GMR Genetics and Molecular Research
Online Journal
ISSN:1676-5680

Identification of a major quantitative trait locus for ear size induced by space flight in sweet corn

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Genet. Mol. Res. 13 (2): 3069-3078 (2014)
Received February 5, 2012
Accepted August 16, 2013
Published April 17, 2014
DOI http://dx.doi.org/10.4238/2014.April.17.3

ABSTRACT. The development of molecular markers has contributed to progress in identifying the gene(s) responsible for favorable variations in maize studies. In this study, quantitative trait locus (QTL) mapping was conducted using simple sequence repeat markers in an F_2 sweet corn population from a cross between parental line 1132 and space flight-induced mutant line 751 to identify the loci contributing to an increase in some yield traits. A primary mutated genomic region was located on chromosome 9. In total, 26 QTL were detected for eight yield-related traits and assembled into three clusters on chromosome 9. The largest QTL cluster at bin 9.02/03, primarily contributing to >10% of the phenotypic variation in ear and cob diameters, was likely due to a major QTL. Desired alleles of these QTL were provided by the mutant line 751. The primary action of the major mutant allele was an additive effect. Another mutant locus, which was induced in bin 9.01, increased cob and ear diameters by dominant genetic action.

Key words: Ear size; Quantitative trait locus; Space flight; *Zea mays*

INTRODUCTION

Yield is the most important economic trait in maize, but is also the most complex trait to manipulate due to its quantitative nature. Many studies have focused on the genetic characteristics and molecular mechanisms that affect yield, and many quantitative trait loci (QTL) for yield-related traits have been identified (Berke and Rocheford, 1995; Austin and Lee, 1996; Graham et al., 1997; Ajmone-Marsan et al., 2001; Lima et al., 2006; Yan et al., 2006; Sabadin et al., 2008; Lu et al., 2006, 2011). Because most of these QTL are minor QTL, it is difficult to utilize them for pyramiding favorable alleles. Hence, the search for functional genes or major QTL that positively affect yield has become an urgent goal in maize genetics and breeding.

Space flight induction is an effective approach to acquire mutations by carrying plant seeds to outer space. During space flight, mutations in plant genomes can be induced by cosmic radiation, microgravity, or other factors (Cyranoski, 2001; Li et al., 2007). As a result, new genetic variations are generated, from which desired mutants can be selected (Novak and Brunner, 1992). Although the genetic mechanism of the induced mutations is unknown, space flight is considered an effective approach for acquiring new favorable alleles and improving elite germplasm for breeding and is used to induce mutations in seeds of *Arabidopsis* (Kranz, 1986), wheat (Tripathy et al., 1996), rice (Yu et al., 2007), and other plants (Nechitailo et al., 2005).

Progress has been made in the molecular characterization of mutations induced by space flight, and in identifying the genes responsible for favorable variations, particularly in rice. For example, space environment-induced mutations were shown to occur preferentially at polymorphic sites (Li et al., 2007). Furthermore, space flight-induced transposable element transposition (Long et al., 2009) and DNA methylation (Ou et al., 2009) was discovered in the rice genome. Recently, a gene that induces resistance to the fungal disease rice blast was identified from a space-induced rice mutant and was finely mapped to chromosome 11 (Xiao et al., 2011).

In maize, the impact of the space environment on roots (Moore et al., 1987a,b), leaves, and flowers (Mei et al., 1994, 1998) was studied, even though little was known about the molecular characterization of mutations induced by space flight. In this study, simple sequence repeat (SSR) markers were used in an F_2 population from a cross of a space-induced mutated line and an original control line to 1) find the primary mutated genomic region in the maize genome, 2) locate the QTL responsible for the variation in yield component traits, 3) estimate the gene effect and other genetic parameters of these QTL.

MATERIAL AND METHODS

Plant materials and field trials

Sweet corn inbred line 1132 is an elite line with good eating quality and agricultural performance, but low yield. In 2003, seeds of 1132 were flown on a recoverable satellite for 18 days, while others were kept on the ground as controls. The satellite was at an altitude of 200-350 km, pressure of 10^{-9}-10^{-5} Pa, microgravity of 10^{-3}-10^{-5} *g*; the temperature was 10°-30°C in the seed capsule during the spaceflight. After returning to earth, the seeds were germinated and planted. Obvious decreases in emergence rate and seedling growth vigor were observed in the 1st generation. Many phenotypic variations emerged in the 2nd generation, with positive or negative effects on agronomic traits. Subsequently, inbred line 751, which showed significant

differences in yield-related traits compared with the original control line 1132, was developed by five generations of selfing and selection from these mutated plants. These changes included decreases in plant height, increases in stem diameter, ear diameter (ED), kernel row number (KRN), and ear weight (EW), among others.

To construct a population for QTL mapping, 342 F_2 plants derived from a cross between lines 1132 and 751, together with the two parental lines, were planted in Guangzhou in the fall of 2008. Nine yield-related traits were measured after harvest: ear length (EL), ED, kernel weight per ear (KW), EW, KRN, kernel number per row (KN), 100-kernel weight (100-KW), cob diameter (CD), and kernel depth (KD). Analyses of phenotypic data for the yield traits were conducted based on parental and F_2 population data using the SAS 9.0 software (SAS Institute Inc., 1999).

Population genotyping and linkage map construction

Genomic DNA from each of the F_2 plants and the parental lines was isolated from fresh leaf tissue (Saghai-Maroof et al., 1984). Genotyping was performed using SSR markers. Sequences of all SSR markers were obtained from the Maize Genetics and Genomics database (http://www.maizegdb.org). The SSR markers, which were polymorphic between lines 1132 and 751, were screened using SSR markers covering the entire maize genome. These polymorphic markers were then used for genotyping the F_2 population. A genetic linkage map was constructed with MAPMAKER/EXP Version 3.0 (Lander et al., 1987; Lincoln et al., 1993).

QTL mapping

The phenotype data, in combination with the linkage map, were used to conduct composite interval mapping (CIM) to locate QTL for the traits listed above. CIM analysis was performed with Windows QTL Cartographer V2.5 (Wang et al., 2011) with the following parameters: Model 6 (standard) CIM model, a walk speed of 1.0 cM, and a log-likelihood threshold value of 2.5. The logarithm of odds (LOD) peak for each significant QTL was identified. The gene effect and the percentage of phenotypic variation attributable to each QTL were estimated at the peak. The gene actions of mapped QTL were estimated according to Stuber et al. (1987).

RESULTS

Phenotypic data analysis

The differences in yield-related traits between the mutant line 751 and the wild-type line 1132 are shown in Table 1. Among the nine traits, 100-KW and KN showed significant differences between the two parents, whereas EL, ED, KRN, EW, 100-KW, and CD showed highly significant differences. KD was not measured for line 1132. Except for 100-KW, significant positive correlations between the other eight traits were observed in the F_2 population, ranging from 0.2258 to 0.9815 (Table 2). KD exhibited the highest correlation coefficient with ED. Significant negative correlations occurred between 100-KW and KRN (-0.2991) or KN (-0.3321). No significant association was observed between 100-KW and the other traits.

Table 1. Differences in yield-related traits between the mutant and original control line.

Trait	Control (1132)	Mutant (751)	P
Ear length (EL, cm)	10.5 ± 0.71	12.75 ± 0.27	0.000359**
Ear diameter (ED, cm)	2.95 ± 0.71	3.78 ± 0.12	0.000091**
Kernel depth (KD, cm)	-	0.78 ± 0.07	-
Kernel row number (KRM)	9 ± 1.41	15 ± 1.67	0.004104**
Kernel number per row (KN)	22 ± 4.24	28.5 ± 2.81	0.042245*
Ear weight (EW, g)	28.15 ± 1.2	50.38 ± 5.01	0.001035**
Kernel weight (KW) per ear (g)	21.85 ± 1.06	40.58 ± 4.24	0.001065**
100-KW (g)	11.95 ± 0.21	10.3 ± 0.64	0.014573*
Cob diameter (CD, cm)	2.95 ± 0.07	2.22 ± 0.12	0.000187**

*Significant at 0.05; **significant at 0.01; (-) = data missing.

Table 2. Correlation coefficients between yield-related traits.

	EL	ED	KD	KRN	KN	EW	KW	100-KW
ED	0.5196**							
KD	0.4501**	0.8625**						
KRN	0.2607**	0.5717**	0.3555**					
KN	0.6470**	0.6040**	0.6048**	0.2992**				
EW	0.7307**	0.8159**	0.7130**	0.4535**	0.7374**			
KW	0.7089**	0.8133**	0.7357**	0.4447**	0.7668**	0.9815**		
100-KW	-0.0236	-0.0811	-0.0854	-0.2991**	-0.3321**	0.0068	-0.0271	
CD	0.3545**	0.6877**	0.2258**	0.5907**	0.2952**	0.5477**	0.5103**	-0.0336

*Significant at 0.05; **significant at 0.01; ns = not significant. For abbreviations, see Table 1.

Linkage map construction

For polymorphic marker screening, 397 markers that were evenly distributed across the maize genome were used (Figure 1). Only 57 polymorphic markers were used for genotyping the F_2 population. After excluding markers that were monomorphic or segregation distorted among the F_2 lines, 47 markers were used for genetic map construction. The distribution of polymorphic markers across the chromosomes was imbalanced (Figure 1).

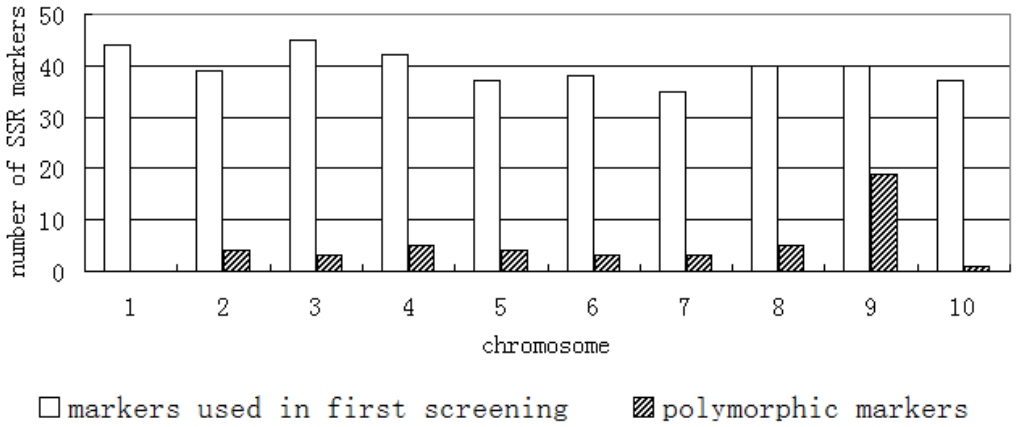

Figure 1. Number of polymorphic markers among 10 chromosomes used in this study.

The percentage of polymorphic markers that were located on chromosome 9 was 47.5%, whereas very low percentages of polymorphic markers (or an absence of markers in the case of chromosome 1) were located on the other chromosomes (Figure 1). This suggested that a higher genomic mutation rate occurred on chromosome 9 after space flight in the 1132 line. Preliminary map construction and QTL mapping showed a significant QTL region located on this chromosome (data not shown). Therefore, regardless of the other chromosomes, 40 markers on chromosome 9 were added based on information provided by the IBM2 2008 neighbors map in the Maize Genetics and Genomics database (http://www.maizegdb.org) and were used for the population genotyping to increase marker density of the genetic map for chromosome 9. Finally, a linkage map consisting of 28 marker loci on chromosome 9 was constructed using the genotype data identified in the F_2 population. The total length of the genetic map was 389 cM, with an average distance between markers of 14.4 cM (Figure 2).

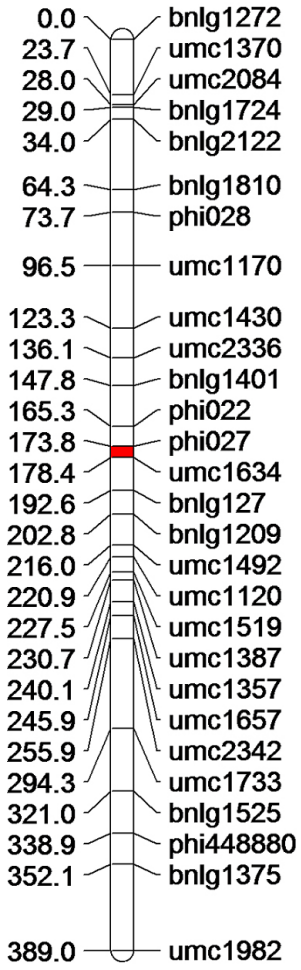

Figure 2. Linkage map of chromosome 9 and the location of the major QTL. The red region indicates the marker interval between two flanking markers of the major QTL peak.

Mapping of QTL for traits relating to yield

In total, 26 QTL, which were located in several clusters, were detected for eight yield-related traits in the F_2 population of 1132 x 751 using the WinQTLCart v2.5 software (Wang et al., 2011) (Table 3). No QTL were detected for KN based on the significant threshold LOD scores. The largest QTL cluster was between bnlg1401 and bnlg127, including 13 QTL for six traits (ED, KD, KRN, EW, 100-KW, and CD). Among these QTL, three ED QTL and three CD QTL had the highest LOD scores and accounted for >10% of the phenotypic variation. In fact, these connected QTL peaks were likely due to a major QTL (Figure 3). In addition, several QTL for KRN, KD, EW, and KW were located at bin 9.02/03 and overlapped with the major QTL for ED and CD. The 2nd QTL cluster was located at bin 9.01-02. The qED1 and qCD2 peaks almost coincided with each other (qED1: QTL indicated as "q + trait name + number", see Table 3) (Figure 3). In an adjacent region, three QTL for EL, ED, and CD (qEL1, qED2, and qCD3, respectively) overlapped and had a similar LOD curve (Figure 3).

Table 3. Genetic parameters associated with QTL for the yield-related traits detected in the F_2 population of 1132 x 751.

Trait	QTL[a]	Chromosome bin	Marker[b]	Position (cM)[c]	LOD score	R^2%[d]	Gene effect		Gene action[e]	Source of desired allele
							Additive	Dominance		
EL	qEL1	9.01	Bnlg2122	42.0	2.6772	10.13	-0.5462	0.1687	PD	751
	qEL2	9.03-04	Bnlg1209	202.9	4.5222	7.25	-0.3187	0.2486	PD	751
	qEL3	9.06	Umc1733	318.3	3.5848	5.82	0.2796	-0.2856	D	1132
ED	qED1	9.01	Bnlg1724	29.0	3.7604	0.13	-0.0394	-0.1076	OD	751
	qED2	9.01	Bnlg2122	44.0	2.9413	0.32	-0.0416	-0.1230	OD	751
	qED3	9.02	Bnlg1401	157.9	6.9840	11.49	-0.1490	0.0142	A	751
	qED4	9.02	Phi027	175.9	8.6194	11.13	-0.1435	0.0087	A	751
	qED5	9.03	Umc1634	183.5	8.8951	13.23	-0.1557	0.0144	A	751
	qED6	9.07	Phi448880	348.9	2.6060	4.43	-0.0717	0.0565	PD	751
KD	qKD1	9.03	Umc1634	183.5	5.0759	7.88	-0.0445	0.0044	A	751
	qKD2	9.07	Bnlg1375	351.9	2.5606	3.89	-0.0270	0.0126	PD	751
KRN	qKRN1	9.02	Bnlg1401	155.9	3.0076	6.19	-0.5432	0.1613	PD	751
	qKRN2	9.03	Phi027	173.9	5.1695	8.70	-0.5907	0.2412	PD	751
	qKRN3	9.03	Umc1634	184.5	4.9123	9.19	-0.6338	0.2084	PD	751
EW	qEW1	9.02	Bnlg1401	151.9	4.8848	8.69	-4.1178	1.5029	PD	751
	qEW2	9.03	Umc1634	183.5	5.4870	9.11	-4.5800	0.8289	A	751
KW	qKW1	9.02	Bnlg1401	151.9	4.5347	7.99	-3.3625	1.2197	PD	751
100-KW	q100-KW1	9.05	Umc1387	232.8	4.3131	6.98	0.6358	-0.1713	PD	1132
	q100-KW2	9.05	Umc1657	246.0	4.7254	6.06	0.6451	-0.0333	A	1132
CD	qCD1	9.01	Bnlg1272	6.0	2.8142	1.12	-0.0270	-0.0451	OD	751
	qCD2	9.01	Bnlg1724	29.0	3.8477	1.44	-0.0309	-0.0362	D	751
	qCD3	9.01	Bnlg2122	48.0	3.2876	2.04	-0.0362	-0.0410	D	751
	qCD4	9.02	Bnlg1401	159.9	6.7583	12.17	-0.0798	0.0132	A	751
	qCD5	9.02	Phi022	172.4	8.0680	11.62	-0.0750	0.0125	A	751
	qCD6	9.03	Umc1634	185.5	7.3517	10.83	-0.0755	0.0055	A	751
	qCD7	9.06	Umc1733	316.3	2.5416	4.02	0.0346	-0.0245	PD	1132

[a]QTL indicated as "q + trait name + number". [b]Marker: left-flanking marker to the QTL peak. [c]Position from the left telomere of the current chromosome. [d]Phenotypic variation. [e]Gene action as determined by the ratio dominance effect/additive effect (D/A): <0.2 indicates additive gene action (A), 0.2-0.8 indicates partial dominance (PD), 0.8-1.2 indicates dominance (D), and >1.2 indicates over-dominance (OD). For abbreviations, see Table 1.

Several other QTL were located on chromosome 9 in different regions from the two large QTL-rich regions. Two QTL (qEL3 and qCD7) overlapped at bin 9.06, with desired alleles from parental line 1132. In addition, two 100-KW QTL were identified at bin 9.05, both of which were

likely due to two peaks of the same QTL and were also contributed by 1132. Similarly, two minor QTL (qED6, qKD2) were detected at bin 9.07 and showed partial dominance. Most of the QTL clustered at bin 9.03-04 showed an additive effect or partial dominance. In particular, all six of the largest QTL for ED and CD showed additive effects. The additive effect was the primary action for the major QTL. At bin 9.01, two ED QTL (qED1 and qED2) and two CD QTL (qCD1 and qCD2) showed over-dominance or dominance, suggesting that a mutant locus that increased CD and ED by dominant genetic action was induced in this genomic region.

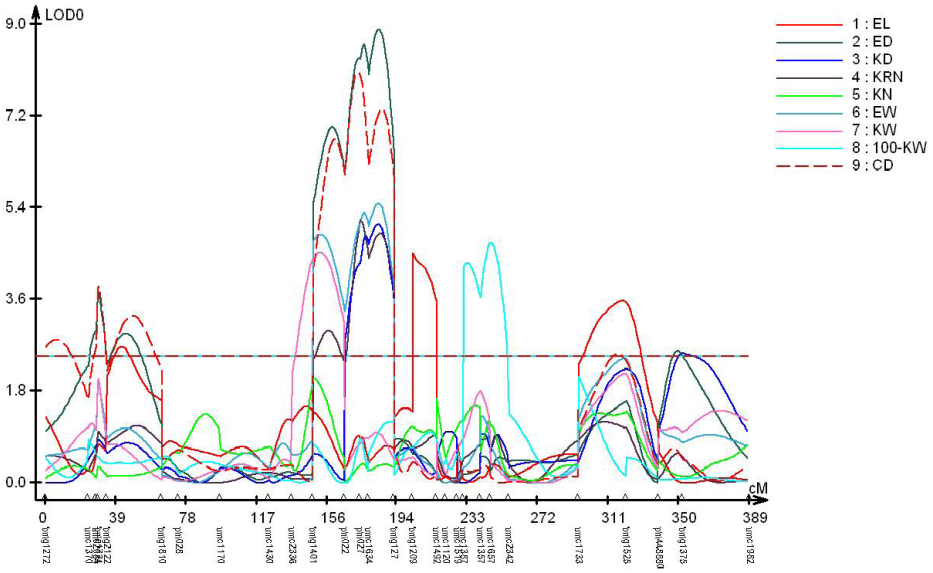

Figure 3. LOD curves of QTL for yield-related traits obtained by WinQTLCart v2.5. The chromosome and associated markers are listed on the x-axis. The horizontal line indicates the significance threshold of LOD score for identifying putative QTL. A peak above the threshold line indicates a QTL. For abbreviations, see Table 1.

Among the 26 QTL, mutant line 751 contributed the desired alleles of 22 QTL including all the QTL for ED and KD and most of the CD QTL. Line 751 was the primary genetic donor for enlarging ear size. In contrast, parent 1132 contributed the favorable alleles at four QTL loci, including two 100-KW QTL. This result was consistent with the phenotypic data showing that 100-KW was lower in line 751 than in 1132. In the mutant line 751, 100-KW decreased as ear size and kernel number increased. Nonetheless, the positive effect from increasing ear size was greater than the negative effect from decreasing 100-KW. As a result, desired alleles of all three QTL for EW and KW identified in this study were provided by line 751.

DISCUSSION

Space flight plays a positive role in germplasm improvement

Genetic variation of useful traits is required for germplasm improvement in crop breeding. However, the desired variation is inadequate in natural resources. The induction

of mutations by the environment in space is a proven approach for creating variation (Mei et al., 1998; Li et al., 2007). Generally, after genomic mutation induced during space flight, a long progress of selection is conducted to find desired heritable variations and utilize them for germplasm improvement. As a powerful tool, molecular marker-assisted selection (MAS) can be used to accelerate this process when the molecular characterization of the induced mutations is known. In fact, the gene responsible for space flight-induced variations has been successfully identified in rice (Xiao et al., 2011). Our results indicated that some favorable mutant alleles increasing yield component traits were induced by the space environment and that a major QTL cluster on chromosome 9 was responsible for the trait variation. Hence, fine mapping for the QTL to identify these alleles and promote high-yield germplasm improvement by MAS will be implemented in future studies.

A major QTL for ear size in maize

Many studies have identified QTL for traits relating to increased ear size in maize (Berke and Rocheford, 1995; Veldboom and Lee, 1996; Austin and Lee, 1996; Graham et al., 1997; Ajmone-Marsan et al., 2001; Lima et al., 2006; Yan et al., 2006; Sabadin et al., 2008; Lu et al., 2006, 2011). A total of 45 ED, 36 CD, 25 KD, and 27 KRN QTL were retrieved, but no QTL for ear size traits was found at bin 9.03 of chromosome 9 by conducting a QTL search for these traits in the Maize Genetics and Genomics Database (www.maizegdb.org). However, the major QTL at bin 9.02/03 in this study was located in a similar genomic region where a partial dominance effect QTL for KRN was mapped in a recent study (Lu et al., 2011). Associated traits and similar regions have also suggested a possible relationship between these two QTL. Although the primary genetic variation occurred on chromosome 9 in this study, mutated genomic regions that correlate with yield-related traits may have also been induced on the other chromosomes. QTL mapping was conducted on chromosome 9 prior to the mapping of other chromosomes because of its significantly high proportion of polymorphic markers (Figure 1).

Genetic characterization of identified QTL

Yield is a function of KN and KW (Elmore and Abendroth, 2006). Increasing the KN is particularly important in sweet corn because it fills poorly and hence has a low 100-KW. Of the two kernel-number components (KRN and KN), the KRN has a relatively high average heritability estimate (57.0%) (Hallauer et al., 2010). Hence, it is easier to utilize genetic variation to increase KRN for germplasm improvement as a source of favorable alleles. Two QTL for KRN at 9.02/03 were identified in this study, explaining 14.89% of the total phenotypic variation. This result indicated that the increase in KRN represents valuable genetic variation among the mutations induced by space flight.

It is well known that ED is determined by CD and KD. A large QTL cluster for ED, CD, KRN, KD, and other traits was identified in the same region in this study (Figure 3 and Table 3). The peaks of most QTL curves were coincident. This result was consistent with a high correlation between these traits (Table 2) and with results of previous studies (Hallauer et al., 2010). There was, however, a subtle difference between the QTL result and correlations between traits in this study. Among the QTL peaks at bin 9.02/03, the ED QTL showed the

highest LOD and accounted for 13.23% of the phenotypic variation, closely following the QTL for CD. In contrast, KD exhibited the highest correlation coefficient with ED among all traits. Hence, it is difficult to determine whether CD or KD was mostly responsible for the observed increase in ear size. Further studies will be conducted to clarify this uncertainty.

In this study, a mapping population was constructed using 342 F_2 plants with only one trial under one environmental condition. However, the results should be credible because of the strong disequilibrium of polymorphic marker distribution on these chromosomes and the high coherence between identified QTL and investigated phenotypic data. Future fine mapping for the QTL will be performed by constructing secondary populations to reveal detailed QTL information such as 1) whether a major QTL or multiple minor QTL lie on the QTL cluster region of bin 9.02/03, and 2) which mutations of functional genes are responsible for the QTL. Future research will resolve these questions and utilize the major QTL in a molecular breeding program.

ACKNOWLEDGMENTS

Research supported by the Foundation of the President of the Guangdong Academy of Agricultural Sciences (#201010), the Natural Sciences Foundation of Guangdong Province (#080021003), the Science and Information Technology Bureau of Guangzhou (#2009J1-C521), the Sciences and Technology Project of Guangdong Province (#2009A020102003), and the Guangdong CHAN-XUE-YAN Fund (#2009B090300297).

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