Theor Appl Genet (2000) 101:823–829

Y.F. Tan · Y.Z. Xing · J.X. Li · S.B. Yu · C.G. Xu
Qifa Zhang

Genetic bases of appearance quality of rice grains in Shanyou 63, an elite rice hybrid

Received: 20 February 2000 / Accepted: 21 March 2000

Abstract Appearance quality of the rice grain represents a major problem of rice production in many rice-producing areas of the world, especially in hybrid rice production in China. In this study, we conducted a molecular marker-based genetic analysis of the traits that are determinants of the appearance quality of rice grains, including traits specifying grain shape and endosperm opacity. The materials used in the analysis included an $F_{2:3}$ population and an F_{10} recombinant inbred line population from a cross between the parents of Shanyou 63, the most widely grown rice hybrid in China. Molecular marker-based QTL (quantitative trait locus) analyses revealed that grain length and grain width were each controlled by a major QTL accounting for a very large proportion of the genetic variation, plus one or two minor QTLs each explaining a small proportion of the genetic variation. The major QTLs can be detected in both the $F_{2:3}$ and recombinant inbred line population using both paddy rice and brown rice, whereas the minor QTLs were detected only occasionally. The QTL located in the interval of RG393-C1087 on chromosome 3 is the major locus for grain length, and the one in the interval RG360-C734a on chromosome 5 plays a major role in determining grain width. Similarly, white belly, which largely determines the opacity of the endosperm, is almost entirely controlled by a major locus on chromosome 5, located in the same genomic region as the major QTL for grain width. The implications of the results with respect to hybrid rice improvement were discussed.

Key words Rice quality · Grain shape · Endosperm opacity · Genetic analysis · Molecular marker

Communicated by P.M.A. Tigerstedt

Y.F. Tan · Y.Z. Xing · J.X. Li · S.B. Yu · C.G. Xu · Qifa Zhang (✉)
National Key Laboratory for Crop Genetic Improvement,
Huazhong Agricultural University, Wuhan 430070, China
Fax: 86 27-87287092
e-mail: qifazh@public.wh.hb.cn

Introduction

Quality rice varieties are preferable by consumers and producers alike. Although the preferences for rice grain characteristics vary with different consumer groups, long and slender rice is generally preferred by many consumers in China, USA and most of the Asian countries (Unnevehr et al. 1992; Juliano and Villareal 1993). Long-grain quality varieties tend to produce dry, fluffy and separated cooked grains, whereas the medium- and short-grain varieties tend to produce clumped, moist and chewy grains after cooking (Webb 1980; Juliano 1985). For all shapes of grains, the endosperm of quality rice should be free of opaqueness and strongly translucent.

Appearance quality of the rice grain represents a major problem of rice production in many rice-producing areas of the world, and this is especially the case in hybrid rice production in China. Currently, there is a strong emphasis in China on improving the quality of hybrid rice varieties, especially the quality of indica hybrids. The most serious problems lie in eating quality, cooking quality and appearance quality and, to some extent, in milling quality and processing quality. According to our present knowledge, cooking and eating qualities are mostly determined by the amylose content, gelatinazation temperature and gel consistency of the grain endosperm. Appearance quality is mostly determined by grain shape as specified by grain length, grain width, the length-width ratio and the translucency of the endosperm.

We previously conducted a molecular marker-based analysis of the genetic control of the three endosperm traits – namely, amylose content, gelatinazation temperature and gel consistency – that determine the eating and cooking quality of the rice grain in a cross between the parents of an elite hybrid, Shanyou 63 (Tan et al. 1999). This is the best hybrid that has been widely grown in China for almost two decades, demonstrating high yield, wide adaptability but relatively poor quality. We were able to show that these three traits are almost perfectly correlated with each other and mainly controlled by the

Wx locus located on chromosome 6. Such results were immediately useful in improving the eating and cooking quality of this elite hybrid.

In the study reported in this paper, we performed a molecular marker-based analysis of quantitative trait loci (QTLs) for the traits that determine appearance quality of the grains, using populations derived from the cross between Zhenshan 97 and Minghui 63, the parents of Shanyou 63. The traits studied included grain length, grain width, length to width ratio and endosperm opacity. The objective was to determine the genetic control of these traits in this cross in order to formulate a strategy for improving the appearance quality of this hybrid.

Materials and methods

Genetic materials

The genetic materials used in this study included Zhenshan 97 and Minghui 63, the parents of Shanyou 63, the best hybrid in rice production in China, and two populations derived from a cross between the two parents. The first population consisted of 241 F_2 individuals, and the second population contained 238 F_{10} recombinant inbred lines (RILs) derived from the 240 F_2 plants by the single-seed descendent method.

Measuring the traits of appearance quality

Harvested paddy rice was dried and stored at room temperature for at least 3 months before processing. Twenty fully filled paddy rice grains from each F_2 individual, referred to as an $F_{2:3}$ family, and RILs were lined up length-wise along a vernier caliper to measure the length, after which the grains were arranged in the breadth to measure the width. The values were averaged and used as the measurements for length and width of individual grains. The length-width ratio of the grains was calculated as grain length divided by width, a measurement which reflects the shape of the grains.

Rough rice was de-husked and milled using a miller (manufactured by Jiading Food and Oil Machinery Factory, Shanghai, China) according to the National Standards NY 147–88. Twenty randomly selected unbroken brown rice grains of each $F_{2:3}$ family or RIL were lined up to measure the length, width and length-width ratio in the same way as described in the previous paragraph.

The measurement of opacity or chalkiness was carried out as follows. One hundred milled head rice grains of each $F_{2:3}$ family or RIL were randomly selected. The chalky grains, including those with a white belly, white core and white back, were counted by visual assessment. The percentages of the chalky grains were used as the measurement of opacity. In the RIL population white belly and white core were further separated and counted. Very few grains had a white back in this population and this type of chalkiness was ignored. All measurements were replicated four times.

Molecular markers, linkage map construction and QTL surveys

Two classes of molecular markers were used in assaying the polymorphisms of the populations, restriction fragment length polymorphisms (RFLPs) and simple-sequence repeats (SSRs). The dataset of molecular markers for the F_2 population was essentially the same as that described by Yu et al. (1997), consisting of 150 markers, including 131 RFLP and 19 SSR loci covering all 12 chromosomes. A total of 171 molecular markers, including 166 RFLPs and 5 SSRs, were employed in the assay of the RIL population; these were largely the same as those used in the $F_{2:3}$ assay (Xing 1999). The molecular marker linkage maps were constructed using MAPMAKER/EXP 3.0 (Lander et al. 1987; Lincoln et al. 1992a).

Interval mapping was carried out to scan the whole genome for putative QTLs controlling the quality traits using MAPMAKER/QTL 1.1 with a LOD threshold of 2.4 (Lincoln et al. 1992b). If two or more QTLs were detected in nearby regions, the QTL with the largest effect was fixed, and the rest of the genome was re-scanned to confirm the existence of the other QTLs. When an QTL was detected in an interval exceeding 20 cM in length in the linkage map, the existence of the QTL was confirmed using composite interval mapping (Zeng 1994) as well as one-way analysis of variance using genotypes of the adjacent markers as the groups.

Results

Distribution of the trait measurements in segregating populations

The distributions of grain length, grain width, length-width ratio and chalkiness of the $F_{2:3}$ and RIL populations are shown in Fig. 1. The two parents, Minghui 63 and Zhenshan 97, showed large differences in all of the traits examined. Transgressive segregations occurred in all of the traits in both $F_{2:3}$ and RIL populations. However, the distribution mode of chalkiness was very different from those of the other three traits, with the former showing an apparent bimodal distribution in both the $F_{2:3}$ and RIL populations and the latter uni-modal in both populations (Fig. 1B).

QTLs for paddy rice grain traits

Grain length

Analysis of the $F_{2:3}$ population resolved three QTLs for grain length of paddy rice, located on chromosomes 2, 3 and 7, respectively (Table 1, Fig. 2). The QTL located in the interval RG393-C1087 on chromosome 3 showed the largest effect on the trait with a LOD score of 41.0 and explaining 63.8% of the phenotypic variance. The effects of the other two QTLs were much smaller. In all three QTLs, alleles from Minghui 63 contributed to the increase in grain length.

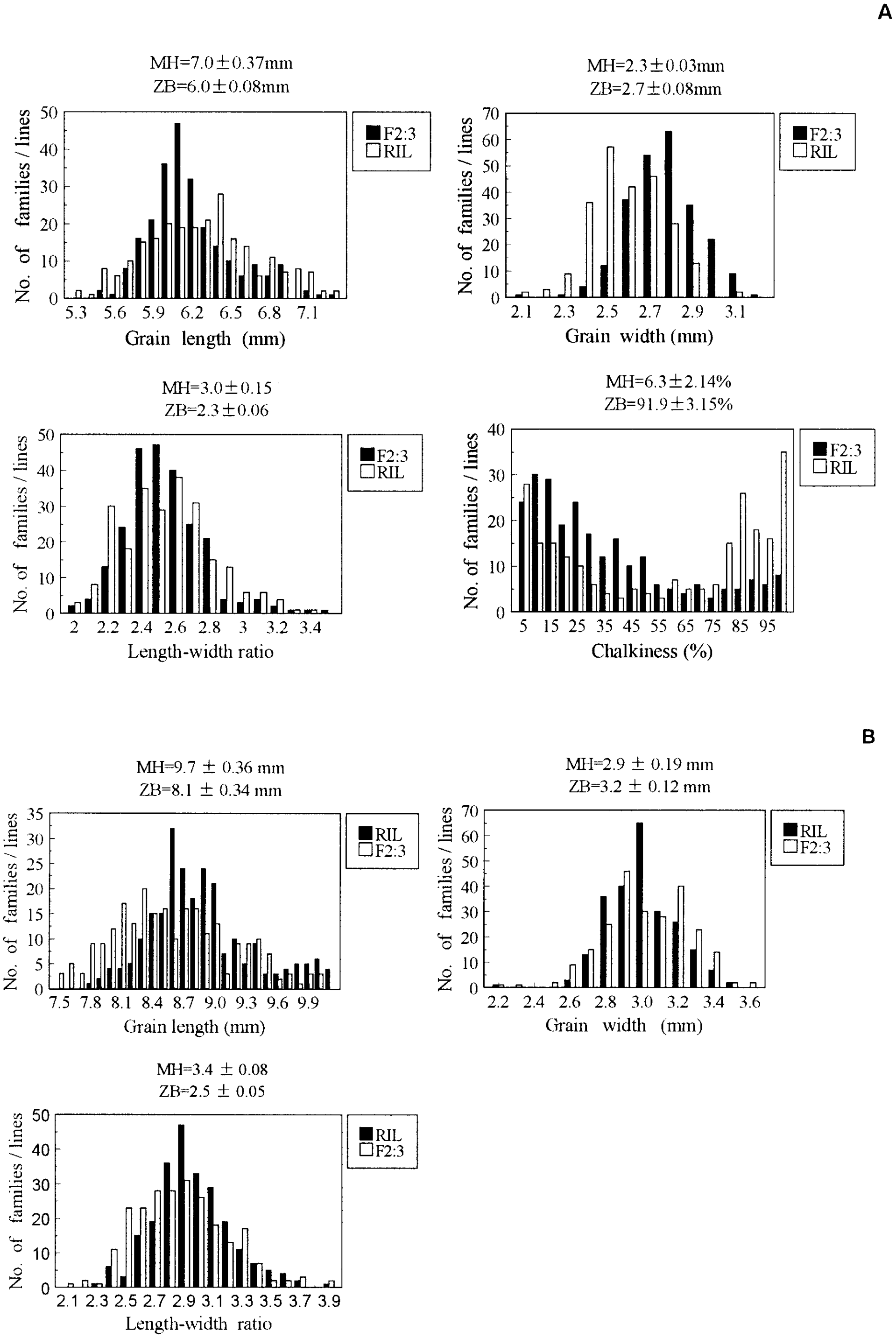
Two QTLs, located on chromosomes 3 and 11, were detected for grain length of paddy rice in the RIL population (Fig. 2). The major QTL was the same as the one located in the $F_{2:3}$ population in the interval RG393-C1087 on chromosome 3, with a LOD score of 33.8 and explaining 57.6% of the variation (Table 1). The effect of the other QTL, located on chromosome 11, was much smaller. In both cases, alleles from Minghui 63 were in the direction of increasing grain length.

Thus, four QTLs were detected for grain length of paddy rice. One locus, the major one, was detected in both of the $F_{2:3}$ and RIL populations, and the remaining three were observed in only one of the populations.

Grain width

Three QTLs were detected for grain width of paddy rice (Table 1, Fig. 2). Two of the QTLs, located on chromo-

Fig. 1A, B Distributions of grain length, grain width, length-width ratio and milled rice chalkiness of paddy (**A**) and brown (**B**) rice in the $F_{2:3}$ and RIL populations. *MH* Minghui 63, *ZB* Zhenshan 97



somes 5 and 6, respectively, were detected in both the $F_{2:3}$ and RIL populations, and one QTL, located on chromosome 1, was detected only in the $F_{2:3}$ population. The QTL detected on chromosome 5 showed the largest effect in both populations. The effects of the other two QTLs, including the one detected in both populations and the other one detected in only one population, were much smaller. Alleles with increasing and decreasing effects were detected from both parents at these QTLs (Table 1).

Length-width ratio

Two QTLs located on chromosomes 3 and 5, respectively, were detected for the length-width ratio in both the $F_{2:3}$ and RIL populations (Table 1, Fig. 2), both of which had large effects on the trait (Table 1). In both cases, alleles from Minghui 63 contributed to the increase in the length-width ratio.

These two QTLs were located in the same vicinities as the two QTLs that assumed major effects on grain

Table 1 QTLs detected for appearance quality traits of paddy rice grains analyzed using the $F_{2:3}$ and RIL populations from a cross between Zhenshan 97 and Minghui 63 by interval mapping at LOD threshold 2.4

Trait	Chromosome	Interval	LOD	% Var [a]	Add [b]	Dom [c]
$F_{2:3}$ population						
Grain length	2	R1843-RMD1	3.1	6.5	–0.18	–0.06
	3	RG393-C1087	41.0	63.8	–0.57	–0.30
	7	RG128-C1023	3.9	15.4	–0.27	0.07
Total			46.8	68.9		
Grain width	1	C161-R753	3.8	13.7	0.02	0.08
	5	RG360-C734a	20.6	55.2	0.18	–0.05
	6	RG424-C962	2.6	10.4	–0.09	0.04
Total			27.9	68.6		
Length-width ratio	3	RZ403-R19	21.0	36.4	–0.24	–0.12
	5	RG360-C734a	11.3	37.8	–0.22	0.01
Total			40.1	75.1		
RIL population						
Grain length	3	RG393-C1087	33.8	57.6	–0.88	
	11	G44-G257	3.1	7.2	–0.34	
Total			37.3	62.3		
Grain width	5	RG360-C734a	16.5	44.0	0.31	
	6	RZ667-RG424	2.5	4.6	–0.12	
Total			20.8	49.4		
Length-width ratio	3	RG393-C1087	11.7	25.4	–0.32	
	5	RG360-C734a	11.5	33.3	–0.37	
Total			26.6	59.6		

[a] Variance explained by the QTL

[b] Additive effect: positive values of additive effects indicate that alleles from Zhenshan 97 are in the direction of increasing the trait scores, and negative values of additive effects indicate that alleles from Minghui 63 are in the direction of increasing the trait scores

[c] Dominance effect

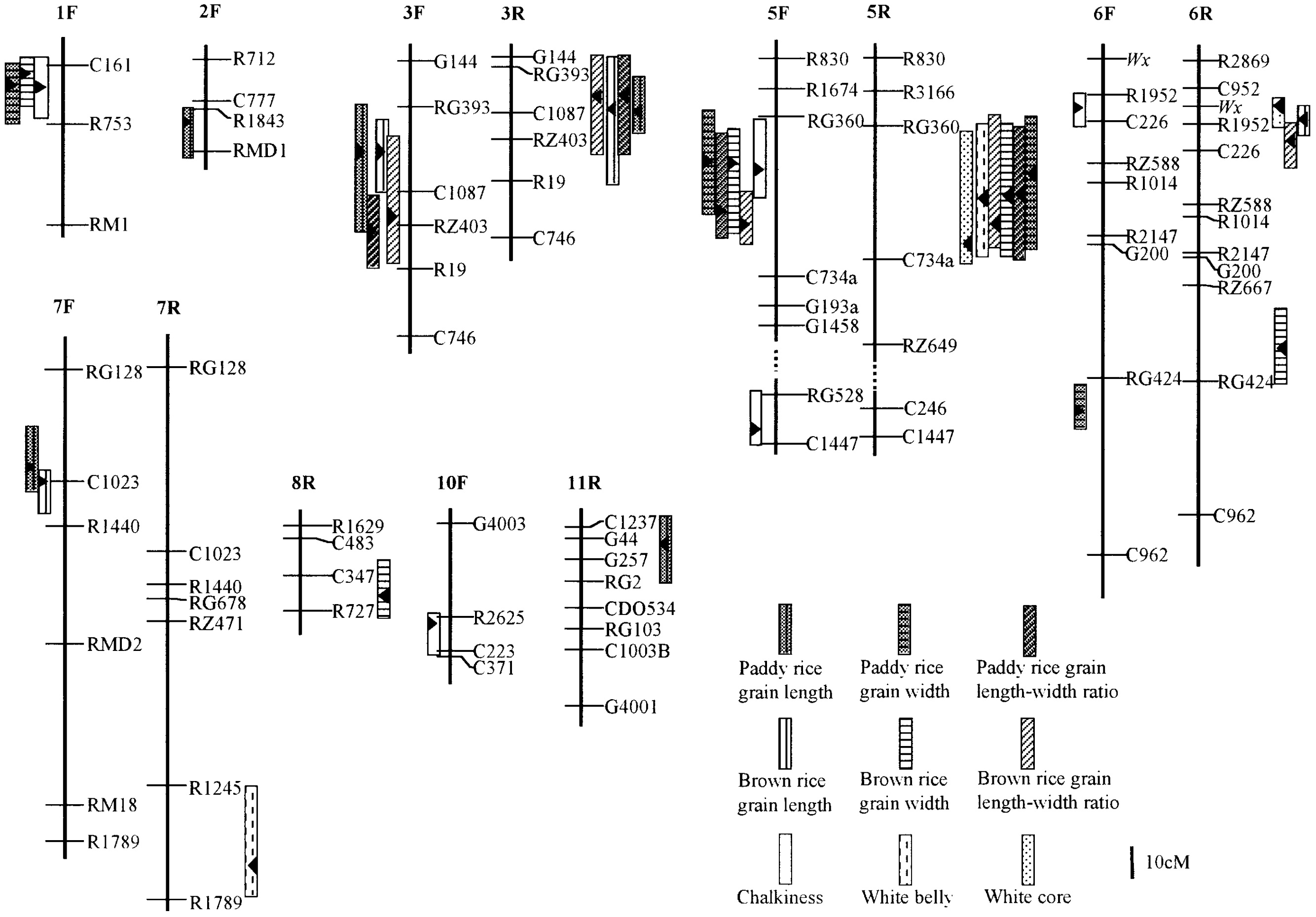


Fig. 2 Locations of the QTLs for appearance quality traits of rice grains. Only those portions of the linkage maps where QTLs were detected are shown. The *number* at the top indicates the chromosome number with affixes of *F* for the $F_{2:3}$ and *R* for the RIL populations, respectively. The *bars* indicate the 1-LOD support intervals of the QTLs identified with $F_{2:3}$ (on the *left side* of the chromosomes) and RIL (*right*) populations. *Small triangles* indicate peaks of the LOD contours

Table 2 QTLs detected for appearance quality traits of brown rice grains analyzed using the $F_{2:3}$ and RIL populations from a cross between Zhenshan 97 and Minghui 63 by interval mapping at LOD threshold 2.4

Trait	Chromosome	Interval	LOD	% Var [a]	Add [b]	Dom [c]
$F_{2:3}$ population						
Grain length	3	RG393-C1087	32.7	59.0	–0.42	–0.24
	7	C1023-R1440	2.7	5.1	–0.08	0.14
Total			33.8	59.9		
Grain width	1	C161-R753	4.1	15.2	0.04	0.11
	5	RG360-C734a	19.9	52.3	0.16	–0.04
Total			21.8	55.9		
Length-width ratio	3	C1087-RZ403	12.8	29.4	–0.18	–0.10
	5	RG360-C734a	9.9	31.3	–0.17	–0.02
Total			30.1	62.4		
Chalkiness	1	C161-R753	2.6	8.9	1.97	16.33
	5	RG360-C734a	29.3	70.3	30.91	–20.73
	5	RG528-C1447	5.8	11.3	13.74	–5.19
	6	R1952-C226	2.5	5.0	8.24	3.11
	10	R2625-C223	2.5	4.9	8.57	0.94
Total			36.8	73.2		
RIL population						
Grain length	3	RG393-C1087	19.8	40.7	–0.55	
	6	Wx-R1952	4.0	8.0	0.24	
Total			25.5	48.6		
Grain width	5	RG360-C734a	15.3	41.6	0.22	
	8	C347-R727	2.5	4.9	0.08	
Total			17.2	44.7		
Length-width ratio	3	RG393-C1087	9.6	21.8	–0.25	
	5	RG360-C734a	10.2	30.0	–0.30	
	6	R1952-C226	2.4	5.1	0.12	
Total			26.1	61.1		
White belly	5	RG360-C734a	35.2	87.2	72.9	
	7	R1245-R1789	2.7	9.5	24.5	
Total			36.6	87.9		
White core	5	RG360-C734a	4.5	11.6	–12.2	
	6	Wx-R1952	4.0	7.5	9.8	
Total			8.8	17.5		

[a, b and c] See Table 1 for explanations

length and grain width as described above. This is quite understandable because length-width ratio is a secondary trait derived by dividing the measurement of length by the measurement of width.

QTLs for brown rice grain traits

Grain length

Two QTLs each were detected for grain length in both the $F_{2:3}$ and RIL populations (Table 2, Fig. 2). The one located in the interval RG393-C1087 of chromosome 3 was observed in both populations and detected the largest effect in both cases (Table 2). Of the other two QTLs, the one located between C1023 and R1440 on chromosome 7 was detected only in the $F_{2:3}$ population, and the one located in the interval *Wx*-R1952 of chromosome 6 was detected only in the RIL population; both had much smaller effects.

Grain width

Two QTLs each were detected for grain width in both the $F_{2:3}$ and RIL populations (Table 2, Fig. 2). The one on chromosome 5 was in common between the two populations and showed the largest effect in both populations (Table 2). The other two QTLs, one on chromosome 1 and the other on chromosome 8, were each detected in only one population and had much smaller effects.

Length-width ratio

Two and three QTLs, respectively, were detected for length-width ratio in the $F_{2:3}$ and RIL populations (Table 2, Fig. 2). The two QTLs, one coincided with the QTL for grain length on chromosome 3 and the other coincided with the QTL for grain width on chromosome 5, appeared to have large effects on the trait in both of the populations (Table 2). A third QTL, located in the interval R1952-C226 on chromosome 6, was detected in the RIL population, which was also in good agreement with a QTL for grain length detected in this population.

Chalkiness

The two component traits, white belly and white core, for chalkiness were analyzed separately. Although the measurements of the traits by no means followed normal distribution, the results of QTL analysis were nonetheless very informative. Two QTLs for white belly were detected, one on chromosome 5 in the interval RG360-C734a and the other on chromosome 7 in the interval R1245-R1789 (Table 2, Fig. 2). The one on chromosome 5 was a major locus explaining 87.2% of the variation, and the other QTL played only a minor role in specifying this trait (Table 2). In both cases, alleles from Zhenshan 97 increased the opacity of the grains.

Two QTLs were detected for white core (Table 2, Fig. 2). The one located on chromosome 5 was in the same interval (RG360-C734a) as the major locus for white belly. However, the allele from the same parent at this locus contributed to white belly and white core in opposite directions; the allele from Zhenshan 97 was in the direction of increasing white belly but decreasing white core. The QTL on chromosome 6 resided right on top of the *Wx* locus that controls amylose content of the endosperm (Wang et al. 1995; Tan et al. 1999); the allele from Zhenshan 97 contributed to the increase of white core (Table 2).

When chalkiness was analyzed as one trait in the $F_{2:3}$ population (Table 2), it was shown that the locus on chromosome 5 played a predominant role in chalkiness of the grain endosperm, although altogether five QTLs were detected in this population.

Confirming the QTLs

The above analyses suggested a likely pleiotropic effect of the subterminal region of chromosome 5 in the interval R360-C734a on grain width, length-width ratio and chalkiness (Fig. 2). However, this interval is 35.8 cM in length in the linkage map constructed using the F_2 data and 27.2 cM in length in the map using the RIL data. Such a gap could possibly induce spurious QTLs (‘‘ghost’’ QTLs, Lander and Botstein 1989) by interval mapping. One-way analysis of variance and composite interval mapping were conducted to confirm the QTLs detected in this region; all the QTLs resolved by interval mapping were also detected by both of the two methods (data not shown), indicating the reality of the QTLs resolved in this region.

Discussion

Grain shape and endosperm opacity are the two main attributes that determine the appearance quality of the rice grains. Grain shape is largely specified by the ratio of grain length to grain width, and opacity, or chalkiness, consists of three subtraits: white belly, white core and white back. The present study has characterized the genetic bases of all the components, except white back, that are related to the appearance quality of rice grains, using populations from a cross between the parents of Shanyou 63, an elite hybrid widely grown in China.

The general picture that emerged from the genetic analyses of grain shape is that grain length and grain width are each controlled by a major QTL accounting for a very large proportion of the genetic variation, plus one or two minor QTLs each explaining a small proportion of the genetic variation. Thus, as expected, length-width ratio is almost completely specified by these two loci according to the results of QTL analyses. Similarly, white belly, which largely determines the opacity of the endosperm, is almost entirely controlled by one major locus. In contrast, white core, which plays only a minor role in determining the opacity, is controlled by two minor QTLs. Very interestingly, the major QTL for grain width and the ones for white belly and white core are located in the same genomic region, such that the chromosomal segment from Zhenshan 97 increases grain width and at the same time greatly increases the white belly and slightly decreases the white core. Whether this is the result of pleiotropy or tight linkage remains to be determined in future studies.

Compared with the results of previous studies, it can be deduced that the major QTL for grain length detected in this study on chromosome 3 should be the same locus as the one reported by Huang et al. (1997), which is also likely to be the same as the one reported by Lin et al. (1995). However, the QTL for grain length reported by Redoña and Mackill (1998) around RG476 on chromosome 4 is certainly a completely different locus for grain length that was not detected in the present study. For grain width, it is highly likely that the QTL detected in this study on chromosome 5 is the same as the one reported in Lin et al. (1995). However, this QTL is certainly different from those of Huang et al. (1997) and Redoña and Mackill (1998).

It is also interesting to note that, based on the syntenic relationship in the grass family (Ahn et al. 1993; Gale and Devos 1998), it is highly likely that the QTL for grain length on chromosome 5 may be orthologous to the QTLs for grain size on maize chromosomes 1 and 5 and the one on sorghum linkage group C (Paterson et al. 1995). This QTL may also be syntenic to the QTL for grain size of wheat on chromosome 5L (Snape et al. 1985).

The findings of this study have significant implications for the improvement of this hybrid. With respect to grain quality improvement, it is clear that grain length and opacity of the hybrid can be independently modified, since the major QTLs for these two traits are located in different chromosomes. It is also clear that opacity and grain width can be simultaneously improved; reducing the grain width would almost certainly decrease the opacity, as indicated by the co-location of the QTLs for these two traits. Furthermore, all of the traits for appearance quality can be modified with little influence on cooking and eating quality, the latter being mostly controlled by the *Wx* locus on chromosome 6 (Tan et al. 1999).

With respect to improving yield potentials, a previous study on the same cross (Yu et al. 1997) detected QTLs for grain weight in both of the genomic regions on chromosomes 3 and 5 where the major QTLs for grain length and width were detected in this study. Grain length was positively associated with grain weight according to the effect estimated for the genomic region containing the major QTL for grain length detected in this study. However, the effects estimated for the genomic region on chromosome 5, in which the major QTL for grain weight was detected in this study and also a QTL for grain weight was detected in the previous study, suggested a positive association between grain width and grain weight. Such results clearly indicate that, in general, increasing grain length would also increase grain weight and, conversely, decreasing grain width would also reduce grain weight. Thus, a compromise has to be reached among grain length, grain width and grain weight in the improvement of this hybrid.

In summary, the results from this study can be useful in many ways for improving the appearance quality of this hybrid: to increase grain length, to decrease grain width, to reduce chalkiness of the endosperm and, at the same time, not to affect the yield. The closely linked markers that flank the QTLs identified should be very useful when transferring genes in breeding programs.

Acknowledgements The authors wish to thank Dr. S.D. Tanksley's group of Cornell University and the Japanese Rice Research Program for kindly providing the RFLP probes. This research was supported by a grant from the National Key Program on Basic Research Development (973) and a grant from the National Natural Science Foundation of China

References

Ahn S, Anderson JA, Sorrells ME, Tanksley SD (1993) Homoeologous relationships of rice, wheat and maize chromosomes. Mol Gen Genet 241:483–490

Gale MD, Devos KM (1998) Plant comparative genetics after 10 years. Science 282:656–659

Huang N, Parco A, Mew T, Magpantay G, McCouch S, Guiderdoni E, Xu J, Subudhi P, Angeles ER, Khush GS (1997) RFLP mapping of isozymes, RAPD and QTLs for grain shape, brown planthopper resistance in a doubled haploid rice population. Mol Breed 3:105–113

Juliano BO (1985) Rice chemistry and technology, 2nd edn. American Association of Cereal Chemists, Inc, St. Paul, Minn.

Juliano BO, Villareal CP (1993) Grain quality evaluation of world rices. International Rice Research Institute, Manila, The Philippines

Lander ES, Botstein D (1989) Mapping mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–198

Lander ES, Green P, Abrahamson J, Barlaw A, Daly M, Lincoln SE, Newburg L (1987) MAPMAKER: An interactive computer package for maps of experimental and natural populations. Genomics 1:174–181

Lin HX, Min SK, Xiong ZM, Qian HR, Zhuang JY, Lu J, Huang N, Zheng KL (1995) RFLP mapping of QTLs for grain shape traits in indica rice (*Oryza sativa* L. subspec. *Indica*) (in Chinese with English abstract). Sci Agric Sin 28:1–7

Lincoln S, Daly M, Lander ES (1992a) Construction genetic maps with MAPMAKER/EXP 3.0. Whitehead Institute Technical Report, 2nd edn., Whitehead Institute, Cambridge, Mass.

Lincoln S, Daly M, Lander ES (1992b) Mapping genes controlling quantitative traits with MAPMAKER/QTL 1.1. Whitehead Institute Technical Report, 2nd edn., Whitehead Institute, Cambridge, Mass.

Paterson AH, Lin YR, Li ZK, Schertz KF, Doebley JF, Pinson S RM, Liu SC, Stansel JW, Irvine J (1995) Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. Science 269:1714–1718

Redoña ED, Mackill DJ (1998) Quantitative trait locus analysis for rice panicle and grain characteristics. Theor Appl Genet 96:957–963

Snape JW, Law CN, Parker BB, Worland AJ (1985) Genetical analysis of chromosome 5 A of wheat and its influence on important agronomic characters. Theor Appl Genet 71:581–526

Tan YF, Li JX, Yu SB, Xing YZ, Xu CG, Zhang Q (1999) The three important traits for cooking and eating quality of rice grains are controlled by a single locus. Theor Appl Genet 99:642–648

Unnevehr LJ, Duff B, Juliano BO (1992) Consumer demand for rice grain quality. International Rice Research Institute, Manila, The Philippines and International Development Research Centre, Ottawa, Canada

Wang ZY, Zhen FQ, Shen GZ, Gao JP, Snustad P, 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

Webb BD (1980) Rice quality and grades. In Luh BS (ed) Rice: production and utilization. Avi Publ Co, Westport, Conn., pp 543–565

Xing YZ (1999) Molecular dissection of genetic bases of important agronomic traits in rice. PhD thesis, Huazhong Agricultural University, Wuhan, China

Yu SB, Li JX, Xu CG, Tan YF, Gao YJ, Li XH, Zhang Q, Saghai Maroof MA (1997) Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. Proc Natl Acad Sci USA 94:9226–9231

Zeng ZB (1994) Precision mapping of quantitative trait loci. Genetics 136:1457–1468