QTL mapping of grain quality traits in rice

Jue Lou, Liang Chen, Gaohong Yue, Qiaojun Lou, Hanwei Mei, Liang Xiong, Lijun Luo

Abstract

Grain quality improvement is one of the most important goals in a rice breeding program. An indica variety with small grain size was crossed to a japonica variety with large grain size to construct a set of recombinant inbred lines (RILs) which was used to identify quantitative trait loci (QTLs) controlling eight grain quality traits. A pleiotropic main effect QTL (M-QTL) flanked by RM3204 and RM16 on chromosome 3 influences the grain length (GL), length width ratio (LWR) and head rice ratio (HRR), explaining the phenotypic variation of 46.0, 36.1 and 29.7%, respectively. A total of 18 epistatic QTLs were identified for all the traits except MRR, distributed on all the chromosomes except chromosome 10. Two M-QTLs for GL and one M-QTL for GW were involved in epistatic QTL. No significant interaction between M-QTL or epistatic QTL and environment was detected except AC having significant M-QTL by environment interaction with minor effect. GL and LWR have a significant negative relation with HRR which might make it difficult to develop long grain with higher HRR in the rice breeding practice.

1. Introduction

Rice is one of the major staple cereal foods, feeding more than half of the world population. Both yield potential and grain quality are the priority traits in a rice breeding program. Selection on grain quality traits based on direct observation in the field is inefficient because the quality traits are very complex and easily affected by the environment. With the recent development of DNA markers and linkage maps of rice, it has become possible for complex polygenic traits to be dissected into single Mendelian quantitative trait loci (QTL). Many QTLs for traits of agronomic importance have been detected and used in rice improvement by marker-assisted selection (MAS) (Bernardo, 2008).

The primary components of rice grain quality influencing the commercial value include appearance quality, milling quality, cooking–eating quality and nutritional quality, which are determined by their physical–chemical properties and other socio-cultural factors.

Generally, the appearance quality of rice grain is essentially composed of grain length (GL), grain width (GW), grain thickness, grain shape defined as length:width ratio (LWR), the chalkiness of the endosperm and the translucency of the endosperm. The genetic basis of rice grain size has been studied extensively in the last decade (Aluko et al., 2004; Huang et al., 1997; Li et al., 2004a; Tan et al., 2000; Wan et al., 2005, 2006;). Among them, one QTL for GL was consistently detected around the pericentromeric region of chromosome 3, usually explaining the largest phenotypic variation. Eventually, GS3 underlying the QTL was cloned by using a BcF2 population from a cross between Minghui63 and Chuan7 (Fan et al., 2006). Recently, GW2 (Song et al., 2007) for grain width and qSW5 (Shomura et al., 2008) for seed width were cloned.

Milling quality is assessed by using three principal characteristics – brown rice ratio (BRR), milled rice ratio (MRR), and head rice ratio (HRR). Much research on QTL mapping for milling quality has been reported (Aluko et al., 2004; Dong et al., 2004; Keipiro et al., 2008; Li et al., 2004a,b; Mei et al., 2002; Septiningsih et al., 2003; Tan et al., 2001). Some of it has studied the milling quality and appearance quality simultaneously.

The eating–cooking quality of rice is usually evaluated by three major physical and chemical characteristics of the starch as indirect indices: amylose content (AC), gel consistency, and gelatinization temperature. The AC of rice, recognized as one of the most important determinants of eating–cooking quality, has been reported to be mainly controlled by the Wx gene on chromosome 6 (Fan et al., 2005; Tan et al., 1999; Wang et al., 2007).

Abbreviations: AC, amylose content; BRR, brown rice ratio; GL, grain length; GW, grain width; HRR, head rice ratio; LWR, length width ratio; MAS, marker-assisted selection; M-QTL, main-QTL; MRR, milled rice ratio; QTL, quantitative trait locus; PC, protein content; PCR, polymerase chain reaction; RIL, recombinant inbred line.

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There are several components influencing nutritional quality of rice such as protein content (PC), amino acid content and fat content. Among them, PC has been considered as a main component. Although various researchers have so far shown different results on the genetic basis of PC, this trait displayed typical normal distribution and was affected by many small effect QTLs (Aluko et al., 2004; Hu et al., 2004; Tan et al., 2001). QTLs for PC on chromosome 1 and 6 have been detected repeatedly in those investigations.

However, the studies mentioned above mainly focused on grain appearance and AC. Less attention was paid to grain milling and PC while fewer researchers have studied the four kinds of grain quality traits simultaneously and analyzed the mutual relationships among these traits. Here we report the QTL mapping of eight quality traits by using an RIL population derived from an indica/japonica cross grown under three environments, and analyzing the correlations among the eight quality traits.

2. Materials and methods

2.1. Plant materials and field experiments

A set of 286 F8 recombinant inbred lines (RILs) of rice was developed from a cross between indica cultivars Chuan7 (1000-grain weight is 10.4 g) and japonica variety Nanyangzhan (1000-grain weight is 41.6 g). In October of 2004 in Shanghai (E1), this RIL population and parents were used for genotypic analysis and phenotypic evaluation. Then these 286 lines and parents were used for trait investigation in October of 2006 in Shanghai (E2) and May of 2007 in Hainan (E3), respectively. Each plot consisted of three rows of 21 plants at a spacing pattern of 25 cm (between rows) by 20 cm (within rows). The field trial was arranged in a randomized block design with three replications. Field management followed normal field production practice. At maturity, each plot was harvested in bulk.

2.2. Quality evaluation

Fully filled grains of individual lines were used for grain quality evaluation. BRR, MRR and HRR were measured in E2 and E3 while other traits were evaluated in three environments.

GL and GW were measured by using a video system (Jeda801). The milling quality traits were investigated according to Chinese National Standard NY 147-88. Hulls were removed from 100 g of grains in duplicate by using a huller (SDL-A; CNRRI, Hangzhou, Zhejiang) to obtain brown rice. BRR is the ratio of brown rice weight to rice grain weight. Brown rice samples (50 g × 2) were processed into milled rice in a desk-top rice miller (JNMJ 6; Taizhou, Zhejiang, China) removing embryo and bran. MRR is the ratio of milled rice weight to rice grain weight. Head rice includes the whole kernels and those having 80% of the complete kernels in milled rice. HRR is the ratio of head rice weight to rice grain weight.

To measure AC and PC, brown rice was placed in a dry room with a constant humidity of 12% for 1 week to balance the moisture content. Samples were scanned by Vector 22/N-I FT-NIR (Bruker Optics, Germany). AC and PC were predicted from models of amylose content and protein content developed by Zhang et al. (2005) and Wu et al. (2006), respectively.

2.3. DNA preparation and PCR amplification

DNA was extracted from fresh leaves of 286 RIL individuals and their parents using the CTAB method as described by Murray and Thompson (1980). The extracted DNA was dissolved in TE buffer and tested for quality and quantity using a DU 640 nucleic acid and protein analyzer (Beckman Coulter Co.). Then these 286 DNA samples were diluted into 25 ng/μl with sterilized double distilled water and stored at 4 °C for the polymerase chain reaction (PCR). PCR was performed with an initial 5-min period at 94 °C, followed by 35 cycles of 30 s of denaturing at 94 °C, 30 s of annealing at 55 °C, and 45 s of extension at 72 °C, and a final 5-min extension at 72 °C. PCR products with large difference were separated on 3% agarose gel and detected by using a UV-GIS detection system (Shanghai Tanon Science and Technology Co., Ltd.). Otherwise, PCR products were separated on 5% denatured polyacrylamide gel electrophoresis and detected by silver staining (Xu et al., 2002).

2.4. Linkage map construction and data analysis

A total of 185 SSR markers covering all 12 chromosomes were analyzed for this population. The genetic linkage map was constructed by using MapMaker/Exp V3.0 (Lincoln et al., 1992). It spanned a total of 1585.6 cM of genome size, with an average interval of 8.57 cM between adjacent markers.

Phenotypic correlation analysis was calculated by using S-Plus for Windows V6.1. QTL analysis was conducted by QTLMapper V1.6 on the basis of the mixed model approach (Wang et al., 1999). A threshold of P ≤ 0.005 and LOD ≥ 2.5 was used to declare the significant main effect QTL (M-QTL), digenic epistatic QTLs, and QTL (M-QTL or epistatic QTL × environment interaction). Contribution rate ($H^2$) was estimated as percentage of variance explained by each locus or epistatic pair in proportion to the total phenotypic variance. QTLs were named following the popular nomenclature but in alphabetic order for QTLs on the same chromosome (McCouch et al., 1997).

3. Results

3.1. Trait performance of the parents and RILs

There were distinct differences between parents on GL, GW, LWR, HRR, and moderate differences on BRR, MRR, AC and PC (Table 1, Figs. 1 and 2). Nanyangzhan grain is twice as long as that of Chuan7. The mean LWR of Chuan7 and Nanyangzhan are 2.27 and 3.63, respectively. Chuan7 has an HRR of 67.1% in E2 and 45.1% in E3, whereas the HRR of Nanyangzhan is only 10.4% in E2 and 5.7% in E3. The distributions of the eight traits in the population were continuous, indicating quantitative inheritance of these characters. Transgressive segregation with one or both directions occurred in all of the traits except GL in E3 (Table 1, Fig. 2). GL, LWR and HRR seemed to have bimodal distribution while GW, BRR, MRR, AC and PC showed a unimodal normal distribution (Fig. 2).

3.2. Correlations among eight rice quality characters

The pairwise phenotypic correlation coefficients were generally consistent in different environments (Table 2). On the whole, there were significant correlations between appearance quality and milling quality, appearance quality and nutritional quality. GL and LWR had weaker positive relation with BRR, but had a significant negative relation with MRR and a very strong negative relation with HRR. The correlation coefficients between GL, LWR and HRR were −0.582, −0.490 in E2 and −0.840, −0.797 in E3, respectively. GW had no significant correlation with grain milling quality traits. Among the three appearance quality traits, GL was significantly positively correlated with LWR and not significantly correlated with GW. GW had a significant negative relation with LWR. For the three
Table 1
Performance of eight grain quality traits of the parents and their RI population in three crossing seasons.

<table>
<thead>
<tr>
<th>Traits</th>
<th>GL (mm)</th>
<th>GW (mm)</th>
<th>LWR (%)</th>
<th>BRR (%)</th>
<th>MRR (%)</th>
<th>HRR (%)</th>
<th>AC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHUAN7</td>
<td>6.13±0.15</td>
<td>2.61±0.21</td>
<td>2.38±0.21</td>
<td>13.01±0.41</td>
<td>13.19±0.23</td>
<td>19.61±0.20</td>
<td>11.54±0.17</td>
</tr>
<tr>
<td>NANYANGZHAN</td>
<td>5.79±0.21</td>
<td>2.61±0.21</td>
<td>2.38±0.21</td>
<td>13.01±0.41</td>
<td>13.19±0.23</td>
<td>19.61±0.20</td>
<td>11.54±0.17</td>
</tr>
<tr>
<td>PARENTS</td>
<td>6.11±0.44</td>
<td>2.61±0.21</td>
<td>2.38±0.21</td>
<td>13.01±0.41</td>
<td>13.19±0.23</td>
<td>19.61±0.20</td>
<td>11.54±0.17</td>
</tr>
</tbody>
</table>

3.3. QTL mapping

A total of 16 QTLs were identified for the eight traits across the three environments, distributed on six chromosomes with LOD values varying from 4.17 to 90.10. The phenotypic variation of QTLs ranged from 1.90 to 46.00%. No significant QTL by environment interaction was detected except AC.

Two QTLs were detected for GL, collectively accounting for 48.45% of the total phenotypic variation. The larger effect QTL, qGL-3, flanked by RM6283 and RM16 on chromosome 3, explained 46% of the variation, indicating that this QTL played a decisive role for GL in the RIL population. The allele from Nanyangzhan increased grain length by 0.99 mm with a LOD value of 90.1. Another QTL mapped to RM588–RM540 on chromosome 6 had a contribution of 2.45% of the phenotypic variation. The allele from Nanyangzhan had a positive additive effect for qGL-6 by 0.23 mm.

Four QTLs for GW on chromosomes 2, 6 and 9 totally explained 8.99% of the phenotypic variance, including two flanked by RM221–RM526 (qGW-2a) and RM3874–RM5651 (qGW-2b) on chromosome 2, one mapped to RM541–RM3183 (qGW-6) on chromosome 6 and the other located between RM541–RM3183 (qGW-9) on chromosome 9. These QTLs accounted for 2.11–2.44% of the variance with LOD values varying from 4.17 to 5.14. The Nanyangzhan allele at each locus could increase GW by 0.04 mm.

Only one QTL mapped to RM6283–RM16 on chromosome 3 was detected for LWR. The major QTL, qLWR-3, accounted for 36.09% of the variation with an LOD score of 43.1. The allele from Nanyangzhan had a positive effect, which could increase LWR by 0.04 mm.

Two QTLs for BRR were identified. The major QTL, qBRR-3, in the interval of RM572–RM582 explained 1.9% of the variation with a LOD value of 4.47. Another QTL (LOD = 8.04), qBRR-3, located in the interval of RM16–RM6266 explained 3.19% of the phenotypic variation. The additive effect of alleles from Nanyangzhan increased BRR by 0.30 and 0.39%, respectively.

A minor QTL qMRR-3 flanked RM3204–RM6283 on chromosome 3 was detected for MRR and accounted for 6.65% of the total variation. An allele from CHUAN7 contributed the positive effect for MRR at this locus by 0.86%.

A major QTL qHRR-3 was associated with HRR (Table 3, Fig. S1). This locus in the interval of RM3204–RM6283 on chromosome 3...
explained 29.74% of the variation. The Chuan7 allele had a positive additive effect of 8.39% for HRR.

In total, three QTLs were detected for AC. They were designated as qAC-2, qAC-6a and qAC-6b, respectively. The total contribution was 13.22% (Table 3, Fig. S1). qAC-2 (LOD = 10.7) was identified in the region of RM525–RM221 on chromosome 2, which explained 2.55% of the total phenotypic variation. The allele from Nanyangzhan had an additive effect of 0.54%. The other two QTLs on chromosome 6 accounted for 2.84 and 7.83% of the variation with LOD values of 14 and 26.7. Chuan7 alleles could increase the AC value at these two loci by 0.56 and 0.94%.

All of the three loci were detected with significant QTL by environment interaction, totally explaining 7.30% of the phenotypic variance. Interaction between individual QTL and environment accounted for from 1.83 to 3.58% of the phenotypic variation. Significant additive effects of AEi are listed in Table 3. Compared with the total effect of M-QTLs, the effect of QTL by environment interaction was smaller, implying that AC was influenced by some M-QTLs in this RI population.

Two QTLs for PC were detected, collectively explaining 7.19% of the variance (Table 3, Fig. S1). One was flanked by RM588–RM540 on chromosome 6 and accounted for 4.5% of the variation. The Chuan7 allele at this locus increased PC by 0.30%.

Another QTL qPC-7 was responsible for 2.69% of the total variation. The Nanyangzhan allele could increase the PC at this locus by 0.23%.

**Fig. 2.** Phenotypic distribution of eight traits in the Chuan7/Nanyangzhan RI population across three environments. Mean values of Chuan7 (open arrow) and Nanyangzhan (Closed arrow) from three environments were shown above. White, grey and black columns represent traits evaluation in E1, E2 and E3, respectively.
4.1. QTL mapping of eight rice grain quality traits

A total of 16 M-QTLs for the eight rice grain quality traits were identified in the present study (Table 3, Fig. S1). Three QTLs, qGW-9, qBRR-1 and qPC-7, were novel compared with previous research (Huang et al., 1997; Li et al., 2004a,b; Redoña and Mackill, 1998; Tan et al., 2000; Yu et al., 1997). Three QTL clusters were observed on chromosomes 3, 2 and 6. The first QTL cluster flanked by RM3204 and RM6266 covering the centromeric region of chromosome 3 contained five QTLs for GL, LWR, BRR, MRR and HRR. The allele from Nanyangzhan at these loci increased GL, LWR and BRR, but decreased MRR and HRR. qGL-3 explained the largest phenotypic variation of 46% for GL. G53 was initially mapped to the interval as qGL-3 by using a population derived from Minghu63 and Chuan7 which was also used in the present study (Fan et al., 2005, 2006). Therefore, G53 and qGL-3 should be the same locus. The second QTL cluster was flanked by RM525 and RM526 on chromosome 2 including qGW-2a, qAC-2 and qGW-2b. The QTLs in this cluster explained 4.66% of phenotypic variation for GW and 2.55% for AC. The Nanyangzhan allele of these QTLs could increase GW and AC. The third QTL cluster located to the interval of RM584–RM540 on chromosome 6 spanned the Wx locus. It harbored QTLs for AC, GL and PC with small effect. The Chuan7 allele had a positive effect on AC and PC, but a negative effect on GL.

Main effect QTLs for AC were not identified in this research. It may be due to the fact that Chuan 7 and Nanyangzhan contain the same indica Wx allele and have a similar amylase content. This result was also found by Bao et al. (2002) and Wan et al. (2004). QTLs with major effect for PC were not detected in the present research as others have reported (Aluko et al., 2004; Hu et al., 2004; Tan et al., 2001; Wang et al., 2007).

Epistasis has been demonstrated as an important factor in the genetic basis for rice flowering time and heterosis (Yamamoto et al., 2000; Yu et al., 1997). In this research, epistatic interaction also played an important role in determining rice grain quality (Tables 3 and 4). Among the eight traits surveyed, only MRR was not influenced by epistatic interaction. Epistatic QTLs explained a larger proportion of the phenotypic variation than M-QTLs for GW. As to QTL × environment interaction, only AC was affected significantly by M-QTL × environment interaction which explained 7.3% of the variation.

### 4.2. Quality improvement through marker-assisted selection based on QTL mapping

QTL mapping results and correlation analysis showed that grain appearance quality had a close relation with milling quality in the present study. A QTL flanked by RM6283 and RM16 had a major impact on QTL mapping.

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**Table 2**

<table>
<thead>
<tr>
<th>Trait</th>
<th>QTL</th>
<th>Chr.</th>
<th>Interval</th>
<th>LOD</th>
<th>A1</th>
<th>A2</th>
<th>H2(A1)</th>
<th>H2(A2)</th>
<th>H2(A1/A2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GL</td>
<td>qGL-3</td>
<td>3</td>
<td>RM6283–RM16</td>
<td>90.13</td>
<td>-0.99</td>
<td>64.00</td>
<td>48.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GW</td>
<td>qGW-6</td>
<td>6</td>
<td>RML88–RM540</td>
<td>7.79</td>
<td>-0.23</td>
<td>2.44</td>
<td>8.99</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LWR</td>
<td>qLWR-3</td>
<td>3</td>
<td>RM6283–RM16</td>
<td>43.13</td>
<td>-0.32</td>
<td>36.09</td>
<td>36.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRR</td>
<td>qBRR-1</td>
<td>3</td>
<td>RM572–RM582</td>
<td>4.47</td>
<td>0.30</td>
<td>1.90</td>
<td>5.09</td>
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<td></td>
</tr>
<tr>
<td>MRR</td>
<td>qMRR-3</td>
<td>3</td>
<td>RM204–RM6283</td>
<td>6.69</td>
<td>0.86</td>
<td>6.65</td>
<td>6.65</td>
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<tr>
<td>HRR</td>
<td>qHRR-3</td>
<td>3</td>
<td>RM204–RM6283</td>
<td>35.90</td>
<td>8.39</td>
<td>29.74</td>
<td>29.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>AC</td>
<td>qAC-2</td>
<td>2</td>
<td>RM525–RM221</td>
<td>10.71</td>
<td>-0.54</td>
<td>2.55</td>
<td>1.89</td>
<td>13.22</td>
<td>7.30</td>
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<tr>
<td>PC</td>
<td>qPC-2</td>
<td>6</td>
<td>RM588–RM540</td>
<td>9.03</td>
<td>0.30</td>
<td>4.00</td>
<td>7.19</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a: A1 and A2 are the additive effects of QTL. Positive values of additive effects indicate that the Chuan7 genotype have a positive effect on that trait.

b: A1 and A2 are the additive effects of the environmental interaction from A1 and E1, A2 and E2, A3 and E3, respectively.

c: H2(A1/A2) are the percentage of the phenotypic variation explained by A1 and A2.

d: H2(A1/A2) are the percentage of the phenotypic variation explained by A1 and A2 for the trait.
Table 4
Digenic epistasis involved in rice grain quality traits in an RILs population derived from the cross of Chuan7 × Nanyangzhan across different environments.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Ch-In i</th>
<th>Interval i</th>
<th>QTL</th>
<th>Ch-In j</th>
<th>Interval j</th>
<th>QTL</th>
<th>LOD</th>
<th>Ai</th>
<th>Aj</th>
<th>AAij</th>
<th>H2(Ai)</th>
<th>H2(Aj)</th>
<th>H2(AAij)</th>
<th>H2(AA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>GL</td>
<td>3–5</td>
<td>RM282–RM6080</td>
<td>3–11</td>
<td>RM6283–RM16</td>
<td>qGL-3</td>
<td>92.83</td>
<td>0.11</td>
<td>0.972</td>
<td>0.32</td>
<td>0.22</td>
<td>0.32</td>
<td>0.27</td>
<td>0.04</td>
<td>1.1</td>
</tr>
<tr>
<td>GW</td>
<td>1–6</td>
<td>RM582–RM5759</td>
<td>7–4</td>
<td>RM1377–RM542</td>
<td>8.42</td>
<td>0.05</td>
<td>0.34</td>
<td>1.07</td>
<td>2.77</td>
<td>10.12</td>
<td></td>
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<tr>
<td>HRR</td>
<td>2–5</td>
<td>RM3874–RM5651</td>
<td>8–13</td>
<td>RM547–RM556</td>
<td>6.39</td>
<td>0.04</td>
<td>0.03</td>
<td>2.19</td>
<td>0.93</td>
<td>0.73</td>
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<tr>
<td>LWR</td>
<td>1–1</td>
<td>RM24–RM562</td>
<td>8–1</td>
<td>RM3120–RM3155</td>
<td>6.49</td>
<td>0.09</td>
<td>0.04</td>
<td>2.44</td>
<td>5.85</td>
<td></td>
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<tr>
<td>BR</td>
<td>3–10</td>
<td>RM1204–RM2683</td>
<td>11–17</td>
<td>RM2064–RM224</td>
<td>7.26</td>
<td>0.26</td>
<td>0.25</td>
<td>1.25</td>
<td>2.72</td>
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<tr>
<td>AC</td>
<td>2–13</td>
<td>RM29–RM6639</td>
<td>4–7</td>
<td>RM252–RM1223</td>
<td>7.55</td>
<td>0.42</td>
<td>0.04</td>
<td>1.66</td>
<td>4.50</td>
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<tr>
<td>HRR</td>
<td>2–5</td>
<td>RM3874–RM5651</td>
<td>9–1</td>
<td>RM316–RM219</td>
<td>8.48</td>
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<td>2.02</td>
<td>1.26</td>
<td>2.88</td>
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<tr>
<td>PC</td>
<td>2–18</td>
<td>RM8977–RM6247</td>
<td>3–5</td>
<td>RM282–RM6080</td>
<td>6.69</td>
<td>0.19</td>
<td>0.22</td>
<td>2.06</td>
<td>3.41</td>
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</tbody>
</table>

Notes:
- Ai and Aj are the additive effects of the test points i and j, respectively. Positive values of Ai and Aj imply that the Chuan7 genotype has a positive effect on that trait.
- AAij is the effect of additive-by-additive interaction between points i and j; a positive value indicates that the parental two-locus genotypes have a positive effect and that the recombinants had a negative effect.
- H2(Ai) is the collective percentage of the phenotypic variation explained by Ai for the trait.
- H2(Aj) is the collective percentage of the phenotypic variation explained by Aj for the trait.
- H2(AAij) is the collective percentage of the phenotypic variation explained by AAij for the trait.
- H2(AA) is the collective percentage of the phenotypic variation explained by AA for the trait.

References


References


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Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jcs.2009.04.005.
population derived from the Oryza sativa variety IR64 and the wild relative O. rufipogon. Theoretical and Applied Genetics 107, 1433–1441.


