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# Identification of Quantitative Trait Loci Associated with Rice Eating Quality Traits Using a Population of Recombinant Inbred Lines Derived from a Cross between Two Temperate *japonica* Cultivars

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**Improved eating quality is a major breeding target in *japonica* rice due to market demand. In this study, we performed genetic analysis to identify quantitative trait loci (QTLs) that control rice eating quality traits using 192 recombinant inbred lines (RILs) derived from a cross between two *japonica* cultivars, 'Suweon365' and 'Chucheongbyeo'. We evaluated the stickiness (ST) and overall evaluation (OE) of cooked rice using a sensory test, the glossiness of cooked rice (GCR) using a Toyo-taste meter, and measured the amylose content (AC), protein content (PC), alkali digestion value (ADV), and days to heading (DH) of the RILs in the years 2006 and 2007. Our analysis revealed 21 QTLs on chromosomes 1, 4, 6, 7, 8, and 11. QTLs on chromosomes 6, 7, and 8 were detected for three traits related to eating quality in both years. QTLs for ST and OE were identified by a sensory test in the same region of the QTLs for AC, PC, ADV, GCR and DH on chromosome 8. QTL effects on the GCR were verified using QTL-NILs (near-isogenic lines) of $BC_3F_{4-6}$ in the Suweon365 background, a low eating quality variety, and some $BC_1F_3$ lines. Chucheongbyeo alleles at QTLs on chromosomes 7 and 8 increased the GCR in the NILs and backcrossed lines. The QTLs identified by our analysis will be applicable to future marker-assisted selection (MAS) strategies for improving the eating quality of *japonica* rice.**

## INTRODUCTION

Rice (*Oryza sativa* L.) is the staple food for half of the world's population. The eating quality of cooked rice is one of the most important breeding objectives suitable for growers of *japonica*, an important commercial rice variant with a significant market. Eating quality has usually been evaluated using sensory tests but this is difficult to perform in early generations of $F_3$ to $F_5$ populations due to the requirement for several hundred grams of milled rice and well-trained specialists. Physicochemical characteristics such as the alkali digestion value (ADV), amylose content (AC), protein content (PC), and amylographic characteristics of polished rice are alternative indirect methods for determining rice eating quality, particularly when selecting for this trait in early generations. It has been suggested that amylose content is related to specific aspects of eating quality, such as glossiness and stickiness (Juliano et al., 1965; Tanaka et al., 2006) and that the amylose content was mainly controlled by the waxy (Wx) gene located on chromosome 6 (Ishima et al., 1974). The eating quality of rice is therefore under complex genetic control (Yamamoto and Ogawa, 1992), but is also influenced by environmental factors, such as the air temperature during the ripening period (Nishimura et al., 1985) and the nitrogen levels in the soil (Ishima et al., 1974).

The available genetic information on eating quality in *japonica* rice varieties is currently limited (Yamamoto and Ogawa, 1992) although several studies have been carried out to identify QTLs that are associated with this trait. Five stable QTLs and 21 additional QTLs associated with eating quality were previously identified using chromosome segment substitution lines (CSSLs) derived from a cross of Asominori (*japonica*) and IR24 (*indica*), and by using backcross inbred lines (BILs) derived from a cross of Koshihikari/Kasalath (*indica*)//Koshihikari and CSSLs, respectively (Ebitani et al., 2005; Wan et al., 2004). A few studies have also identified QTLs for eating quality in doubled haploid (DH)lines or RILs derived from crosses between different *japonica* strains (Kobayashi and Tomita, 2008; Suh et al., 2006; Takeuchi et al., 2008; Tanaka et al., 2006; Wada et al., 2008). DNA markers closely linked to these QTLs have made it possible to more efficiently develop rice cultivars with a higher eating quality (Lestari et al., 2009).

Recently, DNA marker-assisted selection (MAS) has been used to develop new rice cultivars or NILs with particular agronomic traits, and resistant to biotic and abiotic stresses. MAS has now been used to introduce resistance genes for blast,

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bacterial blight, brown planthopper, lodging resistance, yield potential, and submergence tolerance (Ashikari et al., 2005; Hayashi et al., 2004; Kwon et al., 2008b; Neeraja et al., 2007; Singh et al., 2001; Sugiura et al., 2004; Suh et al., 2011; Wang et al., 2005). The effectiveness of the MAS system depends on the reliability of markers linked to the target gene/QTL loci from diverse genetic backgrounds in high eating quality *japonica* rice varieties. The objective of our present study was to identify QTLs associated with eating quality by employing a saturated genetic linkage map of a recombinant inbred population derived from a cross between two temperate *japonica* varieties.

## MATERIALS AND METHODS

### Plant materials

A total of 190 $F_{12\text{-}14}$ recombinant inbred lines (RILs) derived from a cross between Suweon365 (*japonica*) and Chucheongbyeo (*japonica*) by means of the single seed descent method were analyzed in this study. Suweon365 is derived from a cross between Seonambyeo and Iri353, and is a high yielding semi-dwarf plant type, resistance to blast with medium eating quality [National Institute of Crop Science (NICS), 1988]. Chucheongbyeo or Akibare in Japanese (developed from a cross between Mandainishiki as the female parent and an $F_5$ line from a cross of Wakaba/Kinmaze as the male parent) was introduced from Japan in 1969. This is a late flowering tall variety with good eating quality but highly susceptible to blast (RDA, 1975). The $F_1$ plants were self-pollinated to produce $F_2$ seeds, and 231 $F_{11}$ lines were developed from the resultant $F_2$ plants via single-seed descent method (Kwon et al., 2008a). This RIL population was advanced from $F_{12}$ generations to $F_{14}$, and 190 RILs were selected to construct a saturated genetic linkage map using SSR markers and thereby evaluate traits for eating quality.

To verify the allelic effects of the QTLs detected by Chucheongbyeo alleles for the glossiness of cooked rice, several RILs containing these QTLs were successively backcrossed with the Suweon365 variety of low eating quality, and advanced from $BC_3F_3$ in 2005 to $BC_3F_5$ in 2007 via selection using linked SSR markers. Seven $BC_1F_1$ lines from backcrosses with the variety Palgongbyeo and one $BC_1F_1$ line from a backcross with Hopyeongbyeo were developed to validate the effectiveness of QTLs for eating quality from the Chucheongbyeo alleles. These lines were advanced to $BC_1F_3$ based on marker-assisted selection for the QTL regions. The Palgongbyeo cultivar developed from a cross between HR1591-43-2-2-2 and 6542B2-16-3-B, is stably resistant to blast but is of low eating quality (Kim et al., 2004; Lestari et al., 2009). Hopyeongbyeo was developed from a cross between Hitomebore and Hwajinbyeo, is highly susceptible to leaf blast, but has a high eating quality that is comparable to Chucheongbyeo (Lee et al., 2007).

### Cultivation and harvesting of seeds

One hundred and ninety RILs and two parents were grown in an experimental plot at NICS, Suwon for two years (2006-2007). Seeds were sown on 25 April and seedlings were transplanted on 25 May in each year. The planting density was 22.22 $m^{-2}$ (15 cm $\times$ 30 cm) over both years and N-$P_2O_5$-$K_2O$ fertilizers were applied at the level of 90 - 45 - 57 kg/ha in each year. Parental cultivars were planted with one replication for every 38 RILs, with six replications in total. Fifty-six plants for the two lines were raised using a randomized block design with two replications in each year. Forty-eight out of 56 plants per line were harvested at forty-five days after heading. Days to heading (DH), which sometimes affects eating quality, was calculated as the number of days from transplanting to heading. All seeds were threshed, and air-dried in a shaded greenhouse. Fully matured grains were used for evaluation of chemical properties and eating quality.

To verify the allelic effects of the detected QTLs, three advanced backcrossed progenies of $BC_3F_{4\text{-}6}$, on the basis of the SSR marker genotypes that were homozygous for the Chucheongbyeo alleles in QTL regions of chromosomes. 6, 7, and 8 in the homozygous Suweon365 genetic background, were cultivated in 2007, 2008, and 2009. The seeding, transplanting and application of fertilizers were as used for the RILs. One-hundred and twelve plants of four lines were raised using a randomized block design with two replications in each year. Forty-eight plants in the middle two lines were harvested at forty-five days after heading. Seventy four and 16 $BC_1F_2$ lines from crosses of Palgongbyeo and Hopyeongbyeo, respectively were genotyped with SSR markers to select homozygotes for the Chucheongbyeo alleles on QTL regions from chromosomes 6, 7, and 8. Each plant was harvested at maturity using the same method applied to the RIL population.

All seeds were threshed, air-dried in a shaded greenhouse, and hulled. Fully matured grains were used for evaluation of chemical properties and eating quality. Each of the lines and the parents were evaluated for agronomic traits and yield potential.

### Evaluation of chemical properties for grain quality

Alkali digestion values (ADV) were determined visually using the scale (1-7) of spreading method of Little (1958) and by the clearing of milled rice kernel soaked in 1.4% KOH solution for 23 h at a constant temperature of 30°C. The amylose content (AC) was determined by the relative absorbency of a starch-iodine blue color in a digested solution of 100-mesh rice flour. For these measurements we used a Rapid Flow Autoanalyzer according to the method of Juliano (1971). The protein content (PC) was measured using the Micro-Kjeldahl method (FOSS: 2300 Kjeltec Analyzer, Sweden). A nitrogen conversion factor of 5.95 was used to estimate the PC in rice flour samples. The glossiness of cooked rice (GCR) was determined with two replications using the Toyo-taste meter (model: MA-90A and 90B) in accordance with the operation manual (TRCM Co., Japan).

### Sensory test for rice eating quality

Rice grains were polished and cooked, as described in the manual 'A guide to rice breeding' (Choi, 2006). The grains were polished to a yield of appropriately 90% using a rice miller, the polished rice was transferred to insert bowls and washed five times with water. After washing, the rice was soaked in water for a further 30 min and then cooked in the rice cooker at a 1.3 (w/w) ratio of water to polished rice. Cooked rice for each line was evaluated by a panel of five judges who had been trained to distinguish differences in glossiness and stickiness of cooked rice. The eating quality of each line was evaluated according to the determination of stickiness (ST), and overall evaluation (OE). For each property, seven scores -3, -2, -1, 0, +1, +2, and +3 were designed corresponding to worst, worse, bad, the same, good, better, and best, respectively, in comparison with the control variety, Chucheongbyeo. The average scores for taste and palatability were used for the QTL analysis.

### QTL analysis

The *japonica* linkage map of 188 SSR markers used to analyze the RIL population from the cross between Suweon365 and Chucheongbyeo had a total length 1,902 cM with an average distance of 10.1 cM. This map was constructed using the basic data published by Kwon (2008) and was used to analyze

**Table 1.** Seven traits related to grain quality and eating quality of *japonica* RILs and parental lines

| Trait | Year | Parents[a/] | | RILs | | Correlation between years[b/] |
|---|---|---|---|---|---|---|
| | | SS | CC | Mean | Range | |
| Days to heading (DH) | 2006 | 109.3 | 120.0 | 118.3 ± 4.5 | 108-130 | 0.88** |
| | 2007 | 108.3 | 122.2 | 117.4 ± 5.3 | 107-129 | 0.88** |
| Alkali digestion value (ADV) | 2006 | 6.1 | 6.3 | 6.0 ± 0.6 | 4.1-6.9 | 0.47** |
| | 2007 | 6.1 | 6.7 | 6.5 ± 0.2 | 5.9-6.9 | 0.47** |
| Amylose content (AC, %) | 2006 | 17.2 | 19.7 | 19.1 ± 0.9 | 16.1-21.7 | 0.44** |
| | 2007 | 15.2 | 18.1 | 17.1 ± 1.3 | 13.0-19.3 | 0.44** |
| Protein content (PC, %) | 2006 | 6.5 | 5.9 | 6.2 ± 0.5 | 4.8-7.5 | 0.60** |
| | 2007 | 8.5 | 7.2 | 7.7 ± 0.5 | 6.0-9.3 | 0.60** |
| Glossiness of cooked rice (GCR) | 2006 | 63.2 | 68.9 | 67.4 ± 3.9 | 57.2-78.8 | 0.63** |
| | 2007 | 60.3 | 66.6 | 64.0 ± 3.7 | 55.6-74.4 | 0.63** |
| Stickiness (ST) | 2007 | -0.75 | 0.0 | -0.02 ± 0.60 | -1.67-1.67 | - |
| Overall eating quality (OE) | 2007 | -1.05 | 0.0 | 0.02 ± 0.70 | -2.00-1.67 | - |

[a/]SS, Suweon365; CC, Chucheongbyeo

[b/]*, **, significance at the 5% and 1% levels, respectively

QTLs for characteristics related to eating quality in *japonica* rice. The chromosomal locations of the QTLs were determined by single-point analysis (SPA) and composite interval mapping (CIM). Primary analysis using SPA was performed using the QGene program (Nelson, 1997). In SPA, a QTL was identified if the phenotype was associated with a marker locus at $P < 0.001$ or with two adjacent marker loci at $P < 0.05$. To identify additional QTLs and to increase the resolution of QTL locations, CIM were performed using QTL Cartographer 2.0 (Basten et al., 1997). Significance thresholds for CIM were determined using 1,000 permutations for each trait. For CIM, the experiment-wise significance level of $P < 0.01$ corresponded to an average LOD > 3.80, whereas the level $P < 0.05$ corresponded to an LOD > 2.52. The QTLs reported in this study was detected using both the methods. The proportions of observed phenotypic variations attributable to a particular QTL were estimated using the coefficient of determination ($R^2$). The total phenotypic variance explained was estimated by simultaneously fitting to a model including all putative QTLs for the respective trait.

## RESULTS

### Phenotypic variations in parental japonica cultivars and RILs

Phenotypic variations for DH, ADV, AC, PC, GCR, ST, and OE in RILs and *japonica* parental cultivars are shown in Table 1. Five phenotypic variations for DH, ADV, AC, PC, and GCR were significantly different between Suweon365 and Chucheongbyeo throughout the two-year period of these experiments. The DH, ADV, AC, PC and GCR traits showed highly significant correlation coefficients over this time frame. Two traits, ST and OE, showed significant difference between Suweon365 and Chucheongbyeo in 2007. The frequency distributions of the RILs for DH, ADV, AC, PC, GCR, ST, and OE are shown in Figs. 1 and 2. Four traits, DH, AC, PC, and GCR, in the RILs showed continuous variation with transgressive segregations over two years. The mean value of the RILs for each trait exhibited similar to the mid-parental value (Table 1). Frequency distributions for the ST and OE for cooked rice by panel testing showed a nearly normal distribution (Fig. 2). The difference in the DH among the RILs was 22 days in the years, 2006 and 2007. The average temperature during the ripening period, 20 days after heading, was 21.4°C and 22.2°C in 2006 and 2007, respectively. Differences in the average temperature during the ripening period among the early and late flowering RILs were 9.8°C and 7.8°C in 2006 and 2007, respectively.

### Correlation analysis

Correlation coefficients among the DH, ADV, AC, PC, GCR, ST and OE are shown in Table 2. The PC was negatively correlated with all other traits. Six traits DH, ADV, AC, GCR, ST and OE were found to be positively correlated with each other. Correlation coefficients between DH and ADV, and ADV and GCR, were higher than those between DH and other traits. Correlation coefficients between GCR and ST, and GCR and OE were 0.51 and 0.49, respectively. The correlation coefficient between ST and OE showed the highest value at 0.90.

### Identification of QTLs for eating-quality in japonica

A total of 21 QTLs associated with DH, ADV, AC, PC, GCR, ST and OE which are related to the eating quality of cooked rice were identified (Table 3 and Fig. 3). For DH, ADV, AC, PC and GCR, only eight QTLs were detected by interval mapping (IM) and composite interval mapping (CIM) analyses over the two-year experimental period. Other QTLs were detected in only one year, or in one of the IM and CIM analyses. For the DH, four QTLs, *qDH6*, *qDH8*, *qDH11.1* and *qDH11.2*, were identified on chromosomes 6, 8 and 11. All four QTLs were detected by IM and CIM analyses for both the years. Two QTLs *qDH6* and *qDH8* had a major impact and explained 27.3% and 25.3%, and 34.9% and 35.5% of the total phenotypic variations in 2006 and 2007, respectively. These same two QTLs were associated with an extended heading time by a Suweon365 and Chucheongbyeo allele, respectively. Two further QTLs *qDH11.1* and *qDH11.2* on chromosome 11 showed effects by CIM in both the years and an extended heading time by a Chucheongbyeo allele. For the ADV trait, four QTLs, *qADV6*, *qADV7*, *qADV8* and *qADV11*, were identified on chromosomes 6, 7, 8 and 11. The *qADV6* and *qADV8* QTLs were detected in both the years and could explain 27.4% and 12.4%, and 32.6% and 13.6% of the total phenotypic variations, respectively, in the CIM analysis. *QADV7* was found to be an effective QTL by IM in 2007, whereas *qADV11* was effective QTL by CIM in 2006. The Chucheongbyeo alleles at *qADV7*, *qADV8*, and *qADV11* increased the ADV, whereas the Suwon365 allele increased this trait at *qADV6*.

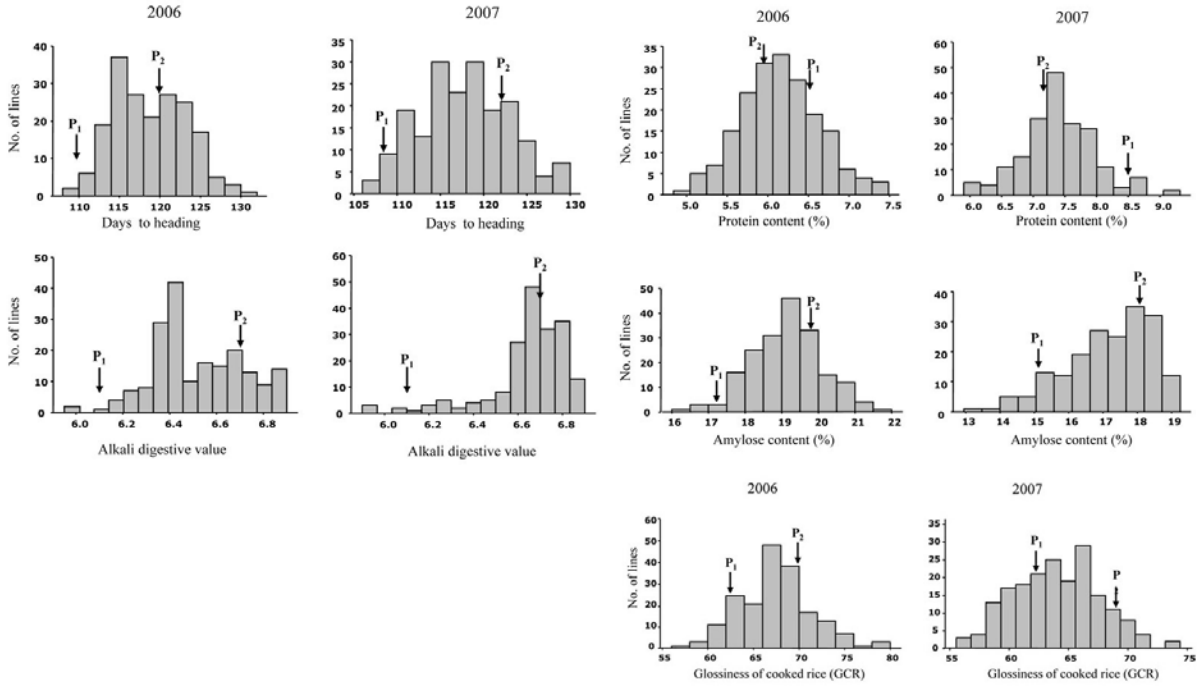


**Fig. 1.** Frequency distribution of the physicochemical properties and glossiness of cooked rice (GCR) determined by Toyo taste-meter analysis of the RIL population derived from a cross between Suweon365 and Chucheongbyeo in 2006 and 2007. $P_1$ and $P_2$ indicate two parental lines Suweon365 and Chucheongbyeo, respectively.

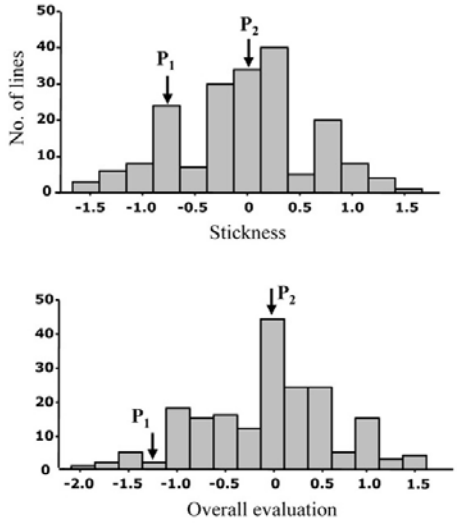


**Fig. 2.** Frequency distribution of stickiness (ST) and overall evaluation (OE) of eating quality in the RIL population derived from a cross between Suweon365 and Chucheongbyeo in 2007. $P_1$ and $P_2$ indicate two parental lines Suweon365 and Chucheongbyeo, respectively.

**Table 2.** Correlation coefficients among seven traits related to eating quality of cooked rice

| Traits | Year | DH | ADV | AC | PC | GCR | ST |
|---|---|---|---|---|---|---|---|
| ADV | 2006 | 0.81** | | | | | |
| | 2007 | 0.61** | | | | | |
| AC | 2006 | 0.43** | 0.56** | | | | |
| | 2007 | 0.34** | 0.31** | | | | |
| PC | 2006 | -0.18* | -0.23** | -0.43** | | | |
| | 2007 | -0.27** | -0.23** | -0.44** | | | |
| GCR | 2006 | 0.57** | 0.56** | 0.52** | -0.40** | | |
| | 2007 | 0.54** | 0.18* | 0.38** | -0.41** | | |
| ST | 2007 | 0.38** | 0.38** | 0.35** | -0.30** | 0.51** | |
| OE | 2007 | 0.40** | 0.40** | 0.35** | -0.26** | 0.49** | 0.90** |

* and **, significance at 0.05 and 0.01 levels, respectively.

For AC, five QTLs were identified on chromosomes 6, 7, 8, and 11. Two QTLs, *qAC6.1* and *qAC6.2* on chromosome 6 were detected in 2007 and 2006, respectively. *QAC6.1* was effective for the Suweon365 allele in the IM analysis, and *qAC6.2* from the Chucheongbyeo allele was effective in the CIM. A further QTL, *qAC7*, was detected only by IM in both 2006 and 2007, and explained 11.2% and 8.8% of the total phenotypic variations, respectively. A major QTL, *qAC8*, was detected consistently for two years and explained 27.4% and 34.0% of the total phenotypic variation in the CIM, respectively. An additional QTL, *qAC11*, explained 8.4% of the total phenotypic variation but was detected only in 2007. Chucheongbyeo alleles for *qAC7*, *qAC8* and *qAC11* were found to be associated with an amylose content increased. For the PC trait, two QTLs, *qPC1* and *qPC8*, were detected on chromosomes 1 and 8. A further QTL, *qPC1*, was identified in the interval between RM486 to RM8049 in both years. This QTL explained 17.2% and 16.0% of the total phenotypic variations in 2006 and 2007, respectively. The QTL *qPC8* was effective in both the IM and CIM analysis in 2006, but detectable in only the IM in 2007. This QTL was found to explain 15.3% and 11.1% of total phenotypic variation in the IM analysis in both years. For these

**Table 3.** QTLs for six traits related to eating quality detected in 190 *japonica* RILs

| Trait | QTLs | Year | Chr. | Flanked marker | Interval mapping | | | Composite interval mapping | | | Threshold[a/] | Positive parent[b/] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | LOD | RSq (%) | Add. | LOD | RSq (%) | Add. | | |
| DTH | *qDH6* | 2006 | 6 | RM190- | 5.19 | 13.0 | 1.65 | 16.23 | 27.3 | 2.45 | 3.0 | S |
| | | 2007 | | RM3370 | 4.22 | 10.6 | 1.73 | 15.09 | 25.3 | 2.72 | 3.0 | |
| | *qDH6* | 2006 | 6 | RM190- | 5.19 | 13.0 | 1.65 | 16.23 | 27.3 | 2.45 | 3.0 | S |
| | | 2007 | | RM3370 | 4.22 | 10.6 | 1.73 | 15.09 | 25.3 | 2.72 | 3.0 | |
| | *qDH8* | 2006 | 8 | RM5556- | 10.8 | 36.0 | 2.72 | 18.26 | 34.9 | 2.72 | 3.0 | C |
| | | 2007 | | RM547 | 11.39 | 31.9 | 2.97 | 19.63 | 35.5 | 3.19 | 3.0 | |
| | *qDH11.1* | 2006 | 11 | RM1761- | 3.87 | 13.0 | 1.64 | 6.87 | 12.0 | 1.61 | 3.0 | C |
| | | 2007 | | RM332 | 3.34 | 10.1 | 1.67 | 3.56 | 5.4 | 1.29 | 3.0 | |
| | *qDH11.2* | 2006 | 11 | RM5857- | - | - | - | 3.19 | 7.8 | 1.37 | 3.0 | C |
| | | 2007 | | RM229 | - | - | - | 7.15 | 20.0 | 2.45 | 3.0 | |
| ADV | *qADV6* | 2006 | 6 | RM589- | 8.60 | 20.2 | 0.09 | 17.22 | 27.4 | 0.10 | 2.8 | S |
| | | 2007 | | RM253 | 3.14 | 7.9 | 0.05 | 6.44 | 12.4 | 0.07 | 3.0 | |
| | *qADV7* | 2007 | 7 | RM234- RM5720 | 3.60 | 8.3 | 0.06 | - | - | - | 3.0 | C |
| | *qADV8* | 2006 | 8 | RM5556- | 9.14 | 32.6 | 0.11 | 15.25 | 32.6 | 0.11 | 2.8 | C |
| | | 2007 | | RM547 | 4.06 | 11.9 | 0.06 | 6.11 | 13.6 | 0.07 | 3.0 | |
| | *qADV11* | 2006 | 11 | RM5857- RM229 | - | - | - | 3.55 | 9.8 | 0.06 | 2.8 | C |
| AC | *qAC6.1* | 2007 | 6 | RM589- RM253 | 2.65 | 6.6 | 0.25 | 7.65 | 12.3 | 0.46 | 2.8 | S |
| | *qAC6.2* | 2006 | 6 | RM50- RM539 | 2.66 | 6.8 | 0.25 | 3.35 | 6.3 | 0.19 | 2.9 | C |
| | *qAC7* | 2006 | 7 | RM3555- | 4.75 | 11.2 | 0.32 | 2.07 | 3.3 | 0.18 | 2.9 | C |
| | | 2007 | | RM5720 | 3.38 | 8.8 | 0.37 | - | - | - | 2.8 | |
| | *qAC8* | 2006 | 8 | RM5556- | 10.50 | 39.8 | 0.52 | 10.55 | 27.4 | 0.51 | 2.9 | C |
| | | 2007 | | RM547 | 10.15 | 29.7 | 0.68 | 14.60 | 34.0 | 0.74 | 2.8 | |
| | *qAC11* | 2007 | 11 | RM1761- RM552 | 2.88 | 9.5 | 0.39 | 3.88 | 8.4 | 0.37 | 2.8 | C |
| PC | *qPC1* | 2006 | 1 | RM486- | 4.42 | 11.6 | 0.19 | 6.35 | 17.0 | 0.23 | 3.1 | S |
| | | 2007 | | RM8049 | 7.03 | 20.7 | 0.28 | 7.64 | 18.4 | 0.29 | 2.9 | |
| | *qPC8* | 2006 | 8 | RM5556- | 4.38 | 15.3 | 0.19 | 4.92 | 13.7 | 0.18 | 2.8 | S |
| | | 2007 | | RM547 | 2.98 | 11.1 | 0.19 | - | - | - | 3.1 | |
| GCR | *qGCR4* | 2007 | 4 | RM2441- RM5709 | 1.83 | 5.8 | 0.89 | 5.14 | 10.6 | 1.22 | 3.0 | S |
| | *qGCR6* | 2006 | 6 | RM589- | 3.80 | 9.8 | 1.25 | 7.90 | 17.6 | 1.69 | 3.1 | S |
| | | 2007 | | RM253 | - | - | - | 3.80 | 6.5 | 0.96 | | |
| | *qGCR7* | 2006 | 7 | RM8261- | 6.04 | 14.1 | 1.50 | - | - | - | 3.1 | C |
| | | 2007 | | RM3555 | 4.09 | 9.9 | 1.17 | - | - | - | 3.0 | |
| | *qGCR8* | 2006 | 8 | RM5556- | 11.44 | 31.2 | 2.20 | 14.44 | 32.9 | 2.28 | 3.1 | C |
| | | 2007 | | RM547 | 9.87 | 22.4 | 1.74 | 10.92 | 19.2 | 1.68 | 3.1 | |
| ST | *qST8* | 2007 | 8 | RM5556- RM547 | 8.98 | 26.1 | 0.32 | 8.52 | 16.3 | 0.26 | 2.9 | C |
| OE | *qOE8* | 2007 | 8 | RM5556- RM547 | 8.39 | 24.4 | 0.35 | 8.13 | 15.8 | 0.29 | 3.0 | C |

[a/]Significance at the 0.05 level
[b/]S, Suweon365; C, Chucheongbyeo

QTLs, the Suweon365 allele was associated with the protein content increased.

For the GCR measurements, four QTLs were detected on chromosomes 4, 6, 7, and 8. The QTL *qGCR4* was detected in 2007, and explained 10.6% of the total phenotypic variations in the CIM. The *qGCR6* QTL detected in the region of the *wx* gene on chromosome 6 was identified in both years in the CIM, and explained 17.6% and 6.5% of the total phenotypic variations in 2006 and 2007, respectively. The *qGCR7* QTL explained 14.1% and 9.9% of the total phenotypic variations at the RM8261-RM3555 interval by IM only in both the years. The *qGCR8* QTL was detected in the RM5556-RM547 region, and explained 32.9% and 19.2% of the total phenotypic variations by CIM in 2006 and 2007, respectively (Table 3). The QTLs,

**Table 4.** Glossiness of cooked rice determined by the Toyo-taste meter in three QTL-NILs

| Lines[a/] | Genotype on QTLs | | | 2007 | | 2008 | |
|---|---|---|---|---|---|---|---|
| | *qGCR6* | *qGCR7* | *qGCR8* | GCR | OE | GCR | OE |
| SCQ04 | CC | SS | CC | 80.5 | 0.2 | 79.8 | 0.2 |
| SCQ07 | SS | CC | SS | 75.8 | -0.4 | 73.3 | -0.2 |
| SCQ14 | CC | SS | SS | 66.2 | -1.4 | 68.3 | -1.2 |
| Suweon365 | | | | 67.1 | -1.2 | 64.6 | -1.0 |
| Chucheongbyeo | | | | 75.8 | 0.0 | 74.5 | 0.0 |

[a/] $BC_3F_4$ in 2007 and $BC_3F_5$ in 2008 from a Suweon365*4 /Chucheongbyeo

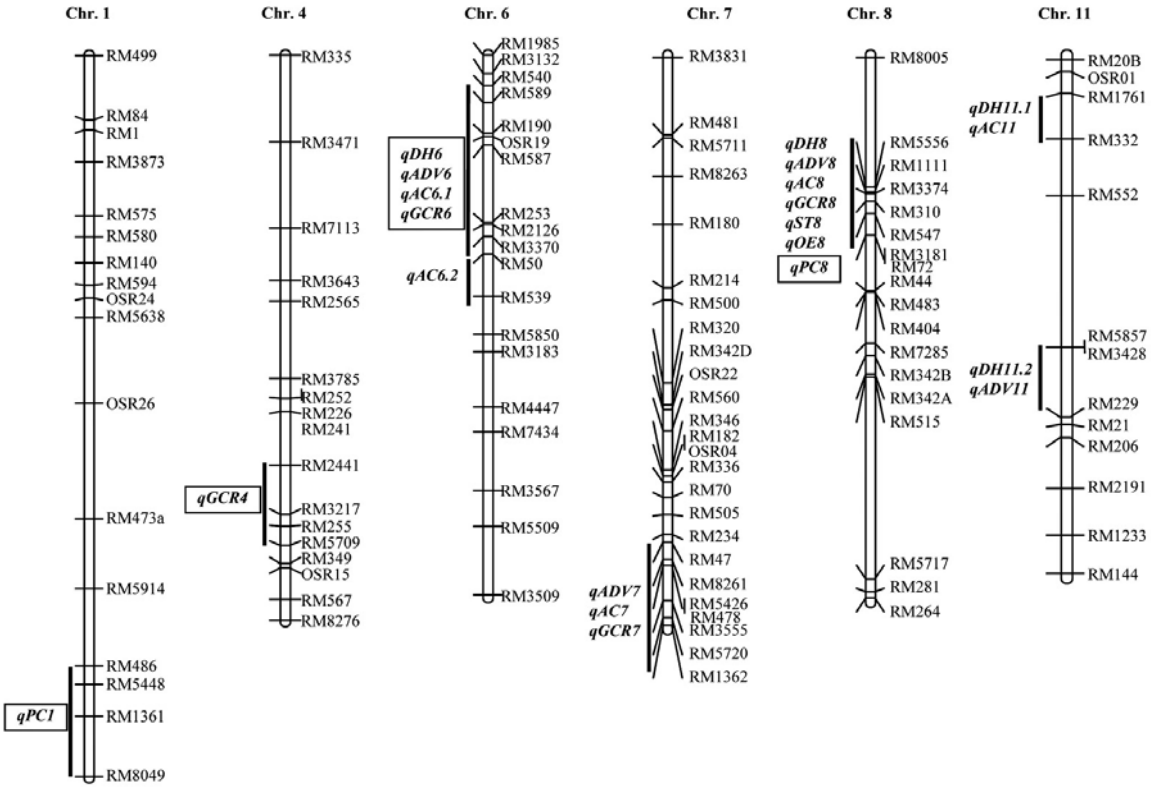


**Fig. 3.** Chromosomal locations of the QTLs for days to heading and six eating quality properties. The boxed QTLs are from the Suweon365 allele. Non-boxed QTLs are from the Chucheongbyeo allele.

*qGCR4* and *qGCR6*, were associated with an increased GCR by the Suwon365 allele, while the Chucheongbyeo allele was associated with an increased GCR by the two QTLs, *qGCR7* and *qGCR8*. For the ST and OE measurements in 2007, the QTLs *qST8* and *qOE8* were detected at the same region in the RM5556 and RM547 interval on chromosome 8. These QTLs explained 16.3% and 15.8% of the total phenotypic variation in the CIM analysis, respectively. The Chucheongbyeo allele at these QTLs on chromosome 8 increased the ST and OE.

**Validation of QTLs for the GCR of cooked rice and physicochemical properties using the QTL-NIL population**

Three QTL-NILs of $BC_3F_4$ were developed in 2007 and of $BC_3F_5$ in 2008 from a Suweon365*4/Chucheongbyeo cross based on the MAS using SSR markers (RM589, RM190, RM587 and RM253 on chromosome 6; RM8261, RM3555, and RM5720 on chromosome 7; RM5556, RM3374, and RM547 on chromosome 8). These QTL-NILs were evaluated for GCR and OE to confirm the QTL effects (Table 4). The SCQ4 line harboring Chucheongbyeo (CC) alleles at *qGCR6* and *qGCR8* and the Suweon365 (SS) allele at *qGCR7* had GCR and OE scores of 80.5 and 0.2 in 2007 and 79.8 and 0.2 in 2008, respectively, which were higher than the donor Chucheongbyeo parent. The SCQ7 line with Chucheongbyeo alleles at *qGCR7* showed GCR and OE scores of 75.8 and -0.4 in 2007 and 73.3 and -0.2 in 2008, respectively. The line SCQ14 with the CC allele only at *qGCR6* showed similar GCR and OE values to the Suweon365 parent in both years. These QTL data indicated that the Chucheongbyeo alleles at *qGCR6* decreased the GCR and those at *qGCR7* and *qGCR8* increase the GCR (Table 3 and Fig. 3). Similarly, the glossiness and overall evaluation of cooked rice of the line SCQ4 were better than those of the Chucheongbyeo parent.

The physicochemical properties of endosperm starch and eating quality of cooked rice associated with three QTL-NILs were evaluated in 2009 (Table 5). The ADV values of three

**Table 5.** Physicochemical properties of endosperm starch and eating quality of cooked rice in three QTL-NILs (2009)

| Lines[a/] | ADV (1-7) | Protein (%) | Amylose (%) | Core/valley (0-7). | Translucency (1-9). | GCR. | Sensory test | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | GL | ST | HD | OE |
| SCQ04 | 6.6 | 6.2 | 17.9 | 0/1 | 1 | 78.8 | 0.0 | 0.2 | -0.2 | -0.2 |
| SCQ07 | 6.6 | 6.8 | 18.9 | 0/1 | 1 | 74.5 | -0.4 | -0.2 | 0.2 | -0.6 |
| SCQ14 | 6.5 | 6.2 | 18.1 | 1/1 | 1 | 64.3 | -0.6 | -1.0 | -0.5 | -0.8 |
| Chucheongbyeo | 6.8 | 5.9 | 16.5 | 0/0 | 1 | 74.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Suweon365 | 6.3 | 6.9 | 19.9 | 1/0 | 1 | 66.5 | -1.2 | -1.2 | -0.7 | -1.0 |

[a/]Three QTL-NILs are $BC_3F_6$ from a Suweon365*4/Chucheongbyeo.

**Table 6.** Effects of GCR-QTLs from Chucheongbyeo when introduced into Palgongbyeo and Hopyeongbyeo varieties (2009).

| Lines[a/] | QTLs[b/] | | | Gen. | No. of line[c/] | GCR | |
|---|---|---|---|---|---|---|---|
| | *qGCR6* | *qGCR7* | *qGCR8* | | | Mean | Range |
| Palgongbyeo*2/SR23577-$F_{12}$-17 | PP | CC | CC | $BC_1F_3$ | 4(3) | 78.8 | 69.7-84.8 |
| Palgongbyeo*2/SR23577-$F_{12}$-100 | PP | PP | CC | 〃 | 12(6) | 71.8 | 63.7-80.5 |
| Palgongbyeo*2/SR23577-$F_{12}$108 | SS | CC | PP | 〃 | 10(2) | 68.9 | 65.0-78.2 |
| Palgongbyeo*2/SR23577-$F_{12}$118 | PP | CC | CC | 〃 | 17(9) | 72.9 | 64.1-79.4 |
| Palgongbyeo*2/SR23577-$F_{12}$147 | SS | CC | CC | 〃 | 8(2) | 68.4 | 62.9-74.6 |
| Palgongbyeo*2/SR23577-$F_{12}$154 | SS | CC | CC | 〃 | 5(3) | 73.2 | 68.2-76.8 |
| Palgongbyeo*2/SR23577-$F_{12}$196 | PP | PP | CC | 〃 | 18(8) | 72.7 | 65.8-81.2 |
| Hopyeongbyeo*2/SR23577-$F_{12}$-17 | HH | CC | CC | 〃 | 16(12) | 79.8 | 69.7-88.7 |
| Chucheongbyeo | CC | CC | CC | | | 72.4 | |
| Suweon365 | SS | SS | SS | | | 66.5 | |
| Palgongbyeo | PP | PP | PP | | | 64.5 | |
| Hopyeongbyeo | HH | HH | HH | | | 73.6 | |

[a/]SR23577 is the number of a cross between Suweon365 and Chucheongbyeo.
[b/]CC, Chucheongbyeo; HH, Hopyeongbyeo; PP, Palgongbyeo; SS, Suweon365.
[c/]The numbers in the parentheses indicate the number of lines that had higher GCR values than that of Chucheongbyeo.

lines were similar to the mean values of the Chucheongbyeo and Suweon365 parents. The PC of SCQ7 was higher than that of the recurrent parent Suweon365. The amylose contents of three QTL-NILs were 17.9-18.9%, which were lower than the recurrent parent Suweon365 (19.9%), but higher than Chucheongbyeo (16.5%). The GCR scores of the QTL-NILs exhibited a similar pattern to the previous results confirming the effects of these QTLs. However, the OE of the QTL-NILs differed from 2007 to 2008, may be attributed to its inconsistency (Lestari et al., 2009).

**QTL effects on the GCR in two japonica varieties**

The QTL effects were analyzed using 90 $BC_1F_3$ lines which were developed from eight cross combinations between seven RILs harboring *qGCR7* and *qGCR8*, and the Palgongbyeo or Hopyeongbyeo alleles. The backcrossed lines were genotyped using the same markers listed in Table 4 for the two QTLs, *qGCR7* and *qGCR8* (Table 6). The GCRs of Palgongbyeo and Hopyeongbyeo were measured at 64.5 and 73.6, respectively. The mean GCR values of the $BC_1F_3$ lines in seven cross combinations with Palgongbyeo were 68.4 to 78.8, and the range was 62.9 to 84.8. Thirty three lines out of 74 derived from cross combinations with Palgongbyeo had higher GCR values than that of Chucheongbyeo (72.4). The mean GCR score of 16 lines derived from cross combinations with Hopyeongbyeo was 79.8 (range 69.7-88.7). Twelve out of 16 lines had a higher GCR values than that of Hopyeongbyeo (73.6).

## DISCUSSION

Eating quality is an important trait in *japonica* rice breeding in Korea. However, this trait is usually evaluated using a sensory test and needs to be done in advanced breeding generations ($F_6$ or later), which is both time consuming and labor intensive. Other selection methods, using as the measurement of physicochemical properties such as the ADV, AC, PC and gel consistency, have been used to evaluate eating quality indirectly (Bao et al., 2000; Kobayashi and Tomita, 2008; Li et al., 2003; Tanaka et al., 2006; Wada et al., 2006). Several studies have identified QTLs for such physicochemical properties and also for the eating quality of cooked rice using *indica*/*japonica* cross populations (Bao et al., 2000; Li et al., 2003; Ogata et al., 1996; Otsuki et al., 1997; Takeuchi et al., 2007; Wan et al., 2004). However, few studies have identified QTLs related to eating quality in the same manner in *japonica*/*japonica* cross populations (Kobayashi and Tomita, 2008; Takeuchi et al., 2007, 2008; Tanaka et al., 2006; Wada et al., 2006; 2008).

In this study, we identified 21 QTLs in seven regions on chromosomes 1, 4, 6, 7, 8 and 11 for seven traits (Table 3, Fig. 3). Of these, three QTL blocks on chromosomes 6, 7 and 8 were detected in which several QTLs for eating quality components were found to be clustered together. These QTLs were consistently detected in two RILs derived from the crosses of Moritawase/Koshihikari (Wada et al., 2008) and Sakihikari/Nipponbare (Kobayash and Tomita, 2008) over two years, sug-

gesting that they are stably expressed under different environmental conditions. Three QTLs, *qADV6*, *qAC6.1* and *qGCR6* mapped to the terminal region of the short arm of chromosome 6, corresponding to the *wx* locus (Harushima et al., 1998; Tan et al., 1999; Wan et al., 2004). This region includes important genes for good eating quality as revealed by several previous studies which have identified QTLs for eating quality near this region (Bao et al., 2000; Kobayashi and Tomita, 2008; Li et al., 2003; Suh et al., 2004; Takeuchi et al., 2007; Tanaka et al., 2006; Wada et al., 2006; Wan et al., 2004). In addition, there are several starch synthase-related genes on the short arm of chromosome 6, including *waxy* (Juliano, 1985; Sano, 1984), *starch synthase I* (Baba et al., 1993; Tanaka et al., 1995), and *starch synthase IIa* (Umemoto et al., 2002). Interestingly, Suweon365 alleles for these QTLs were found to be associated with an increased eating quality, although the Suweon365 variety has a relatively poorer eating quality than Chucheongbyeo. The *qDH6* QTL for heading date was also identified in this region. Since the ADV and AC traits in rice correlate with the temperature during the maturation period, they may be altered by the heading dates (Asaoka et al., 1985). In our analyses, the correlations between ADV and AC, and ADV and DH were highly significant in both 2006 and 2007. Moreover, the *qDH6* QTL coincides with *Hd-3* (Yamamoto et al., 1998).

A region containing three QTLs, *qADV7*, *qAC7* and *qGCR7*, was found to be located in a 95-100 cM region of the long arm on chromosome 7. Interestingly, these QTLs were only identified by interval mapping in 2007 for ADV; however AC and GCR for both 2006 and 2007 explained 8.3-14.1% of total phenotypic variation due to Chucheongbyeo alleles. These are thus minor QTLs that are significantly affected by the cultivation conditions and the environment. However, these QTLs are not linked with those for DH. Two candidate genes, sucrose synthase 3 (*S3*) and trehalose phosphatase (*Tre*), which is thought to be related to eating quality were identified in this QTL region previously (Lestari et al., 2009). Several QTLs for rice quality have also been reported within the same region (Kobayashi and Tomita, 2008; Suh et al., 2004).

A region containing five QTLs, *qADV8*, *qAC8*, *qGCR8*, *qST8* and *qOE8* was identified at RM5556-RM547 (36-40.2 cM), which is near to the centromeric region on chromosome 8. A QTL for PC, *qPC8*, was also identified in the same region, in which the Suweon365 allele was found to be associated with an increased PC. In general, high protein content is one of the reasons for poor eating quality as it increases the hardness of cooked rice (Yu et al., 2008). Chucheongbyeo allele at *qPC8* is associated with the protein content decreased and thus has a positive effect on good eating quality. In addition, *qDH8* QTL for days to heading was detected in this region as a major QTL that accounted for over 30% of the total phenotypic variation in both years under study. In previous studies, a heading date QTL *qHd-5* (Yamamoto et al., 1998) and several others QTLs that affect rice quality (Kobayashi and Tomita, 2008; Wan et al., 2004) have been reported within the same region.

A PC QTL, *qPC1*, was identified in the region RM486-RM8049 on chromosome 1, on which some QTLs for amylographic characteristics and amylose content have also been reported (Kobayashi and Tomita, 2008). Another QTL, *qGCR4*, was identified in our analyses within the region RM2441-RM5709 on chromosome 4 in 2007. Other QTLs for rice quality have been reported in this same region (Kobayashi and Tomita, 2008; Tanaka et al., 2006; Wan et al., 2004). Two QTLs *qAC11* and *qADV11* identified on chromosome 11 appear to be affected by heading date as other QTLs for this trait have been detected previously in the same region. A QTL for glossiness has also been reported by Wada et al. (2008).

Most of the QTLs identified in this study were found to be located at the same or similar chromosomal regions as previously reported QTLs, although the quality components in previous reports were not identical to those found in our current study. If most of the quality components are inter-related in terms of their phenotypic expression, this would suggest that rice quality might be controlled by a few major loci only. However, this will not be clarified until the genes responsible for each quality component are identified. In the present study, twenty-one QTLs were identified by RILs. One possibility was the existence of digenic epistatic between QTLs, especially between minor QTLs. When QTLs with large effects are segregated, it is difficult to detect QTLs with minor effects in populations such as RILs and BILs (Takeuchi et al., 2007). Futhermore, the effects of the 21 QTLs detected in the present study may not be stable over time. The environmental factors such as maturation temperature affected to the traits related with eating quality (Asaoka et al., 1985; Fan et al., 2005). The verification of epistatic relationship would be needed by further analysis of NILs for QTLs under normal, cool and hot conditions.

Three QTLs for GCR, *qGCR6, qGCR7,* and *qGCR8*, were validated by the evaluation of QTL-NILs developed through marker-assisted backcrossing. This indicates that high eating quality varieties can be developed by the accumulation of desirable alleles at each QTL through MAS. We anticipate that our present results will be helpful in future rice breeding programs for better eating quality.

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