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QTL analysis for eating quality-related traits in an $F_{2:3}$ population derived from waxy corn × sweet corn cross

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In order to identify quantitative trait loci (QTL) for the eating quality of waxy corn and sweet corn (*Zea mays* L.), QTL analysis was conducted on an F_2 population derived from a cross between a waxy corn inbred line and a sweet corn inbred line. Ten QTLs for pericarp thickness (PER), amylose content (AMY), dextrose content (DEX) and sucrose content (SUC) were found in the 158 F_2 families. Among them, four QTLs, qAMY4 (10.43%), qAMY9 (19.33%), qDEX4 (21.31%) and qSUC4 (30.71%), may be considered as major QTLs. Three of these, qAMY4, qDEX4 and qSUC4, were found to be located within a region flanked by two adjacent SSR markers on chromosome 4 (umc1088 and bnlg1265), making this SSR marker pair a useful selection tool for screening the eating quality traits of AMY, DEX and SUC. The QTL for amylose content was found to be located between markers phi027 and umc1634, raising the possibility of its identity being the *Wx1* gene, which encodes a granule-bound amylose synthase. The new QTLs identified by the present study could serve as useful molecular markers for selecting important eating quality traits in subsequent waxy corn breeding studies.

Key Words: waxy corn, sweet corn, F_2 population, eating quality, QTL analysis, marker assisted selection.

Introduction

Maize (*Zea mays* L.), wheat and rice, are the three most important staple crops. Maize can be divided into three types based on the starch composition of the endosperm in the seed, normal corn, waxy corn and sweet corn. It is generally considered that the difference between normal corn and waxy corn is the texture or starch content (amylose and amylopectin) of the grain. In addition, sweet corn is a variety of maize with a high sugar content. Sweet corn is the result of a naturally occurring recessive mutation in the genes which control conversion of sugar to starch inside the endosperm of the corn kernel (Carey *et al.* 1984, Nelson and Rines 1962, Sprague *et al.* 1943). Although normal corn is widely cultivated and used in food, forage, industrial and bioenergy, waxy corn or sweet corn, which is a special type of cultivated maize, is only used in food production. As the general population shows an increasing trend of a switch from the traditional rice-based diet to a meat-based Western diet, waxy corn has become a popular and valuable crop in East Asian countries, especially in Korea. Both demand and consumption of waxy corn have soared in recent years (Sa *et al.* 2010). Consumers particularly pay a premium for fresh waxy corn, usually available on the market approximately 25 days after pollination. Along with increased consumption of waxy corn, consumers are also demanding more delicious new cultivars of waxy corn. However, there has been little effort in Korea to develop systematic breeding programs through extensive genetic mapping and quantitative trait loci (QTL) analyses of waxy corn.

Eating quality of maize has been extensively studied by a number of research groups (Azanza *et al.* 1996, Ito and Brewbaker 1981, Simonne *et al.* 1999). In fresh sweet corn, consumers' primary eating quality concerns are sweetness and kernel tenderness (Wann *et al.* 1971). Pericarp thickness has been a major selection target for improving the kernel tenderness in sweet corn (Ito and Brewbaker 1981), as well as the popping ability of popcorn (Babu *et al.* 2006). Due to its close association with grain hardness, a thin pericarp corn strain has been the preferred edible variety (Bailey and Bailey 1938, Ito and Brewbaker 1991, Shmidt and Tracy 1988). Sweetness is largely determined by the kernel sucrose content (Reyes *et al.* 1982). During post-harvest maturation, kernels undergo a rapid turnover of sucrose and glucose into starch with concomitant moisture loss (Carey *et al.* 1984). Therefore, sucrose concentration in the kernel, a key attribute preferred by the sensory evaluation taste panels (Azanza *et*

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al. 1994, Evensen and Boyer 1986), negatively correlates with total starch content of the kernel (Creech 1965).

With the completion of the maize genome project, high-density genetic maps have become essential tools for analyses such as QTL analysis, positional cloning, or physical map construction aimed at deciphering the structure and function of the genome (Azanza *et al.* 1996, Choe and Rocheford 2012, Ku *et al.* 2010, Tanksley *et al.* 1996, Wang *et al.* 2010). Utilizing specialized mapping populations of F_2 or recombinant inbred lines, DNA-based molecular markers have been instrumental in developing fine linkage maps that facilitate crop genetic advances. QTL analysis, gene cloning, and crop molecular breeding by marker assisted selection are all vital tools in agrogenomics (MAS) (Choe and Rocheford 2012, Ku *et al.* 2010, Sa *et al.* 2012, Tanksley *et al.* 1996, Wang *et al.* 2010, Young 1995).

During the past few decades, a number of molecular markers related to agronomically important qualitative and quantitative traits have been developed (Paran and Zamir 2003) and used to improve many crops through genetic mapping and QTL analysis (Azanza *et al.* 1996, Choe and Rocheford 2012, Ku *et al.* 2010, Wang *et al.* 2010, Young 1995). It is necessary to manipulate a mapping population such as F_2 or recombinant inbred lines (RILs) and backcross the populations with recombination around the target loci for linkage mapping and QTL analysis. Among these populations, the F_2 population is particularly useful because it allows us to measure the effects of additive and dominant gene actions at specific loci. This population can be quickly constructed via a simple cross that saves time and money, in addition to showing obvious Mendelian segregation of the allelic characteristics of the parent strains. Due to their co-dominant nature and superior reproducibility (Park *et al.* 2009), simple sequence repeats (SSRs) are generally considered to be one of the best markers for constructing genetic maps and have been extensively used in the analyses of linkage maps and QTLs in F_2, RIL and backcross populations. Using SSR markers, we can construct genetic maps and assess genetic diversity among F_2 segregating mapping population or maize inbred lines due to their high level of allelic variation.

Here we report eating quality traits-related QTLs by employing a genetic linkage map of the $F_{2:3}$ population derived from a cross between a waxy corn inbred line (02S6140) and a sweet corn inbred line (KSS22).

Materials and Methods

Plant materials

A population of 158 F_2 families was developed from a 2004 cross between 02S6140 (an inbred strain derived from a Korean waxy corn landrace) and KSS22 (sweet corn inbred line). Among the parental inbred lines used in our study, 02S6140 is used as one of the parental lines of Korean waxy corn cultivar (cv. Mibackchal), which is extensively cultivated in the area of Gangwon province, while KSS22 is derived from an American commercial sweet corn variety, which is used as an imported sweet corn variety in Korea. These were cultivated for more than 6 years to develop an elite inbred line at the Maize Experiment Station, Gangwon Agricultural Research and Extension Service, Hongcheon (Sa *et al.* 2010).

Phenotypic analysis

The 158 $F_{2:3}$ families were grown at the Maize Experiment Station in 2005. Ten plants per row were sib-mated to create $F_{3:4}$ sib-mated families by two replications. Four eating quality-related traits, such as pericarp thickness (PER), amylose content (AMY), sucrose content (SUC) and dextrose content (DEX), were investigated in seeds of 158 $F_{2:3}$ families. PER (μm) was measured using Saginamiya BGM-3 in five randomly chosen kernels per sample. AMY (%) was evaluated in ten randomly chosen kernels per sample by UV spectroscopy scans at 620 nm using a UVIKON 900 spectrophotometer according to the method of Juliano (1971). In our study, the sample of kernels used for fresh waxy corn was approximately 25 days after pollination. Thus, it may have had slightly higher amylase content (6.6%) than the normal waxy kernel (0.0%) of the dough-ripe stage, approximately 45 days after pollination (See Fig. 1). In addition, in this study, amylose content was measured using whole kernels instead of using pure starch extracted from kernels and this may have affected the higher value of amylose content. Sugar content (g/L), DEX (g/L) and SUC (g/L) were measured in 10 randomly chosen kernels per sample using a YSI 2700 STAT Analyzer.

DNA extraction and SSR genotyping

Genomic DNA from parental and F_2 mapping populations was isolated from young leaves via the method described by Dellaporta *et al.* (1983). SSR amplifications were performed in a total volume of 30 μl and consisted of 20 ng genomic DNA, 1× PCR buffer, 0.3 M of forward and reverse primers, 0.2 mM deoxyribonucleotide triphosphate (dNTP) and 1 unit *Taq* Polymerase. The PCR profile consisted of a 5-minute initial denaturation period at 94°C followed by two cycles each of 1-minute denaturation at 94°C, 1-minute annealing at 65°C and 2-minute extension at 72°C. The annealing temperature was gradually decreased after the second cycle by 1°C following every second cycle until a final temperature of 55°C was reached. The last cycle was then repeated 20 times. Upon completion of the cycles, the reaction was extended for 10 minutes at 72°C.

Five microliters of the final reaction product was mixed with 10 μl electrophoresis loading buffer (98% formamide, 0.02% BPH, 0.02% Xylene C and 5 mM NaOH). After denaturation and immediate cooling, 2 μl of the sample was loaded onto a 6% denaturing (7.5 M urea) acrylamide-bisacrylamide gel (19 : 1) in 1× Tris/borate/EDTA (TBE) buffer and electrophoresed at 1800 volts and 60 watts for 120 min. The separated fragments were then visualized using a silver-staining kit (Promega).

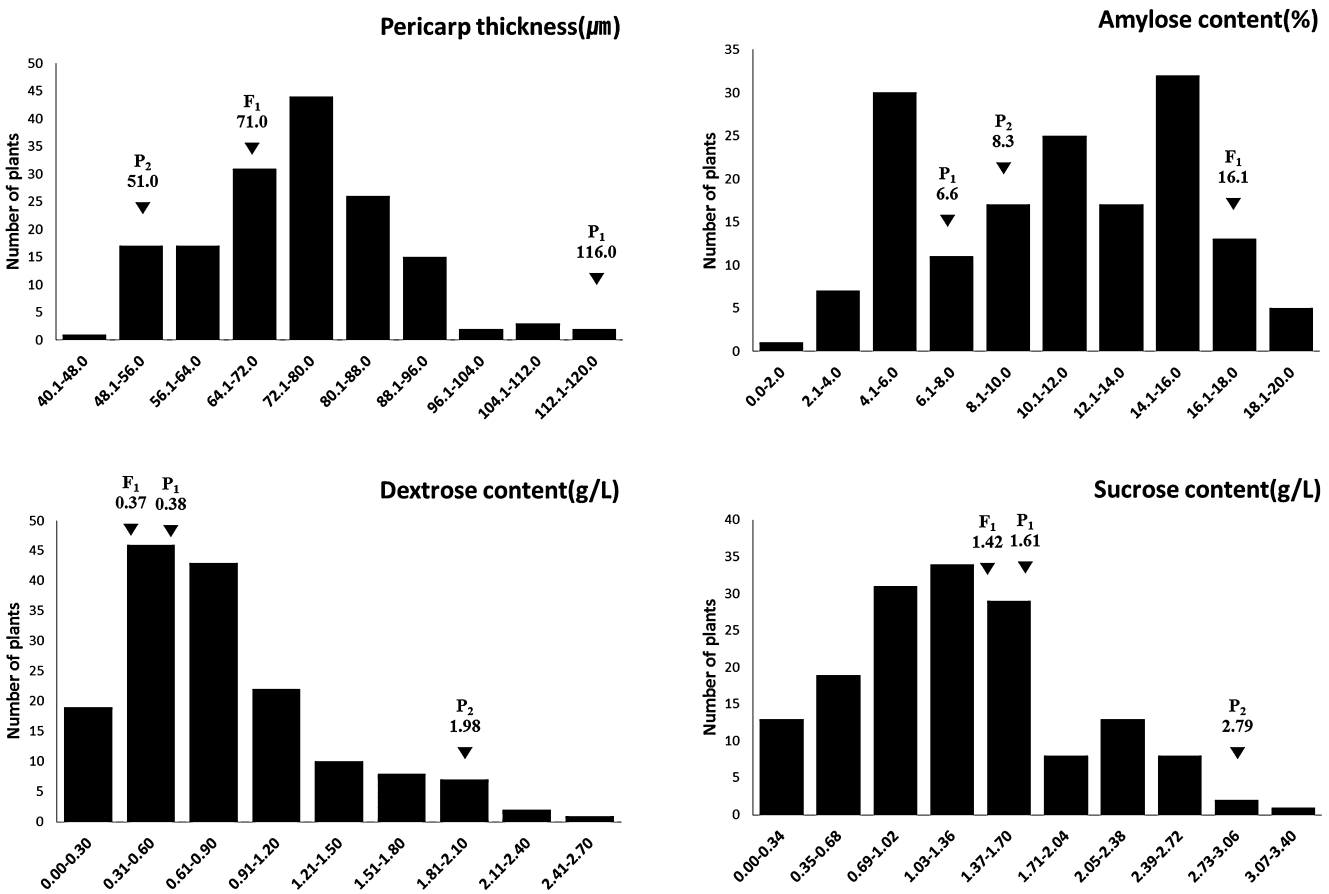

Fig. 1. Frequency distribution of four eating quality-related traits in parents, F_1 and F_2 populations. A population of 158 F_2 families was developed from a cross between 02S6140 (an inbred strain derived from a Korean waxy corn landrace) and KSS22 (sweet corn inbred line).

Construction of a linkage map and QTL mapping

In total, 650 SSR markers covering all 10 chromosomers were tested for parental polymorphisms in the analysis of the population. A linkage map was constructed from the genotype data of polymorphic 295 SSR markers using MAPMAKER/Exp 3.0 (Lander *et al.* 1987). The linkage groups were assigned to the ten chromosomes based on the positioning of the mapped SSRs described by Lawrence *et al.* (2007). QTL mapping for eating quality-related traits was carried out on the cohort of 158 F_2 families by mixed linear model approaches using QTL Mapper 2.0 (Wang *et al.* 1999). This program is based on mixed linear models and allows simultaneous mapping of both main effect and digenic epistatic QTLs in an $F_{2:3}$ population. Digenic epistatic loci were determined at a significance level of $p \leq 0.001$. Gene action was determined by the ratio of the absolute value of the estimated dominance effect divided by the absolute value of estimated additive effect as described by Stuber *et al.* (1987).

Results

Phenotypic evaluation of $F_{2:3}$ seeds and correlation analysis for eating quality-related traits

PER, AMY, DEX and SUC in parental lines, F_1 and $F_{2:3}$ plant families are shown in Fig. 1 and Table 1. The PER of the parent 02S6140 (P_1) was 115.6 μm thicker than that of the parent KSS22 (P_2). In contrast, the AMY, DEX and SUC of the P_1 parent were 6.63%, 0.38 g/L and 1.61 g/L less than those of the P_2, respectively. The values of PER and SUC for the F_1 plants were between those of P_1 and P_2. The values of AMY and DEX obtained for the F_1 population were higher and lower, respectively, than those of both parental lines. The mean PER and DEX values of the $F_{2:3}$

Table 1. The eating quality-related characters of parents, F_1, $F_{2:3}$ populations derived from 02S6140 × KSS22

		PER[a]	AMY[b]	DEX[c]	SUC[d]
P_1 (02S6140)		115.63	6.63	0.38	1.61
P_2 (KSS22)		50.63	8.26	1.98	2.79
F_1 (02S6140 × KSS22)		70.63	16.14	0.37	1.42
$F_{2:3}$	Mean ± SD[e]	74.14 ± 13.54	10.69 ± 4.60	0.80 ± 0.50	1.25 ± 0.66
	Range	41.00~116.67	1.97~19.86	0.19~2.61	0.07~3.37

[a] Pericarp thickness.
[b] Amylose content.
[c] Dextrose content.
[d] Sucrose content.
[e] Standard deviation.

Table 2. Correlation coefficients among eating quality-related traits in 158 $F_{2:3}$ families

	PER	AMY	DEX	SUC
PER	–			
AMY	–0.22**	–		
DEX	0.22**	–0.48**	–	
SUC	0.21**	–0.27**	0.41**	–

** Significance at $P < 0.01$.

families were similar to those of the parent population. AMY was higher in P_1 and P_2 than in F_1 families. DEX was lower in the F_1 population than the parental lines, and mean values for AMY and SUC of F_1 plants were higher and lower, respectively, than the mid-parent value (Table 1).

Correlation coefficients among the PER, AMY, DEX, and SUC are listed in Table 2. PER was positively correlated with DEX (0.22**) and SUC (0.21**). AMY was negatively correlated with PER (–0.22**), DEX (–0.48**) and SUC (–0.27**). Of these correlations, the relationships between AMY and DEX and DEX and SUC showed relatively high correlation coefficients compared to other trait combinations. In particular, the correlation coefficient between AMY and DEX showed the highest value, whereas the relationship between PER and SUC exhibited the lowest correlation coefficient (Table 2).

QTL analysis

The size of the framework map spanned 2,626.5 cM across all 10 linkage groups. The average genetic distance between pairs of markers among all linkage groups was 8.9 cM. Ten QTLs associated with PER, AMY, DEX and SUC, related to eating quality in fresh waxy corn, were mapped to maize chromosomes 4, 5, 6, 8 and 9 (Fig. 2 and Table 3). Of these 10 QTLs, 4 were associated with PER, 2 with AMY, 2 with SUC and 2 QTLs were related to DEX.

As shown on Fig. 2 and Table 3, four QTLs on chromosomes 4, 5, 8 and 9 were associated with PER. One QTL, qPER4 (on chr. 4), showed an additive effect, accounting for 10.43% of the phenotypic variance. The other three QTLs on chromosomes 5, 8 and 9 (qPER5, qPER8 and qPER9, respectively) showed partial dominance and accounted for 6.71%, 6.74% and 7.79% of the phenotypic variance, respectively. Three of the QTLs (qPER4, qPER5, qPER8) conferring the PER increase were contributed to by KSS22, whereas one (qPER9) was provided by the other parent, 02S6140. Two QTLs defining AMY were identified on chromosomes 4 and 9. The QTL on chromosome 4, qAMY4, showed an additive effect, accounting for 4.26% of the phenotypic variance. The chromosome 9 QTL, qAMY9, exhibited partial dominance and accounted for 19.33% of the phenotypic variance. qAMY4 was contributed to by the parental strain 02S6140 and qAMY9 came from the other

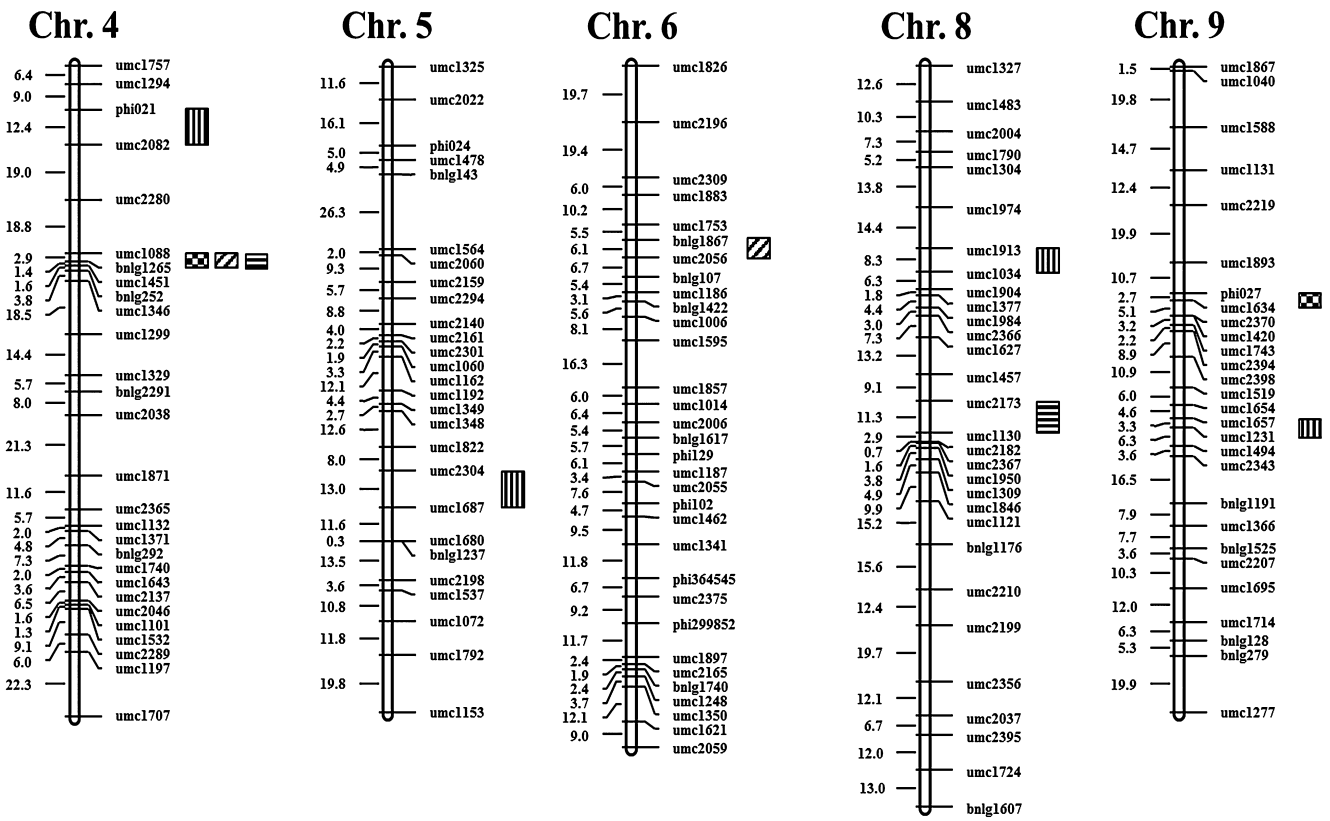

Fig. 2. The genetic map based on SSR markers and QTLs detected in four eating quality-related traits. Map distances (on the left) are given in cM (Kosambi function). ▥: QTL associated with PER, ▩: QTL associated with AMY, ▨: QTL associated with DEX, ▤: QTL associated with SUC.

Table 3. Detection of QTL for various traits in the 158 $F_{2:3}$ families

Trait	Chr	QTL	Interval	LOD	Gene effect		R^2	Gene action[c]	Favorable allele
					A[a]	D[b]			
PER	4	qPER4	phi021-umc2082	8.21	6.27	−0.02	10.43	A	KSS22
	5	qPER5	umc2304-umc1687	5.48	5.03	1.61	6.71	PD	KSS22
	8	qPER8	umc1913-umc1034	5.19	5.04	−1.9	6.74	PD	KSS22
	9	qPER9	umc1657-umc1231	4.87	5.42	−2.05	7.79	PD	02S6140
AMY	4	qAMY4	umc1088-bnlg1265	17.61	2.3	0.09	4.26	A	02S6140
	9	qAMY9	phi027-umc1634	62.62	4.9	2.04	19.33	PD	KSS22
DEX	4	qDEX4	umc1088-bnlg1265	32.02	0.5	−0.17	21.31	PD	KSS22
	6	qDEX6	bnlg1867-umc2056	8.02	0.31	0.02	8.19	A	02S6140
SUC	4	qSUC4	umc1088-bnlg1265	22.25	0.59	−0.14	30.71	PD	KSS22
	8	qSUC8	umc2173-umc1130	5.51	0.29	0.00	7.42	A	KSS22

[a] Additive effect.

[b] Dominant effect.

[c] Gene action was estimated by (d)/(a): A (additive effect) 0–0.20, PD (partial dominance) 0.21–0.80, D (dominance) 0.81–1.20 and OD (over dominance) >1.20.

Table 4. Epistasis interaction detected for eating quality-related traits in an $F_{2:3}$ population

Trait	Chr	Marker interval i	Chr	Marker interval j	LOD	Ai[a]	Aj[a]	AAij[b]	PVE (%)[c]
PER	1	umc1282-bnlg1112	5	umc1348-umc1822	8.88	−1.08	−1.28	8.20	6.47
AMY	4	umc1088-bnlg1265	9	umc1893-phi027	64.74	2.59	−4.48	−1.32	0.70

[a] Ai and Aj represent the additive effect on intervals i and j, respectively.

[b] AAij represents the epistatic effect between intervals i and j as defined by (Mei *et al.* 2003).

[c] PVE (%) is the proportion of phenotypic variation explained by AAij, significant at $P < 0.001$.

parental strain, KSS22. Two QTLs for DEX were detected on chromosomes 4 and 6 (qDEX4 and qDEX6, respectively), which showed partial dominance and additive effects, and accounted for 21.31% and 8.19% of the phenotypic variance, respectively. The enhancement of DEX provided by qDEX4 was contributed to by KSS22, while that of qDEX6 was from 02S6140. Two QTLs on chromosome 4 and 8 were associated with SUC, with partial dominance and additive effects, and accounted for 30.71% and 7.42% of the phenotypic variance, respectively. Both SUC QTLs were contributed to by KSS22.

Interestingly, in our study, we found allelism of QTLs, in that three QTLs (qAMY4, qDEX4 and qSUC4) were located between the SSR markers umc1088 and bnlg1265 on chromosome 4. This result indicated that the co-location of three QTLs for eating quality-related traits showed pleiotropy and/or tight linkage.

QTLs with epistasis effects

In our study, we observed two epistatic interactions in two pairs of loci for traits PER and AMY (Table 4). The interaction for PER trait, which was responsible for 6.47% of phenotypic variance, was observed between the region flanked by the markers umc1282 and bnlg1112 on chromosome 1 and the regions bordered by umc1348 and umc1822 on chromosome 5, while the interaction for AMY trait, which was responsible for 0.7% of phenotypic variance, was observed between the regions flanked by the SSR markers umc1088 and bnlg1265 on chromosome 4 and the regions bordered by umc1893 and phi027 on chromosome 9.

Discussion

The utilization of molecular markers and mapping populations for identifying QTLs related to diverse morphological characteristics is now well established in maize crops (Azanza *et al.* 1996, Choe and Rocheford 2012, Ku *et al.* 2010, Séne *et al.* 2000, Wang *et al.* 2010, Wang and Brewbaker 2001). Similarly to sweet corn, fresh waxy corn 25 days after pollination is generally consumed as food in Korea. Recently, waxy corn hybrids have increased in popularity in Korea, resulting in increased demand for more cultivars of superior taste quality. Thus, eating quality is an important focus of any waxy corn breeding program in Korea. In this study, a construction of a genetic linkage map with SSR markers was performed using a waxy/sweet corn hybrid population of 158 F_2 families derived from a cross between 02S6140 (an inbred line derived from a Korean waxy corn strain) and KSS22 (an inbred derived from an American sweet corn variety). This frame map was then used for QTL mapping to identify chromosomal regions associated with the traits of eating quality, PER, AMY, DEX and SUC. The highest correlation coefficient value was observed between AMY and DEX, whereas the correlation coefficient between PER and SUC was the lowest. This high correlation between AMY and DEX may facilitate the

improvement of traits related to consumer preference via direct and indirect selection in smaller populations (Table 2).

Ten QTLs that are associated with maize eating quality, including PER, AMY, DEX and SUC, were revealed by this study. Three of these, qAMY4, qDEX4 and qSUC4, were found to be located within a region flanked by two adjacent SSR markers on chromosome 4 (umc1088 and bnlg1265), making this SSR marker pair a useful selection tool for screening eating quality traits of AMY, DEX and SUC. Genetic interaction between loci may play an important role in the determinism of some traits (De Vicente and Tanksley 1993). In the previous study, Azanza *et al.* (1996) reported that one QTL, *npi*410, which was located on chromosome 4, was significantly associated with kernel and sensory characteristics of eating quality in sweet corn. In addition, Séne *et al.* (2000) reported that two QTLs, *Brittle* 2 and *Sugary* 1, which are involved in kernel starch biosynthesis, were located on chromosome 4. In our study, three QTLs were within a region flanked by two adjacent SSR markers on chromosome 4. These results might indicate that these region markers were associated with several QTLs linked to waxy or sweet corn eating quality traits in the same chromosomal segment. Furthermore, allelic variation is of major interest in breeding programs. In our study, allelic variation of genes controlling eating quality demonstrated that the co-location of QTL for eating quality traits might mean pleiotropy and/or tight linkage. Previous studies using fine mapping have found that several QTL/genes exhibited pleiotropic effects on multiple yield traits (Fan *et al.* 2006, Fujino and Iwata 2011, Li *et al.* 2011, Song *et al.* 2007, Xue *et al.* 2008). For example, allelic variation of genes controlling heading data demonstrates that photoperiod sensitivity plays an important role in adaptability during diversification of cultivated rice (Fujino and Iwata 2011). In addition, *Ghd7* for grain number, plant height and heading date has a significant role in wide-ranging adaptation across Asia (Xue *et al.* 2008). However, in our study, we did not find the possible effect of agronomic traits such as flowering date on the eating-related QTL (data not shown).

On the other hand, according to Collard *et al.* (2005), a major QTL is defined as one contributing to more than 10% of phenotypic variation. Four QTLs in our study, qAMY4 (10.43%), qAMY9 (19.33%), qDEX4 (21.31%) and qSUC4 (30.71%), may be regarded as major QTLs. Interestingly, qAMY9 is located between the markers phi027 and umc1634 on chromosome 9. It has been shown that phi027 is part of the gene encoding a granule-bound starch synthase, *Wx1*. The role of *Wx1* in determining amylose content in kernels has been well documented by Senior *et al.* (1998). Therefore, it is possible that qAMY9 is identical to the *Wx1* locus or is part of the regulatory element controlling the *Wx1* gene. Furthermore, qAMY4 is located at a similar locus as the *glt1* gene on chromosome 4, which has been previously reported by Pan (2003) to be associated with the amylopectin synthesis pathway. The other QTLs present on chromosome 4, qDEX4 and qSUC4, were mapped to similar loci as *su1* (sugary1, Stinard 2000) and *fl2* (floury2, Stinard 2000), respectively. Additionally, qPER4b (on chromosome 9) and qPER8 (on chromosome 8), may be closely associated with *piple* (plasma membrane intrinsic protein 1, Chaumont *et al.* 2001) and *pebp9* (phospatidylethanolamine-binding protein 9, Danilevskaya *et al.* 2008), respectively. Furthermore, qSUC8 on chromosome 8 may in fact be the locus for *spp1* (sucrose-phosphatase1, Datta *et al.* 2002). However, the four PER QTLs in this study, based on chromosomal position, appear to be different from previously described PER QTLs (Choe and Rocheford 2012) and thus will be useful as new markers in breeding programs optimizing the pericarp thickness of kernels.

Lindhout (2002) and Pilet-Nayel *et al.* (2002) suggested that major QTLs are stable under varying environments, whereas minor QTLs may be environmentally sensitive. However, in our study, we did not survey the influence of different environmental conditions on these quantitative traits due to the limited quantity of seeds in the $F_{2:3}$ family lines. Therefore, all results obtained in this study should be further validated by additional experiments utilizing recombinant inbred lines, near isogenic lines, doubled haploids and other permanent populations under various environments in the future, as suggested by Wang *et al.* (2010). Nevertheless, the results of this study indicate that the introgression of favorable traits in maize can be facilitated using conventional and marker-assisted selection breeding efforts. In breeding programs, the target gene/locus is introgressed into the recipient as a chromosomal segment linked to the target gene/locus by MAS. To perform MAS efficiently, it is important to identify genes or traits on the chromosomal segment linked to the target gene. Thus the detection and confirmation of loci associated with eating quality-related traits presented here may provide greater opportunities for maize breeder to improve quality by MAS.

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