4.6
	qBti-6	6	RM402-RM5963	6.85	-0.09	15.1
	qBti-7	7	RM445-RM11	2.12	0.05	6.6
10 Btime	*qBti-6*	6	RM402-RM5963	2.53	0.05	7.8
	qBti-8	8	RM547-RM310	2.62	0.06	8.3
09 Btemp	*qBte-5*	5	RM413-RM17896	2.35	0.36	4.8
	qBte-6-1	6	RM402-RM5963	5.96	-0.64	13.7
10 Btemp	*qBte-6-2*	6	RM469-RM508	2.54	0.34	7.8
	qBte-6-1	6	RM402-RM5963	2.72	2.72	8.7
09 BAtime	*qBAti-6-1*	6	RM133-RM584	11.96	-0.64	26.3
	qBAti-6-2	6	RM402-RM5963	59.83	0.71	70.0
10 BAtime	*qBAti-5*	5	RM18614-RM164	2.36	-0.18	5.1
	qBAti-6-1	6	RM133-RM584	8.20	-0.61	30.1
	qBAti-6-2	6	RM402-RM5963	31.38	0.72	61.4
	qBAti-11	11	RM26643-RM7120	2.05	0.17	4.0
09 PKV	*qPKV-2*	2	RM13608-RM240	3.14	-11.88	11.4
	qPKV-5	5	RM122-RM413	2.28	-10.57	9.2
	qPKV-6-1	6	RM133-RM584	2.32	11.29	7.2
	qPKV-6-2	6	RM5963-RM136	3.63	10.73	8.3
10 PKV	*qPKV-3*	3	RM7389-RM514	2.68	-10.67	10.1
09 V95	*qV95-2*	2	RM240-RM498	2.15	-4.62	6.0
10 V95	*qV95-6*	6	RM402-RM5963	3.49	11.76	19.0
09 HPV	*qHPV-6-1*	6	RM133-RM584	2.27	-7.01	8.0
	qHPV-11	11	RM27046-RM286	2.16	-5.59	5.6
	qHPV-12	12	RM28010-RM28223	2.47	5.83	6.2
10 HPV	*qHPV-3*	3	RM1256-RM7	2.94	6.63	9.9
	qHPV-6-2	6	RM402-RM5963	5.15	10.36	24.1
09 CPV	*qCPV-5*	5	RM17896-RM405	4.27	6.47	10.0
	qCPV-6-1	6	RM3-RM248	2.36	-4.83	5.7
	qCPV-8	8	RM8243-RM7034	5.28	7.28	12.3
	qCPV-12	12	RM28010-RM28223	2.77	4.89	6.3
10 CPV	*qCPV-6-2*	6	RM402-RM5963	4.15	13.42	22.1
09 FV	*qFV-5*	5	RM413-RM17896	3.70	5.92	8.4
	qFV-8	8	RM8243-RM7034	4.22	6.48	10.0
	qFV-12	12	RM28010-RM28223	2.39	4.55	5.5
10 FV	*qFV-6*	6	RM133-RM584	4.50	14.01	21.9
09 SB	*qSB-5*	5	RM413-RM17896	2.17	8.45	4.6
	qSB-6-1	6	RM133-RM584	2.11	-13.69	10.0
	qSB-6-2	6	RM5963-RM136	4.59	-12.97	10.6
	qSB-7-1	7	RM478-RM22181	2.08	9.72	6.5
10 SB	*qSB-3*	3	RM7389-RM514	2.24	6.37	6.8
	qSB-6-3	6	RM402-RM5963	5.73	11.99	25.8
	qSB-6-4	6	RM136-RM3	3.58	10.46	19.8
	qSB-7-2	7	RM11-RM3394	3.63	9.27	11.8
	qSB-7-3	7	RM3394-RM20916	3.90	10.12	14.3
09 CS	*qCS-4-1*	4	RM3892-RM16335	4.28	-4.40	9.5
	qCS-8	8	RM8243-RM7034	3.41	4.19	7.6
	qCS-11	11	RM26386-RM26643	2.96	3.73	6.5

10 CS	*qCS-4-2*	4	RM335-RM3892	2.92	2.47	8.5
	qCS-6	6	RM133-RM584	6.31	5.20	29.8
09 BD	*qBD-6-1*	6	RM133-RM584	2.03	13.31	7.9
	qBD-6-2	6	RM5963-RM136	4.75	13.88	10.6
	qBD-7	7	RM478-RM22181	2.05	-10.97	7.2
10 BD	*qBD-6-3*	6	RM402-RM5963	3.51	-9.05	16.0
	qBD-6-4	6	RM136-RM3	2.26	-6.88	9.3

#Wax locus = RM133-RM584 and *Alk* locus = RRM402-RM5963. *09 refers to 2009 and 10 to 2010. *Additive: the additive effects of QTL. Positive values of additive effects indicate that the MH63 genotype have a positive effect on that trait and negative values for KDML105 allele effect. *Var%: the percentage of the phenotypic variation explained by the QTL.

across the environment and their small phenotypic variation value. Therefore, further analysis and investigation, including fine mapping of some QTLs using common markers, cloning and sequence comparison of these QTLs, will be required.

Acknowledgments

We are grateful to Dr. Ling-Qiang Wang (Huazhong Agricultural University) for his help and suggestions. This work was supported by grants from the National 863 Project, the National Program on the Development of Basic Research, the National Program on R&D of Transgenic Plants and the National Natural Science Foundation of China.

References

Allahgholipour M, Ali A, Alinia F, Nagamine T, Kojima Y (2006) Relationship between rice grain amylose and pasting properties for breeding better quality rice varieties. Plant Breed 125:357-362

Aluko G, Martinez C, Tohme J, Castano C, Bergman C, Oard J (2004) QTL mapping of grain quality traits from the interspecific cross *Oryza sativa*× *O. glaberrima.* Theor Appl Genet 109:630-639

Bao J, Zheng X, Xia Y, He P, Shu Q, Lu X, Chen Y, Zhu L (2000) QTL mapping for the paste viscosity characteristics in rice (*Oryza sativa* L.). Theor Appl Genet 100:280-284

Bao JS, Wu YR, Hu B, Wu P, Cui HR, Shu QY (2002) QTL for rice grain quality based on a DH population derived from parents with similar apparent amylase content. Euphytica 128:317–324

Bhattacharya K (1979) Gelatinization temperature of rice starch and its determination, Proceedings of the Workshop on Chemical Aspects of Rice Grain Quality. Los Baños, Laguna, Philippines. pp. 231-249

Cagampang GB, Perez CM, Juliano BO (1973) A gel consistency test for eating quality of rice. J Sci Food Agric 24:1589-1594

Chen X, Temnykh S, Xu Y, Cho Y, McCouch S (1997) Development of a microsatellite framework map providing genome-wide coverage in rice (*Oryza sativa* L.). Theor Appl Genet 95:553-567

Fan C, Yu X, Xing Y, Xu C, Luo L, Zhang Q (2005) The main effects, epistatic effects and environmental interactions of QTLs on the cooking and eating quality of rice in a doubled-haploid line population. Theor Appl Genet 110:1445-1452

Gravois KA, Webb BD (1997) Inheritance of long grain rice amylograph viscosity characteristics. Euphytica 97:25-29

He P, Li S, Qian Q, Ma Y, Li J, Wang W, Chen Y, Zhu L (1999) Genetic analysis of rice grain quality. Theor Appl Genet 98:502-508

Juliano BO (1985) Rice: chemistry and technology American Association of Cereal Chemists St. Paul. Minn.

Kaushik R, Khush G (1991) Genetic analysis of endosperm mutants in rice *Oryza sativa* L. Theor Appl Genet 83:146-152

Kharabian-Masouleh A, Waters DLE, Reinke RF, Ward R, Henry RJ (2012) SNP in starch biosynthesis genes associated with nutritional and functional properties of rice. Scientific Reports 2(557): 1-9

Lanceras JC, Huang ZL, Naivikul O, Vanavichit A, Ruanjaichon V, Tragoonrung S (2000) Mapping of genes for cooking and eating qualities in Thai jasmine rice (KDML105). DNA Research 7:93-101

Larkin PD, Park WD (2003) Association of waxy gene single nucleotide polymorphisms with starch characteristics in rice (*Oryza sativa* L.). Mol Breed 12:335-339

Li J, Xiao J, Grandillo S, Jiang L, Wan Y, Deng Q, Yuan L, McCouch SR (1999) QTL detection for rice grain quality traits using an interspecific backcross population derived from cultivated Asian (*O. sativa L.*) and African (*O. glaberrima S.*) rice. Genet 47:697-704

Li T, Takano T, Nagamura Y, Takeda G (1994) Linkage analysis of rice lactate dehydrogenase gene. Rice Genet Newsletter 11:109-111

Li Z, Wan J, Xia J, Yano M (2003) Mapping of quantitative trait loci controlling physico-chemical properties of rice grains (*Oryza sativa* L.). Breed Sci 53:209-215

Lincoln S (1992) Constructing genetic maps with MAPMAKER/EXP 3.0 Whitehead Institute technical report.

Little RR, Hilder GB, Dawson EH (1958) Differential effect of dilute alkali on 25 varieties of milled white rice. Cereal Chem 35:111-126

Martínez Racines CP, Cuevas Pérez FE, Medina LM (1989) Evaluación de la calidad culinaria y molinera del arroz [conjunto audiotutorial].

McCouch SR, Teytelman L, Xu Y, Lobos KB, Clare K, Walton M, Fu B, Maghirang R, Li Z, Xing Y (2002) Development and mapping of 2240 new SSR markers for rice (*Oryza sativa* L.). DNA Research 9:199-207

McKenzie K, Rutger J (1983) Genetic analysis of amylose content, alkali spreading score, and grain dimensions in rice. Crop Sci 23:306-313

Mo H (1995) Identification of genetic control for endosperm traits in cereals. Acta Genetica Sinica **22**(2): 126–132

Pingali PL, Hossain M, Gerpacio RV (1997) Asian rice bowls: the returning crisis? International Rice Research Institute (IRRI) pp. 341

Pooni H, Kumar I, Khush G (1992) A comprehensive model for disomically inherited metrical traits expressed in triploid tissues. Heredity 69:166-174

Sabouri H (2009) QTL detection of rice grain quality traits by microsatellite markers using an indica rice (*Oryza sativa* L.) combination. J Genet 88:81

Sano Y, Katsumata M, Okuno K (1986) Genetic studies of speciation in cultivated rice. 5. Inter-and intraspecific differentiation in the *waxy* gene expression of rice. Euphytica 35:1-9

Septiningsih E, Trijatmiko K, Moeljopawiro S, McCouch S (2003) Identification of quantitative trait loci for grain quality in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. Theor Appl Genet 107:1433-1441

Shu Q, Wu D, Xia Y, Gao M, McClung A (1998) Relationship between RVA profile character and eating quality in *Oryza sativa* L. Sci Agric Sinica 31:25-29

Tan Y, Li J, Yu S, Xing Y, Xu C, Zhang Q (1999) The three important traits for cooking and eating quality of rice grains are controlled by a single locus in an elite rice hybrid, Shanyou 63. Theor Appl Genet 99:642-648

Tanksley SD, Ganal MW, Martin GB (1995) Chromosome landing: a paradigm for map-based gene cloning in plants with large genomes. Trends Genet 11:63-68

Temnykh S, Park WD, Ayres N, Cartinhour S, Hauck N, Lipovich L, Cho YG, Ishii T, Mc Couch SR (2000) Mapping and genome organization of microsatellite sequences in rice (*Oryza sativa* L.). Theor Appl Genet 100:697-712

Tian R, Jiang GH, Shen LH, Wang LQ, He YQ (2005) Mapping quantitative trait loci underlying the cooking and eating quality of rice using a DH population. Mol Breed 15:117–124

Umemoto T, Yano M, Satoh H, Shomura A, Nakamura Y (2002) Mapping of a gene responsible for the difference in amylopectin structure between *japonica*-type and *indica*-type rice varieties. Theor Appl Genet 104:1-8

Wang L, Liu W, Xu Y, He Y, Luo L, Xing Y, Xu C, Zhang Q (2007) Genetic basis of 17 traits and viscosity parameters characterizing the eating and cooking quality of rice grain. Theor Appl Genet 115:463-476

Wang ZY, Zheng FQ, Shen GZ, Gao JP, Snustad DP, Li MG, Zhang JL, Hong MM (1995) The amylose content in rice endosperm is related to the post‐transcriptional regulation of the *Waxy* gene. Plant J 7:613-622

Wrigley C, Morris C (1996) Breeding cereals for quality improvement, Cereal Grain Quality, Springer. pp. 321-369

Wu K-S, Tanksley SD (1993) Abundance, polymorphism and genetic mapping of microsatellites in rice. Mol General Genet 241:225-235

Yan CJ, Li X, Zhang R, Sui JM, Liang GH, Shen XP, Gu SL, Gu MH (2005) Performance and inheritance of rice starch RVA profile characteristics. Rice Sci 12:39-47

Yan CJ, Tian ZX, Fang YW, Yang YC, Li J, Zeng SY, Gu SL, Xu CW, Tang SZ, Gu MH (2011) Genetic analysis of starch paste viscosity parameters in glutinous rice (*Oryza sativa* L.). Theor Appl Genet 122(1):63-76

Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y (2000) Hd1, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the Arabidopsis flowering time gene CONSTANS. Plant Cell Online 12:2473-2483

Zhou P, Tan Y, He Y, Xu C, Zhang Q (2003) Simultaneous improvement for four quality traits of Zhenshan 97, an elite parent of hybrid rice, by molecular marker-assisted selection. Theor Appl Genet 106:326-331

Zhu J, Weir B (1994) Analysis of cytoplasmic and maternal effects. II. Genetic models for triploid endosperms. Theor Appl Genet 89:160-166