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ORIGINAL ARTICLE

Identification of quantitative trait loci for physical and chemical properties of rice grain

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Abstract Quantitative trait loci (QTL) associated with six physical traits of cooked rice and seven chemical properties of rice grain were identified using a recombinant inbred (RI) population of rice evaluated over 3 years at the National Honam Agricultural Research Institute in Korea. The RI population consisted of 164 lines derived from a cross between Milyang23 and Gihobyeo, and the genetic map consisted of 414 molecular markers. A total of 49 QTL were identified for the 13 physico-chemical properties using composite interval mapping. Of these, 13 QTL were identified for 2 or more years, while 36 were detected in only 1 year. Five QTL were identified over all 3 years and will be useful for marker-assisted improvement of rice grain quality in Korea. The two QTL with the highest LOD scores, *adhesiveness1.2* and *potassium content7.1,* provide a valuable starting point for positional cloning of genes underlying these QTL.

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Keywords Physical property · Chemical property · Rice grain

Abbreviations
QTL Quantitative trait locus/loci
CIM Composite interval mapping

Introduction

The analysis of rice grain quality requires evaluation of at least four components, including cooking quality, eating quality, nutritional quality, and grain appearance. Each of these components is a composite trait that can be defined by specific physico-chemical properties of the grain, where the value placed on different properties is a function of cultural preference. Grain quality is a major concern of rice breeders and producers. Knowledge accumulated in the past several decades indicates that cooking and eating quality of rice grains is a major determinant of varietal acceptance and can be assayed based on five physical and chemical characteristics of the endosperm; namely, amylose content (AC) (Juliano 1985; Unnevehr et al. 1992; Webb 1980), protein content (Hsieh and Brunner 1976), gel consistency (GC) (Cagampang et al. 1973), gelatinization temperature (GT) (Little et al. 1958), and physical properties of cooked rice grain.

Eating quality is evaluated by the cohesiveness, tenderness, and volume of steamed rice, characteristics that are largely controlled by AC, GC, GT, and protein content (Bao et al. 2004; Juliano 1964, 1965, 1967, 1972). Despite the fact that levels of protein in milled rice are generally very low (i.e., between 5.8 and 9.4%), rice is the major

source of protein in many rice-consuming regions of the world. Thus, protein content is an important consideration from a nutritional perspective, though high protein levels generally have a deleterious influence on the physico-chemical properties of cooked rice (Hamaker 1994; Juliano 1993; Marshall et al. 1990; Tan et al. 2001; Yanase et al. 1984). Yanase et al. (1984) reported that rice with higher protein content was lower in adhesiveness and in water-uptake ratio, and was also associated with a decrease in the hardness, springiness, and chewiness of cooked rice. Hardness of cooked rice is also affected by the mineral and lipid contents of grain (Kim et al. 1986).

Most grain quality attributes are quantitatively inherited and show continuous variation among the segregating progeny of intervarietal crosses. It is difficult for breeders to select for quality using conventional methods due to lack of discrete phenotypic classes and the tedious and expensive methodologies for quality testing. Assessment of rice grain quality is further complicated by the triploid nature of the endosperm and the effect of environment on the expression of these traits (He et al. 1999). Early studies focused on physico-chemical and sensory evaluation of rice grain with emphasis on AC, alkali spreading value, GC, and chalkiness of the endosperm (He et al. 1999; Lanceras et al. 2000; Redona and Mackill 1998; Tan et al. 1999). More recently, researchers have identified genes and quantitative trait loci (QTL) associated with grain morphology (Fan et al. 2006; Li et al. 2004; Shomura et al. 2008; Takano-Kai et al. 2009), grain weight, and filling (Song et al. 2007; Wang et al. 2008) and cooking quality (Aluko et al. 2004; Amarawathi et al. 2008; Bao et al. 2004; Bradbury et al. 2005; Chen et al. 2006; Li et al. 2004; Liu et al. 2000; Wan et al. 2004; Zheng et al. 2008).

The well-saturated genetic and physical maps of rice (http://www.gramene.org; http://rgp.dna.affrc.go.jp) provide an important scaffold for determining the positions of genes and QTL associated with agronomically important phenotypes. QTL studies that are conducted over several years and locations provide valuable information about which regions of the genome are consistently identified with target traits, and also provide insights about G × E interaction. In rice, a comparison of QTL positions across populations and years allows researchers to develop testable hypotheses about the behavior of genetic factors underlying putative QTL. When mapping QTL that have been evaluated in different locations or years, G × E interaction is shown by variable levels of significance of QTL effects across years and/or locations (Cho et al. 2007; Hittalmani et al. 2003).

The present study utilized a mapping population of recombinant inbred lines (RIL) developed from a cross between two Korean cultivars, Milyang23 and Gihobyeo, to identify regions of the genome associated with 12 physical and chemical properties of rice grain.

Materials and methods

Plant material

A recombinant inbred (RI) population consisting of 164 F_{11} lines was developed from a cross between Milyang 23 (abbreviated as "M23", an *Indica/Japonica* derivative known as the *Tongil* type) as the maternal parent, and Gihobyeo (abbreviated as "Giho", a temperate *Japonica* type) as the paternal parent, at the National Institute of Agricultural Biotechnology in Suwon, Korea, as previously reported by Cho et al. (1998). The mapping population was developed via single-seed descent from an intercross between the genetically divergent parents Milyang 23 and Gihobyeo. F_2 plants were selfed, with generations progressing via single-seed descent (selected randomly) to the F_6 generation. F_7 seeds were planted in single rows in the field, and seeds were harvested from single plants until the F_{11} generation. DNA was extracted from F_{11} lines as the basis for map construction (Cho et al. 1998).

Crosses among *indica* and *japonica* rice varieties have been very successful in Korea, where 39 *tongil* varieties were released by the Rural Development Administration between 1970 and 1985. M23, the maternal parent, was derived from a cross between the *japonica* variety, Suwon 232, and the *indica* variety, IR24, and is considered to be inferior in grain quality within Korea, but contains many favorable genes and is frequently used as a parent in rice breeding programs. Giho, the paternal parent, is a *temperate japonica* variety developed from a cross between two *japonica* parents, Fuji 280 and BL 1. These two progenitors were known for their grain quality characteristics in accordance with Korean cultural preferences. We were interested to evaluate the segregation of traits associated with physico-chemical aspects of grain quality in this RI population.

Field trials

The F_{11}, F_{12}, and F_{13} generations of the M23 × Giho RI population were evaluated at the Honam Agricultural Research Institute (HARI) in Korea during 1995–1997. HARI is located at Iksan (36°N, 126.5°E) in the lowland region of southwestern Korea. It has an average rainfall of 1,058 mm/year and an average temperature of 22.4°C and a relative humidity of 74.4% during the rice growing season from May to September.

The M23 × Giho RI lines and their parents were cultivated in ten rows with two replications at HARI. The seeds of the RI lines and their parents were planted in the seedling nursery in mid-May. Each row consisted of 30 plants with a spacing of 15 cm between the plants and 30 cm

between rows. Fertilizer ($N–P_2O_5–K_2O$) was applied at a rate of 110, 70, and 80 kg/ha, respectively.

Evaluation for physical traits of cooked rice

Bulked seeds from each line were dehulled. Samples of brown rice were dried at 40°C for 48 h. Twenty grams of milled rice with 27 ml water were cooked for 30 min using a rice cooker (CocKoo, SR-3010, Korea). When the cooker automatically shifted to the warm setting to indicate completion of cooking, the rice was held for an additional 20 min at that setting. The mechanical adhesiveness, chewiness, hardness, springiness, gumminess, and cohesiveness of cooked rice were measured using a Texture Analyzer (Texture Analyser TA, XT plus, UK) according to standard procedures (Endo et al. 1976). The sensory evaluation and physical properties of cooked rice were defined according to Holcomb et al. (1998) as shown in Table 1. Cooked rice was tested with a maximum delay of 2 min after removing the samples from the rice cooker. The physical properties of the cooked rice were based on the force (in Newtons) required to express the cooked rice through the plunger of the Texturometer. The definitions of physical properties are as described in Table 1.

Evaluation for chemical properties of rice grain

The contents of ash, fat, amylose, protein, magnesium, and potassium were analyzed by NIR (NIR Systems 6500, USA) (Schenk and Westerhaus 1991). The alkali digestion value as an indication of GT of whole-grain rice was determined in accordance with Little et al. (1958) with minor modifications.

Table 1 Definitions of traits associated with QTL; sensory evaluation and physical properties of cooked rice (adapted from Holcomb et al. 1998)

Characters (in *g*)	Definition
Adhesiveness	The force required to remove cooked rice that adheres to serving utensils and the mouth (especially the teeth) during eating
Chewiness	Relating to the length of time required to masticate cooked rice at a constant rate of force application, to reduce it to a consistency suitable for swallowing
Hardness	The force required to compress cooked rice between the molar teeth on the first chew
Springiness	The degree to which cooked rice returns to its original shape once it has been compressed between the teeth
Gumminess	Denseness that persists throughout mastication; the energy required to disintegrate cooked rice to a state ready for swallowing. This term is a composite of hardness and cohesiveness
Cohesiveness	The internal force holding a grain together before it breaks, when compressed between the teeth

g Force in Newtons

Statistical analysis and QTL mapping

Statistical analyses of field data collected over 3 years in a single environment were conducted using the statistical package SAS (SAS Institute). Year effects were assumed to be random. Based on the variance components estimated from the mean squares in ANOVA (Cochran and Cox 1957), heritabilities (h_n^2) were calculated for physical and chemical properties (Hallauer and Miranda 1988). Correlation analyses were performed using QGene 3.06y (Nelson 1997).

Quantitative trait loci mapping was conducted on the 164 RIL using segregation data from 414 DNA markers. QTL analysis was carried out by composite interval mapping (CIM) using QTL Cartographer v2.0 (Basten et al. 1997) with automatic cofactor selections using a forward/backward regression (forward $P < 0.01$, backward $P < 0.01$). Empirical thresholds for each trait (Churchill and Doerge 1994) were developed using QGene 3.06y and QTL Cartographer 2.0 to calculate empirical LOD thresholds for CIM for each trait. These thresholds were established based on 1,000 permutations at the $P < 0.05$ and QTL identified in 2 or more years were reported. Nomenclature for QTL was as described in McCouch et al. (1997).

Results and discussion

Trait performance and correlations

As illustrated in Fig. 1, all traits showed approximately normal distributions, except for AC, and both positive and negative transgressive variation was observed. Means and variances for the 13 traits are summarized in Table 2. Significant genotype (G) and year (Y) effects were observed for all traits except cohesiveness, for which no QTL were identified (Table 3) (Hoshmand 2006). Eight of the traits, including adhesiveness, chewiness, hardness, gumminess, AC, ash content, potassium content, and magnesium content showed significant G × Y interaction, while no significant interaction was detected for springiness, cohesiveness, protein content, or fat content.

Grain chemical properties such as AC, fat content, and potassium content showed higher heritability than other traits, with values of 0.629, 0.616, and 0.672, respectively.

Correlation coefficients among traits are summarized in Table 4. The highest correlations were observed among chewiness, gumminess, and hardness, suggesting that these attributes are not independent of each other. Percent ash, percent fat, and potassium content are also correlated,

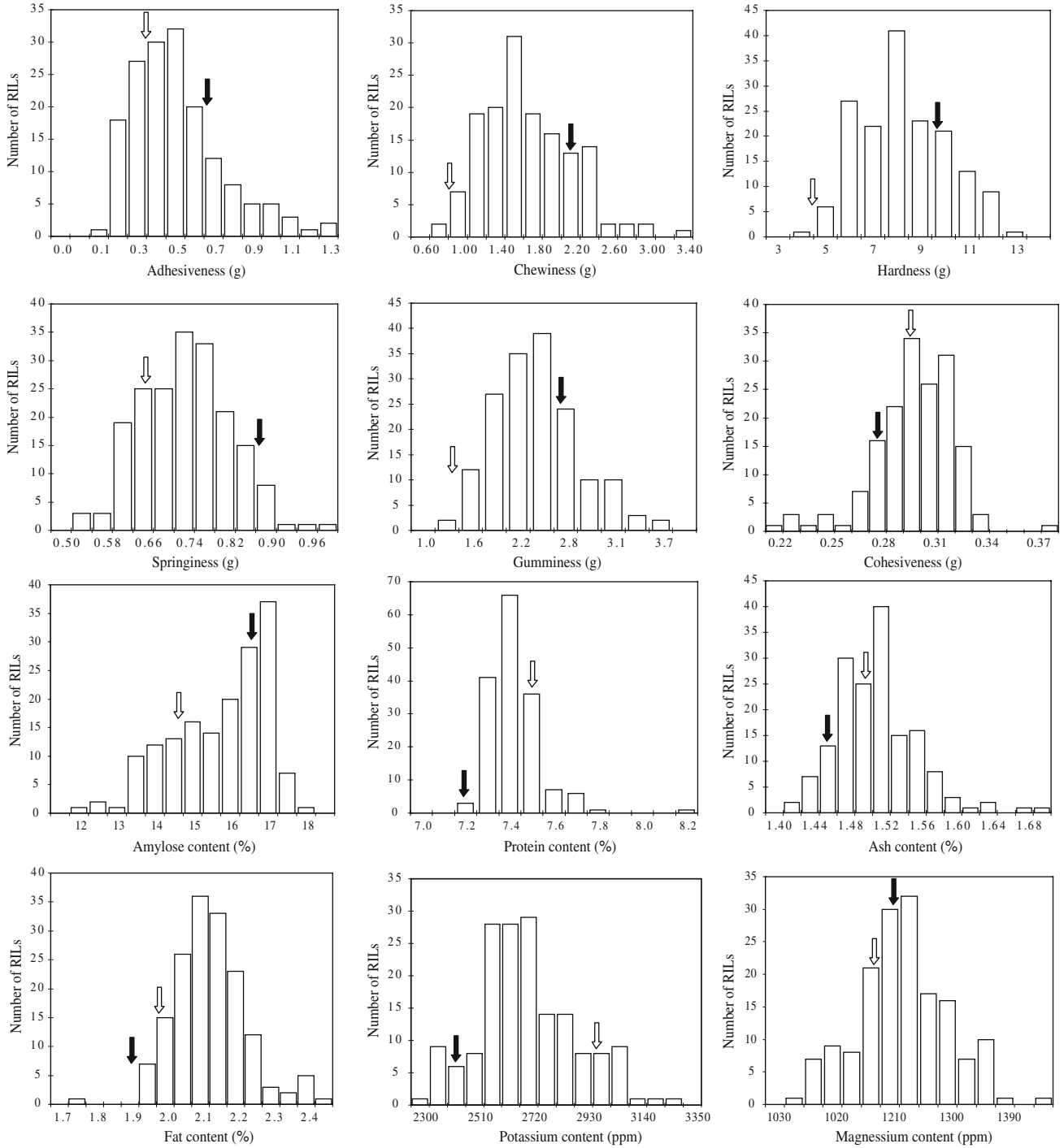


Fig. 1 Frequency distributions of 12 physical and chemical properties of rice grain in a Milyang23 × Gihobyeo RI population, summarized as mean performance over 3 years in Korea. *Black arrows* represent Milyang23 parental means, while *white arrows* indicate Gihobyeo parental means for each trait

consistent with the fact that ash is partly derived from potassium. AC was positively correlated with chewiness, gumminess, and hardness, while it was negatively correlated with percent ash, percent fat, potassium content, and protein content. On the other hand, protein content was positively correlated with adhesiveness, ash, fat, and potassium contents. This suggests that there may be a trade-off in many of the nutritionally important aspects of grain quality between amylose and protein content. These results differ from those reported by Yanase et al. (1984), who observed a negative correlation between protein content and adhesiveness.

Table 2 Means of physical and chemical properties in the Milyang23/Gihobyeo RI population

Traits	Milyang 23			Mean	Gihobyeo			Mean	RIL			Mean
	1995	1996	1997		1995	1996	1997		1995	1996	1997	
Adhesiveness (*g*)	0.39	0.41	0.40	0.40 ± 0.01	0.37	0.37	0.32	0.35 ± 0.03	0.32	0.45	0.45	0.41 ± 0.25
Chewiness (*g*)	2.33	2.39	1.89	2.20 ± 0.27	0.80	0.80	1.16	0.92 ± 0.21	1.85	1.51	1.84	1.73 ± 0.53
Hardness (*g*)	8.90	8.76	8.19	8.62 ± 0.38	4.30	4.30	5.35	4.65 ± 0.61	8.32	7.63	7.71	7.89 ± 1.88
Springiness (*g*)	0.91	0.84	0.91	0.89 ± 0.04	0.65	0.65	0.69	0.66 ± 0.02	0.72	0.69	0.79	0.73 ± 0.08
Gumminess (*g*)	2.55	3.49	2.09	2.71 ± 0.71	1.24	1.24	1.64	1.37 ± 0.23	2.52	2.20	2.25	2.32 ± 0.53
Cohesiveness (*g*)	0.29	0.29	0.26	0.28 ± 0.02	0.29	0.29	0.31	0.30 ± 0.01	0.32	0.45	0.45	0.41 ± 0.04
Alkali digestion value	5.5	5.3	6.7	5.8 ± 0.76	5.0	5.0	6.2	5.4 ± 0.69	4.8	5.8	6.6	5.7 ± 0.25
Amylose (%)	15.7	17.1	18.0	16.9 ± 1.16	13.7	15.3	15.8	14.9 ± 1.10	14.8	15.8	15.9	15.5 ± 1.33
Protein (%)	7.3	7.3	7.1	7.2 ± 0.12	7.5	7.4	7.5	7.5 ± 0.06	7.4	7.3	7.4	7.4 ± 0.15
Ash (%)	1.46	1.47	1.44	1.46 ± 0.02	1.49	1.52	1.48	1.50 ± 0.02	1.51	1.52	1.49	1.51 ± 0.05
Fat (%)	2.03	2.00	1.72	1.92 ± 0.17	2.04	2.08	1.80	1.97 ± 0.15	2.23	2.14	2.97	2.45 ± 0.10
Potassium (ppm)	2,495	2,544	2,228	2,422 ± 170	3,059	2,943	2,844	2,949 ± 108	2,638	2,703	2,680	2,674 ± 184
Magnesium (ppm)	1,321	1,242	1,075	1,213 ± 126	1,462	1,141	968	1,190 ± 251	1,370	1,247	1,044	1,220 ± 77

g Force in Newtons

Table 3 Mean squares and heritability from ANOVA of the 164 RILs combined across 3 years for 12 traits

Source	*df*	Adhe	Chew	Har	Spr	Gum	Coh	Amy	Prot	Ash	Fat	Pot	Mag
Genotype	163	0.381**	1.41**	21.24**	0.037**	1.657**	0.011 NS	10.62**	0.085**	0.0125**	0.065**	205,116**	33,168**
G × Y	326	0.124**	0.78**	8.29**	0.024 NS	0.819**	0.009 NS	1.36**	0.034 NS	0.0018**	0.015 NS	21,248**	9,849**
Pooled error	489 (483)[a]	0.078	0.49	4.84	0.021	0.456	0.0085	0.82	0.034	0.0010	0.012	13,743	6,365
Genetic VC		0.043	0.105	2.157	0.0023	0.140	0.0003	0.154	0.0086	0.0018	0.0084	30,645	3,886
Interaction VC		0.023	0.143	1.728	0.0014	0.182	0.0001	0.269	−0.0003	0.0004	0.0016	3,753	1,742
h^2		0.334	0.163	0.285	0.095	0.213	0.037	0.629	0.202	0.616	0.409	0.672	0.359

df Degrees of freedom, *NS* not significant, *VC* variance component, h^2 heritability

Adhe Adhesiveness, *Chew* chewiness, *Har* hardness, *Spr* springiness, *Gum* gumminess, *Coh* cohesiveness, *Amy* Amylose, *Prot* protein content, *Ash* ash content, *Fat* fat content, *Pot* potassium content, *Mag* magnesium content

[a] Degrees of freedom for Adhe, Chew, Har, Spr, and Gum

** $P < 0.01$

Table 4 Correlation coefficients among physical and chemical grain properties averaged over 3 years in a Milyang23/Gihobyeo RI population

Traits	Adhe	Adv	Amy	Ash	Chew	Coh	Fat	Gum	Har	Pot	Mag	Prot
Adv	−0.33**											
Amy	−0.26**	0.17*										
Ash	0.29**	−0.20*	−0.24**									
Chew	0.42**	NS	0.22**	NS								
Coh	−0.32**	NS	NS	−0.17*	NS							
Fat	0.27**	−0.21**	−0.36**	0.84**	NS	NS						
Gum	0.39**	NS	0.26**	NS	0.88**	NS	NS					
Har	0.54**	NS	0.22**	NS	0.87**	−0.26**	NS	0.94**				
Pot	0.44**	−0.32**	−0.52**	0.82**	NS	−0.20**	0.74**	NS	NS			
Mag	−0.19*	NS	NS	−0.40**	NS	NS	−0.27**	NS	NS	−0.36**		
Prot	0.17*	−0.15*	−0.26**	0.55**	NS	NS	0.49**	NS	NS	0.52**	NS	
Spr	0.53**	NS	NS	NS	0.66**	−0.29**	NS	0.52**	0.67**	NS	NS	NS

Adhe Adhesiveness, *Adv* alkali digestion value, *Amy* amylose content, *Ash* ash content, *Chew* chewiness, *Coh* cohesiveness, *Fat* fat content, *Gum* gumminess, *Har* hardness, *Pot* potassium content, *Mag* magnesium content, *Prot* protein content, *Spr* springiness, *NS* not significant

** $P < 0.01$; * $P < 0.05$

QTL analysis by CIM

A total of 49 QTL were detected at or below $P < 0.05$ for the 12 traits (Table 5; Figs. 2 and 3). Thirteen QTL were identified in two or more years, while 36 QTL were detected in only 1 year. Five QTL associated with four traits, adhesiveness (*adhe1.2*), AC (*amy7.1*), % fat (*fat7.2*), and potassium content (*pot 7.1* and *pot8.1*) were identified in all 3 years.

Physical properties of cooked rice

Adhesiveness (adhe)

Three QTL on two chromosomes were significantly associated with adhesiveness (*adhe1.1, adhe1.2,* and *adhe7.1*) and are the first reported QTL for adhesiveness of cooked rice. The most significant, *adhe1.2*, had a LOD of 9.69 and an R^2 value of 0.208 and was detected in all 3 years and the grand mean (GM). The markers defining this QTL, RZ14 and RM14, provide breeders with a tool to select for specific adhesiveness properties and also offer a valuable starting point for map-based cloning of genes underlying this trait.

Chewiness (chew)

Two QTL on chromosome 4, *chew4.1* and *chew4.2,* were significantly associated with chewiness and are the first reported QTL for chewiness of cooked rice.

Gumminess (gum)

Three QTL on two chromosomes were identified for gumminess. *gum4.1* and *gum4.2* were detected in the same positions on chromosome 4 as *chew4.1* and *chew4.2*. These are the first reported QTL for gumminess of cooked rice.

Hardness (har)

Two QTL, *har4.1* and *har5.1* on chromosome 4 and 5, were significantly associated with hardness of cooked rice. The M23 allele increased hardness by 1.08 *g* ($R^2 = 0.12$).

Springiness (spr)

A single QTL near the centromere on chromosome 8 was identified for springiness and is the first reported QTL for springiness of cooked rice.

Alkali digestion value (adv)

While there was little phenotypic difference between the parents (both had intermediate to low *adv*), four QTL on three chromosomes were identified for alkali digestion value. *adv4.1* was detected in 2 years, while the other three QTL were each detected in a different year. M23 alleles at *adv1.1* and *adv4.1* slowed down the alkali digestion of rice grain in potassium hydroxide solution, while M23 alleles speeded up alkali digestion at both QTL on chromosome 3. *adv3.1* was in the same position as a QTL detected by Aluko et al. (2004) for AC.

Chemical properties of rice grain

Amylose content (amy)

Six QTL on four chromosomes were associated with AC (Table 5; Figs. 2, 3). M23 alleles at *amy1.1, amy7.1*, and

Table 5 QTL identified for nutritional and physical properties of rice over 3 years

QTL	Chromosome	Markers bordering QTL	CIM[a]		Additive effect[c]	Year and GM
			LOD	R^2	CIM	
Adhesiveness (adhe)			3.28[b]			
adhe1.1	1	RG140-RM243	3.68	0.075[d]	0.074	1997[e]
adhe1.2	1	RG317-RM14	9.69	0.208	0.219	1995, 1996, 1997, GM
adhe7.1	7	C507-E25M48.143P2	3.73	0.091	−0.076	1996, 1997, GM
Chewiness (chew)			3.17			
chew4.1	4	E25M59.186P2-RZ740	3.61	0.081	0.241	1995
chew4.2	4	RG620-RG143	5.04	0.118	−0.083	1995, 1996
Gumminess (gum)			3.20			
gum4.1	4	E25M59.186P2-RZ740	5.63	0.125	0.348	1995
gum4.2	4	RG620-RG143	5.41	0.122	−0.086	1995
gum5.1	5	E25M48.219P2-RCD511	3.92	0.083	0.155	1996, GM
Hardness (har)			3.19			
har4.1	4	E25M59.186P2-RM241	5.18	0.124	1.080	1995, GM
har5.1	5	E25M48.219P2-RCD511	3.62	0.081	0.555	1996, GM
Springiness (spr)			3.19			
spr8.1	8	E13M59.152P2-E26M49.158P1	5.15	0.113	0.026	1997, GM
Alkali digestion value (adv)			3.12			
adv1.1	1	C161-RG1028	4.09	0.087	−0.235	1995
adv3.1	3	RG100-RG369	3.24	0.071	0.229	1996
adv3.2	3	RZ745-RZ575	3.46	0.075	0.217	1997
adv4.1	4	RG396B-RZ69	3.50	0.070	−0.094	1995, 1997
Amylose content (amy)			3.11			
amy1.1	1	C161-RG1028	3.60	0.075	−0.483	1995
amy7.1	7	C285-E26M47.213P2	3.24	0.071	−0.381	GM
amy7.2	7	ESTI-4-C507	7.34	0.163	0.582	1995, 1996, 1997, GM
amy10.1	10	E13M59.517P1-RG323	3.68	0.106	0.447	GM
amy10.2	10	E26M47.166P1-CDO94	3.65	0.082	0.382	1997, GM
amy11.1	11	E23M50.M003P2-RG118	3.18	0.087	−0.426	1996
Protein content (prot)			3.02			
prot1.1	1	E13M60.294P2-E26M47.356P2	3.45	0.073	−0.024	1996
prot2.1	2	E13M59.M003P2-G1184B	4.18	0.091	−0.047	1995
prot4.1	4	RZ569B-RG143	4.43	0.133	−0.052	1995
prot6.1	6	RG213-E13M59.270P1	40.1	0.669	−0.995	1997, GM
Ash content (ash)			3.24			
ash1.1	1	RG1028-RM1	4.27	0.077	0.013	1995, 1996
ash1.2	1	RM5-RG462	3.85	0.081	−0.014	1996, GM
ash1.3	1	RG317-RZ14	5.77	0.133	0.017	1996, 1997, GM
ash6.1	6	RG213-E13M59.270P1	4.75	0.281	−0.107	1997
ash7.1	7	E26M47.213P2-RG711	4.93	0.123	−0.016	1996
ash7.2	7	b-Amy-C507	6.31	0.142	−0.019	1995, 1997, GM
ash8.1	8	G1073A-RM210	3.29	0.071	0.014	1995, GM
Fat content: (fat)			3.17			
fat1.1	1	RG317-RZ14	6.76	0.142	0.040	1996
fat4.1	4	E23M50.340P1-RG329	3.72	0.100	−0.033	1995, GM
fat7.1	7	E26M47.213P2-RG711	4.65	0.126	−0.037	1996, GM
fat7.2	7	b-Amy-C507	5.46	0.118	−0.031	1995, 1996, 1997, GM
fat8.1	8	G1073A-RM210	3.71	0.087	0.036	1995

Table 5 continued

QTL	Chromosome	Markers bordering QTL	CIM[a]		Additive effect[c]	Year and GM
			LOD	R^2	CIM	
Potassium content (pot)			3.12			
pot1.1	1	C161-RM84	4.31	0.070	65.56	1995, 1996, GM
pot1.2	1	RG140-ESTI-1	3.12	0.061	61.20	1995
pot1.3	1	RM5-RG303	3.20	0.063	−43.96	1996
pot2.1	2	E23M50.160P1-RM6	3.70	0.056	−45.44	1997, GM
pot4.1	4	RG214-RG161	4.89	0.081	−69.42	1995, GM
pot7.1	7	RG156-C507	11.28	0.196	−83.00	1995, 1996, 1997, GM
pot8.1	8	RM33-RM210	4.16	0.074	51.70	1995, 1996, 1997, GM
Magnesium content (mag)			3.17			
mag2.1	2	E23M50.160P1-E13M59.296P1	5.58	0.128	31.07	1995, GM
mag3.1	3	E25M59.156P1-E26M47.104P2	3.26	0.069	−25.82	1995
mag3.2	3	E24M50.159P2-RZ575	4.88	0.124	37.38	1996, GM
mag8.1	8	RG20-RG885	3.57	0.087	−28.27	1996, GM
mag9.1	9	C397-RM257	6.68	0.147	29.28	1996, 1997, GM

[a] The empirical significance thresholds (underlined) for declaring putative QTL were determined for each trait based on 1,000 permutations at the $P < 0.05$ and $P < 0.01$ significance levels and represent the average across 3 years

[b] LOD and R^2 shown are the highest if QTL detected in more than 1 year

[c] *Additive effect* Positive value indicates that the increasing allele originates in Milyang23

[d] Represent the phenotypic effects for specific QTL

[e] Underlined years correspond to the highest LOD and R^2 values

amy11.1 decreased AC in the RIL, while M23 alleles at *amy7.2, amy10.1*, and *amy10.2* increased the AC of the grain. *amy7.2* was detected in all 3 years and GM, and was the most significant of the QTL for this trait (LOD = 7.34; $R^2 = 0.16$).

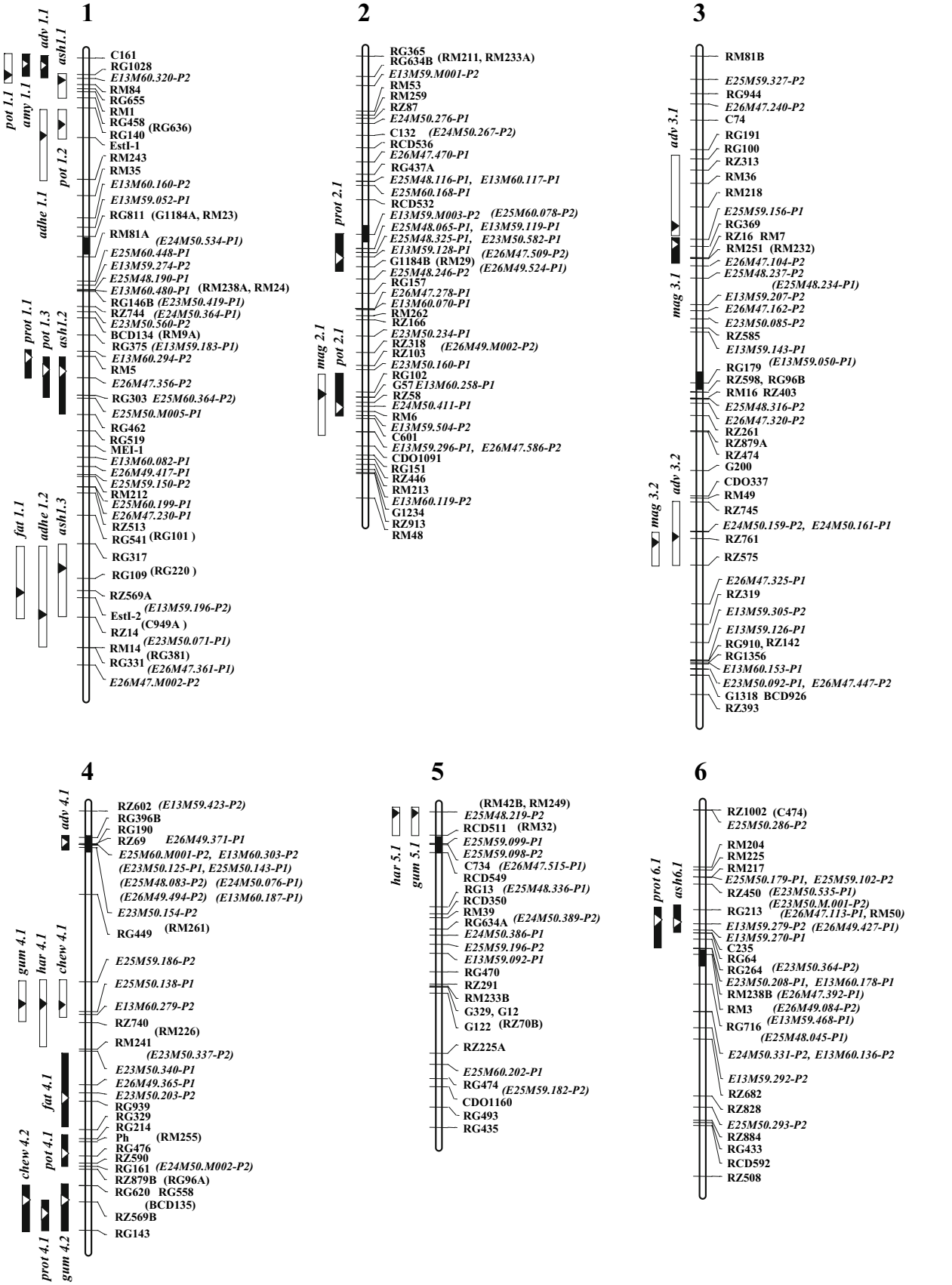
The apparent AC is a major determinant of eating and cooking quality of rice (Juliano 1972). It directly affects water absorption and volume expansion during cooking. Rice grains with medium (20–26%) or high AC (>26%) result in relatively dry, separate and flaky cooked grains, while low amylose rice grains (10–20%) are more tender and sticky when they are cooked. Variation for this trait is largely associated with a single major gene, *Waxy*, with modifications associated with minor genes (Kumar and Khush 1988; McKenzie and Rutger 1983). Particular attention in this study was given to three chromosomal regions known to contain genes associated with starch quality. One region was near the distal end of the short arm of chromosome 6 where the *Waxy* gene is located. This region has been previously known to be associated with AC (Aluko et al. 2004; Tan et al. 1999; Zheng et al. 2008) and GC (Tan et al. 1999). The second region was the distal end of the long arm of chromosome 6 where the starch branching enzyme *I* (Q-enzyme *I*) is located (Harrington et al. 1997). The third region was on the short arm near the centromere of chromosome 2 (Harushima et al. 1998) where the starch branching enzyme *III* (Q-enzyme *III*) is located (Nakamura and Yamanouchi 1992; Nakamura et al. 1994). No significant QTL were detected in any of the regions containing these candidate genes, while five minor QTL were associated with AC in this study. This is likely due to the fact that both parents have similar AC (16.9% for M23 and 14.9% for Giho) and are likely to share similar alleles at the major loci associated with *Waxy* and Q-enzymes *I* and *III*.

Fig. 2 QTL associated with chromosomes 1–6 for 12 physical and nutritional properties of rice analyzed in the Milyang23 × Gihobyeo RI population (164 lines). Marker locations and distances are the same as in Cho et al. (1998); centromeres are indicated by *black bars* on each chromosome. *Filled white boxes* with a *black triangle* indicate increased effects from Milyang23 and *black boxes* with a *white triangle* indicate increased effects from Gihobyeo. The peak of the QTL interval plot is indicated by a *triangle*. The QTL boundaries are defined by the closest flanking markers that reach the empirically determined significance threshold for each trait ($P < 0.05$) ▶

Protein content (prot)

Four QTL were identified for protein content, but each was detected in only 1 year. The QTL with the largest effect was *prot6.1* (LOD = 40.1; $R^2 = 0.67$) with enhanced protein content coming from Gihobyeo. The environmental conditions responsible for its effect are unknown.

In a previous study, Aluko et al. (2004) identified four QTL associated with protein content, and *pro1*


1
pot 1.1
amy 1.1
adv 1.1
ash1.1
adhe 1.1
pot 1.2
C161
RG1028
E13M60.320-P2
RM84
RG655
RM1
RG458 (RG636)
RG140
EstI-1
RM243
RM35
E13M60.160-P2
E13M59.052-P1
RG811 (G1184A, RM23)
RM81A (E24M50.534-P1)
E25M60.448-P1
E13M59.274-P2
E25M48.190-P1
E13M60.480-P1 (RM238A, RM24)
RG146B (E23M50.419-P1)
RZ744 (E24M50.364-P1)
E23M50.560-P2
BCD134 (RM9A)
RG375 (E13M59.183-P1)
E13M60.294-P2
RM5
E26M47.356-P2
RG303 E25M60.364-P2)
E25M50.M005-P1
RG462
RG519
ME1-1
E13M60.082-P1
E26M49.417-P1
E25M59.150-P2
RM212
E25M60.199-P1
E26M47.230-P1
RZ513
RG541 (RG101)
RG317
RG109 (RG220)
RZ569A
EstI-2 (E13M59.196-P2)
(C949A)
RZ14
RM14 (E23M50.071-P1)
(RG381)
RG331 (E26M47.361-P1)
E26M47.M002-P2
prot 1.1
prot 1.3
ash1.2
fat 1.1
adhe 1.2
ash1.3
2
RG365
RG634B (RM211, RM233A)
E13M59.M001-P2
RM53
RM259
RZ87
E24M50.276-P1
C132 (E24M50.267-P2)
RCD536
E26M47.470-P1
RG437A
E25M48.116-P1, E13M60.117-P1
E25M60.168-P1
RCD532
E13M59.M003-P2 (E25M60.078-P2)
E25M48.065-P1, E13M59.119-P1
E25M48.325-P1, E23M50.582-P1
E13M59.128-P1 (E26M47.509-P2)
G1184B (RM29) (E26M49.524-P1)
E25M48.246-P2
RG157
E26M47.278-P1
E13M60.070-P1
RM262
RZ166
E23M50.234-P1
RZ318 (E26M49.M002-P2)
RZ103
E23M50.160-P1
RG102
G57 E13M60.258-P1
RZ58
E24M50.411-P1
RM6
E13M59.504-P2
C601
E13M59.296-P1, E26M47.586-P2
CDO1091
RG151
RZ446
RM213
E13M60.119-P2
G1234
RZ913
RM48
prot 2.1
mag 2.1
pot 2.1
3
RM81B
E25M59.327-P2
RG944
E26M47.240-P2
C74
RG191
RG100
RZ313
RM36
RM218
E25M59.156-P1
RG369
RZ16 RM7
RM251 (RM232)
E26M47.104-P2
E25M48.237-P2
(E25M48.234-P1)
E13M59.207-P2
E26M47.162-P2
E23M50.085-P2
RZ585
E13M59.143-P1
RG179 (E13M59.050-P1)
RZ598, RG96B
RM16 RZ403
E25M48.316-P2
E26M47.320-P2
RZ261
RZ879A
RZ474
G200
CDO337
RM49
RZ745
E24M50.159-P2, E24M50.161-P1
RZ761
RZ575
E26M47.325-P1
RZ319
E13M59.305-P2
E13M59.126-P1
RG910, RZ142
RG1356
E13M60.153-P1
E23M50.092-P1, E26M47.447-P2
G1318 BCD926
RZ393
adv 3.1
mag 3.1
mag 3.2
adv 3.2
4
RZ602 (E13M59.423-P2)
RG396B
RG190
RZ69 E26M49.371-P1
E25M60.M001-P2, E13M60.303-P2
(E23M50.125-P1, E25M50.143-P1)
(E25M48.083-P2) (E24M50.076-P1)
(E26M49.494-P2) (E13M60.187-P1)
E23M50.154-P2
RG449 (RM261)
E25M59.186-P2
E25M50.138-P1
E13M60.279-P2
RZ740 (RM226)
RM241
(E23M50.337-P2)
E23M50.340-P1
E26M49.365-P1
E23M50.203-P2
RG939
RG329
RG214
Ph (RM255)
RG476
RZ590
RG161 (E24M50.M002-P2)
RZ879B (RG96A)
RG620 RG558
(BCD135)
RZ569B
RG143
adv 4.1
gum 4.1
har 4.1
chew 4.1
fat 4.1
chew 4.2
pot 4.1
prot 4.1
gum 4.2
5
(RM42B, RM249)
E25M48.219-P2
RCD511 (RM32)
E25M59.099-P1
E25M59.098-P2
C734 (E26M47.515-P1)
RCD549
RG13 (E25M48.336-P1)
RCD350
RM39
RG634A (E24M50.389-P2)
E24M50.386-P1
E25M59.196-P2
E13M59.092-P1
RG470
RZ291
RM233B
G329, G12
G122 (RZ70B)
RZ225A
E25M60.202-P1
RG474 (E25M59.182-P2)
CDO1160
RG493
RG435
har 5.1
gum 5.1
6
RZ1002 (C474)
E25M50.286-P2
RM204
RM225
RM217
E25M50.179-P1, E25M59.102-P2
RZ450 (E23M50.535-P1)
RG213 (E23M50.M.001-P2)
(E26M47.113-P1, RM50)
E13M59.279-P2 (E26M49.427-P1)
E13M59.270-P1
C235
RG64
RG264 (E23M50.364-P2)
E23M50.208-P1, E13M60.178-P1
RM238B (E26M47.392-P1)
RM3 (E26M49.084-P2)
RG716 (E13M59.468-P1)
(E25M48.045-P1)
E24M50.331-P2, E13M60.136-P2
E13M59.292-P2
RZ682
RZ828
E25M50.293-P2
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prot 6.1
ash6.1

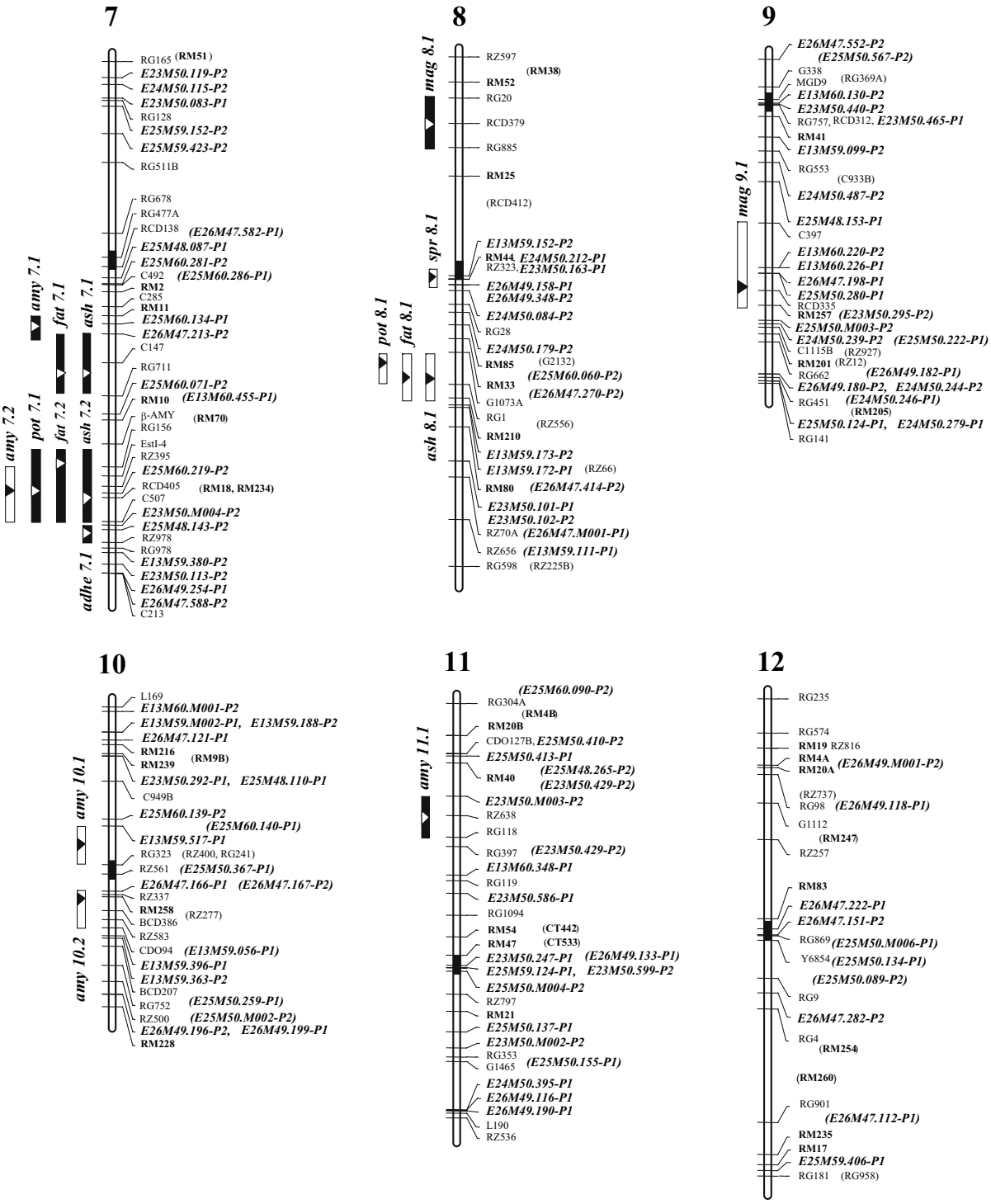

Fig. 3 QTL associated with chromosomes 7–12 for 12 physical and nutritional properties of rice analyzed in the Milyang23 × Gihobyeo RI population (164 lines)

(nomenclature from Aluko et al. 2004) is located in the same region as *prot1.1* (in this study). Protein content was negatively correlated with alkali digestion value and AC, indicating that if protein content is increased, amylose and ADV content may be decreased in rice grain.

Ash content (%ash)

Seven QTL on four chromosomes were significantly associated with ash content in rice grains (Table 5; Figs. 2 and 3). The M23 allele was associated with higher *%ash* at

ash1.1, ash1.3, and *ash8.1,* while the Giho allele increased *%ash* at the other four loci. The locus that explained the highest portion of the phenotypic variation was *ash6.1* ($R^2 = 0.28$).

Three QTL, *ash1.1, ash1.3*, and *ash7.2*, were each identified in 2 years and *ash1.3* (increasing allele from M23) and *ash7.2* (increasing allele from Giho) both had LOD scores >5.0 and R^2 values of 0.13 and 0.14, respectively. This study suggests that markers linked to the QTL for *%ash* may be useful in a marker-assisted selection (MAS) program to either increase or decrease the ash content of rice grain.

Fat content (%fat)

Five QTL on four chromosomes were detected for fat content. Several of these QTL are likely to be of interest for MAS, including *fat7.2,* which was detected in all 3 years, and GM, *fat1.1,* which is in the same location as a fat content QTL detected in a previous study (Hu et al. 2004), and two additional QTL detected on chromosome 7 (*fat7.1* and *fat7.2,* $R^2 = 0.13$ and 0.12, respectively).

Potassium content (pot)

Seven QTL on five chromosomes were associated with potassium content. Three were detected in 2 or more years and GM, and the most significant QTL was *pot7.1* (LOD = 11.28; $R^2 = 0.20$), where the M23 allele was associated with decreased potassium content.

Magnesium content (mag)

Five QTL on four chromosomes were identified for magnesium content. *mag9.1* was detected in 2 years and GM ($R^2 = 0.147$) and the M23 allele conferred increased magnesium content at this locus. Magnesium content is negatively correlated with adhesiveness, ash content, fat content, and potassium content. These are the first reported QTL for magnesium content of rice grain.

Implications for plant breeders

The identification of markers linked with traits of interest provides plant breeders with tools that can be used for MAS. The information also provides the foundation for cloning genes and QTL of interest. The most useful markers for use in breeding are those linked to QTL that are stable across years and environments, including the five QTL in this study that were significant in all 3 years (*adhe1.2*, *amy7.2*, *fat7.2*, *pot 7.1*, and *pot8.1*) .

By comparing the magnitude (R^2 value) and direction (additive effect) of specific alleles, markers that are closely associated with useful alleles can be used to trace the inheritance of specific chromosomal segments in a segregating population. The use of MAS early in the life of a plant can provide the breeder with insights about grain quality traits long before the plant sets seed, making it possible to eliminate unwanted segregants that do not meet commercial grain quality standards, and potentially saving the breeder a generation of progeny testing. Breeders interested in genomic selection may use molecular markers linked to favorable grain quality loci to enhance breeding gains (Heffner et al. 2009). As more genes associated with key grain quality traits are identified, "perfect markers" can be used to enhance the accuracy and efficiency of selection, to identify useful parents in a germplasm collection, and to deepen our understanding of genotype–phenotype relationships.

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