Novel and favorable QTL allele clusters for end-use quality revealed by introgression lines derived from synthetic wheat

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Abstract Wheat quality is an important target trait. Previous studies mainly focus on storage protein, but their contribution to quality is partial, and most loci for quality are still undetected. Wild species of wheat are valuable resources for wheat improvement and introgression lines (ILs) are the ideal materials for detecting quantitative trait loci (QTL). In this study, a set of 82 BC5 F2-6 ILs, carrying a range of introgressed chromosome segments from a synthetic hexaploid wheat Am3 (*Triticum carthlicum* × *Aegilops tauschii*), was developed and genotyped with 170 microsatellite markers. QTL analysis was performed for 14 parameters, sodium dodecyl sulfate sedimentation volume, grain protein content (GPC), grain hardness and 11 mixograph parameters, associated with end-use quality of wheat, using the materials harvested in three environments. This led to the detection of 116 QTL, with c. 95% of the positive alleles contributed by Am3. Six important and novel genomic regions for bread-making quality were found on chromosomes 2D, 3A, 4A, 4B, 5A and 6A. These loci for bread-making quality showed pleiotropy and had large positive effects on several quality parameters with no or very weak negative effect on grain yield, thus demonstrating the value of synthetic wheat as a source of useful genetic variation for the improvement of bread wheat quality.

Keywords Synthetic wheat · Introgression line · Introgressed segment · QTL · Quality

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Abbreviations

AACC	American association of cereal chemists
ANOVA	Analysis of variance
GH	Grain hardness
GPC	Grain protein content
HMW-GS	High-molecular-weight glutenin subunit
IL	Introgression line
LMW-GS	Low-molecular-weight glutenin subunit
GNS	Grain number per spike
K–S	Kolmogorov–Smirnov
MLV	Midline left of peak value
MLW	Midline left of peak width

MPTi	Midline peak time
MPV	Midline peak value
MPW	Midline peak width
MRV	Midline right of peak value
MRW	Midline right of peak width
MT	Mixing tolerance
MTxV	Midline time $x = 8$ min value
MTxW	Midline time $x = 8$ width
NIRS	Near-infrared reflectance spectroscopy
QTL	Quantitative trait locus/loci
SDS–PAGE	Sodium dodecyl sulphate polyacrylamide gel electrophoresis
SNS	Spikelet number/spike
SSD	SDS sedimentation volume
SSR	Simple sequence repeat
TGW	Thousand grain weight
WS	Weakening slope

1 Introduction

Much of the current breeding of bread wheat (*T. aestivum* L.), one of the most important crops in the world, is based on a narrow gene pool composed of historical and current cultivars. This excludes a reservoir of allelic variation from both landraces and wild species, which are rarely used because linkage drag makes it difficult to separate the genes for favorable traits from those for undesirable ones (Paterson et al. 1991; Stalker 1980). To overcome this problem, one approach which has been pioneered in tomato, rice, barley and soybean is to develop sets of introgression lines (ILs) (Eshed and Zamir 1995; Tian et al. 2006; Matus et al. 2003; Concibido et al. 2003). A partial set of ILs, covering 37.7% of the donor genome from a synthetic wheat, has been described by Liu et al. (2006). Using these ILs, they detected 38, 33 and 28 quantitative trait loci (QTL) for nine agronomic traits in three environments, respectively. In addition, a set of 84 bread wheat lines, each containing a single homozygous introgression of the *A. tauschii* genome, was produced in the Chinese Spring background via backcrossing of the D-genome chromosome substitution lines Chinese Spring/Sears's Synthetic 6× with the recurrent parent and subsequent selfing (Pestsova et al. 2006). The development of the lines was accompanied by microsatellite marker-assisted selection. With the exception of three telomeric regions at

chromosomes 1DL, 4DL and 7DS, and a region of <24 cm on the chromosome arm 3DL, the genome of *Ae. tauschii* is fully represented in these lines. The newly developed lines were used for the discovery of morphological and agronomic QTL from the wild species. Fifty-two introgression lines were grown in the field and evaluated for six traits including flowering time, plant height, ear length, spikelet number, fertility and grain weight per ear. Among the 17 detected QTL, *Ae. tauschii* contributed favourable alleles at nine loci for five traits. The whole set of 84 homozygous lines provides a tool for further testing of the effects and stability of the detected QTL and for the evaluation of new traits. However, to date the novel QTL for end-use quality has been rarely discovered from synthetic wheat.

The end-use quality is a vital breeding aim for bread wheat, but its measurement in early generation material is technically demanding. As a result, a number of predictive indirect assays have been developed, including sodium dodecyl sulfate (SDS) sedimentation volume (SSD), grain protein content (GPC), grain hardness (GH) and various mixograph parameters, and these are widely used in breeding programs to evaluate processing quality. The end-use quality is determined by a combination of genetic factors and the growing environment of the crop (Rousset et al. 1992; Peterson et al. 1998). A major contributor to the genetic determination of bread-making quality is due to the allelic variants at the loci encoding the high-molecular-weight glutenin subunits (HMW-GS) (Payne et al. 1984), low-molecular-weight GS (LMW-GS) and gliadins (Payne et al. 1987). The gluten fraction as a whole can account for up to one-third of the variation in bread-making quality (Blackman and Payne 1987; Oury et al. 2010). This leaves more than half of the genetic determination of the end-use quality in wheat as yet undefined.

In the present study, we describe the development of a set of ILs based on the introgression of segments of the synthetic hexaploid wheat Am3 into the commercial cultivar Laizhou 953, and the genotypic characterization of these lines, based on allelic constitution at 170 microsatellite (simple sequence repeat; SSR) loci. The objective of this study was to locate QTL for quality parameters in a BC5 IL population carrying alleles from unadapted genetic resources and to assess the potential of exotic alleles for improving wheat quality parameters.

2 Materials and methods

2.1 Plant materials

Am3 was the donor parent for the IL set, and was derived from the wide cross between the tetraploid AABB species *T. carthlicum* acc. PS5 and the diploid DD species *Aegilops tauschii* acc. Ae38. The ILs were selected from the progenies of the fifth back-cross between Am3 and the recurrent parent Laizhou 953. A set of 82 BC5F2:F6 families were selected by both random selection and phenotype selection during the IL development. The process of generating ILs is showed in Electronic Supplementary Material Fig. 1. This IL set did not duplicate any of the 97 ILs selected randomly from the BC4 of the same population by Liu et al. (2006).

2.2 Field trials

All 82 ILs and two parents were grown 2006 in Beijing, and in 2007 in both Beijing and Luoyang, Henan province, China. Each IL and parent was planted in a 2 m double row plot, with 30 plants per row. An unreplicated randomized complete block design was employed for all three trials. Field management was done in accordance with local practices. Nitrogen fertiliser was applied at 350 kg/ha. No pesticide and fungicide were applied because no severe disease developed during the field trials.

2.3 Quality and yield assay

Using the ILs and parents harvested from all three environments, the SDS sedimentation volume (SSD) was determined using a modified procedure of Axford et al. (1979) and Preston et al. (1982). The SDS-lactic acid reagent was prepared by dissolving 20 g SDS in 1 L water, to which 20 mL dilute lactic acid (1:8lactic acid:water) was added. Each 2 g whole-meal sample was vortexed for 5 min in a graduated 35 ml vial containing 16.7 ml water with some methylene blue dye, after which 16.7 ml SDS-lactic acid reagent was added, and the tubes gently up-ended three times), then mixed for 5 min on a special shaker. The vials were left to settle and the sedimentation volume was scored after 5 min. Grain protein content (GPC) and grain hardness (GH) were measured by near-infrared reflectance spectroscopy

(Perten DA7200) (AACC method 39-70A) using the ILs and parents from two environments, Luoyang 2007 and Beijing 2007, and expressed on a 14% moisture basis. A 10 g mixed whole-meal sample of each IL from Luoyang 2007 and Beijing 2007 was prepared for mixograph analysis. The mixograph parameters recorded were midline peak time (MPTi, min), midline peak value (MPV, %), midline peak width (MPW, %), midline left of peak value (MLV, %), midline left of peak width (MLW, %), midline right of peak value (MRV, %), midline right of peak width (MRW, %), midline time $x = 8$ min value (MTxV, %), midline time $x = 8$ min width (MTxW, %), mixing tolerance (MT, min) and weakening slope (WS, %), in accordance with industry standards (AACC method 54-40A) (Martinant et al. 1998; Liu et al. 2005).

The data of grain number per spike (GNS) and spikelet number per spike (SNS) were collected from mature spikes of the main stems. Thousand grain weight (TGW) was calculated as (grain weight per plant/grain number per plant) × 1,000. Each yield parameter was the mean of ten plants.

2.4 Analysis of variance (ANOVA) and trait correlations

ANOVA of phenotypic data was performed using SPSS15.0 software. The distribution test was performed by using the Kolmogorov–Smirnov (K–S) test. A normal distribution was determined when $P > 0.05$. Pearson's correlation coefficients between traits were calculated based on the average value of Luoyang 2007 and Beijing 2007. Heritability (H^2) was estimated according to the formula: $H^2 = M_1/(M_{1+}M_2)$, where M_1 and M_2 are mean squares for genotype and mean square for residual error, respectively.

2.5 Genotype characterization

DNA was extracted from the leaves at the seedling stage following an improved hydroxybenzene–chloroform method (Sharp et al.1989; Devos and Gale 1992). The informativeness of a large set of established SSR loci was determined by comparing the amplification profiles of the two parents and several pooled samples of ILs, with each pooled sample containing 8–10 ILs. The genetic location of the SSR

loci was based on the consensus map of Somers et al. (2004). The PCR procedure followed Röder et al. (1998), and the amplicons were separated by 5% denaturing polyacrylamide gel electrophoresis, and the gels stained with silver (Röder et al. 1998). Primer sequences were obtained from Röder et al. (1998), Pestsova et al. (2000), Gao et al. (2004) and http://www.wheat.pw.usda.gov. The glutenin composition of Laizhou 953 and Am3 was determined from SDS–PAGE separations of total endosperm proteins, following Singh et al. (1991). The presence of the *Glu-B3j* (null) allele at *Glu-B3* locus was considered to be an indicator of the presence of the 1BL.1RS translocation (Gupta and Shepherd 1992).

2.6 Estimation of the length of the introgressed segments

The linkage map positions of the markers and the distances between markers were inferred from the consensus map of Somers et al. (2004). The genetic linkage map was used to estimate the extent of the Am3 segments presented in each IL, based on graphical genotyping (Young and Tanksley 1989; Hospital 2002.

2.7 QTL analysis

A one-way ANOVA was used to detect QTL using SPSS15.0 software (Liu et al. 2006). A QTL close to a marker locus was declared when the probability of the marker/trait combination occurring by chance was < 0.05. Markers detecting the significant effects within regions of ≤ 20 cm were considered to be associated with the same QTL (Pillen et al. 2003). The additive effect (A) of each significant QTL was estimated by ($BB–AA$)/2 (Monforte and Tanksley 2000), and the additivity percentage ($A\%$) of each significant locus was calculated as $100 \times (BB–AA)/2AA$, where AA denotes the phenotypic mean for individuals homozygous for the Laizhou 953 allele at the specific marker locus, and BB represents the phenotypic mean for individuals homozygous for the Am3 allele. The QTL were designated using the format "QTL + trait + research department + chromosome" in accordance with the recommended international nomenclature for QTL in wheat and related species (McIntosh et al. 1994).

3 Results

3.1 Informativeness of the genotypic assays

Among the six glutenin and 548 SSR loci, distributed across all 21 wheat chromosomes, that were screened to detect the polymorphisms between Am3 and Laizhou 953, four glutenin loci (*Glu-B1*, *Glu-A3*, *Glu-B3* and *Glu-D3*) and 170 SSR loci were informative. The Laizhou 953 glutenin genotype is *Glu-A1c* (null allele), *Glu-B1c* (subunits $7 + 9$), *Glu-D1a* ($2 + 12$), *Glu-A3d*, *Glu-B3j* and *Glu-D3a*, while Am3 has the *Glu-A1c* (null), *Glu-B1b* ($7 + 8$), *Glu-D1a* ($2 + 12$), *Glu-A3a*, *Glu-B3b* and *Glu-D3b* alleles. The map locations of 149 of these 170 SSRs were reported by Somers et al. (2004), 19 were allocated to a chromosome but not mapped intrachromosomally, and two (*barc1031* and *barc1039*) had no prior available genetic location. The number of polymorphic markers per chromosome ranged from 4 (chromosome 4D) to 13 (chromosome 3B). Among homeologous groups, the highest marker density was in group 5 (31 loci), and the lowest in group 4 (19 loci). The mean inter-marker distance was 15.0 cM.

3.2 Number, size and position of introgressed segments

At least one introgressed segment was present in each of the 82 ILs. Each IL carried between one and 15 segments (0–13 segments in the homozygous state and/or 0–7 in the heterozygous state), with an average of 7.6 segments per IL. The genetic size of the individual introgression segments ranged from 1.0 to 79.5 cm, with an average length of 12.9 cM. The proportion of individual Am3 chromosomes represented among the ILs ranged from 26.4 (chromosome 4D) to 93.8% (chromosome 4A), with a mean of 59.4%. The proportion of Laizhou 953 chromatin presented in each IL varied from 87.0 to 99.7% (96.1% on average). The introgressed segments present in each chromosome are shown in Fig. 1.

3.3 Parental and IL phenotypes

The means, standard deviations and coefficients of variation among the 82 ILs for the 14 quality

Fig. 1 Introgressed segments present in the 82 ILs, and the location of QTL for 14 quality parameters on the genetic map. The segments are listed to the *right* of each chromosome according to their location, with *lines dashed lines*, *dotted lines* and *dahed lines with dot* representing homozygous segments, heterozygous segments and introgressed segments detected by Liu et al. (2006) but not represented in the present set of ILs, respectively. Segments not located on the consensus map are shown at the *bottom* of the Figure
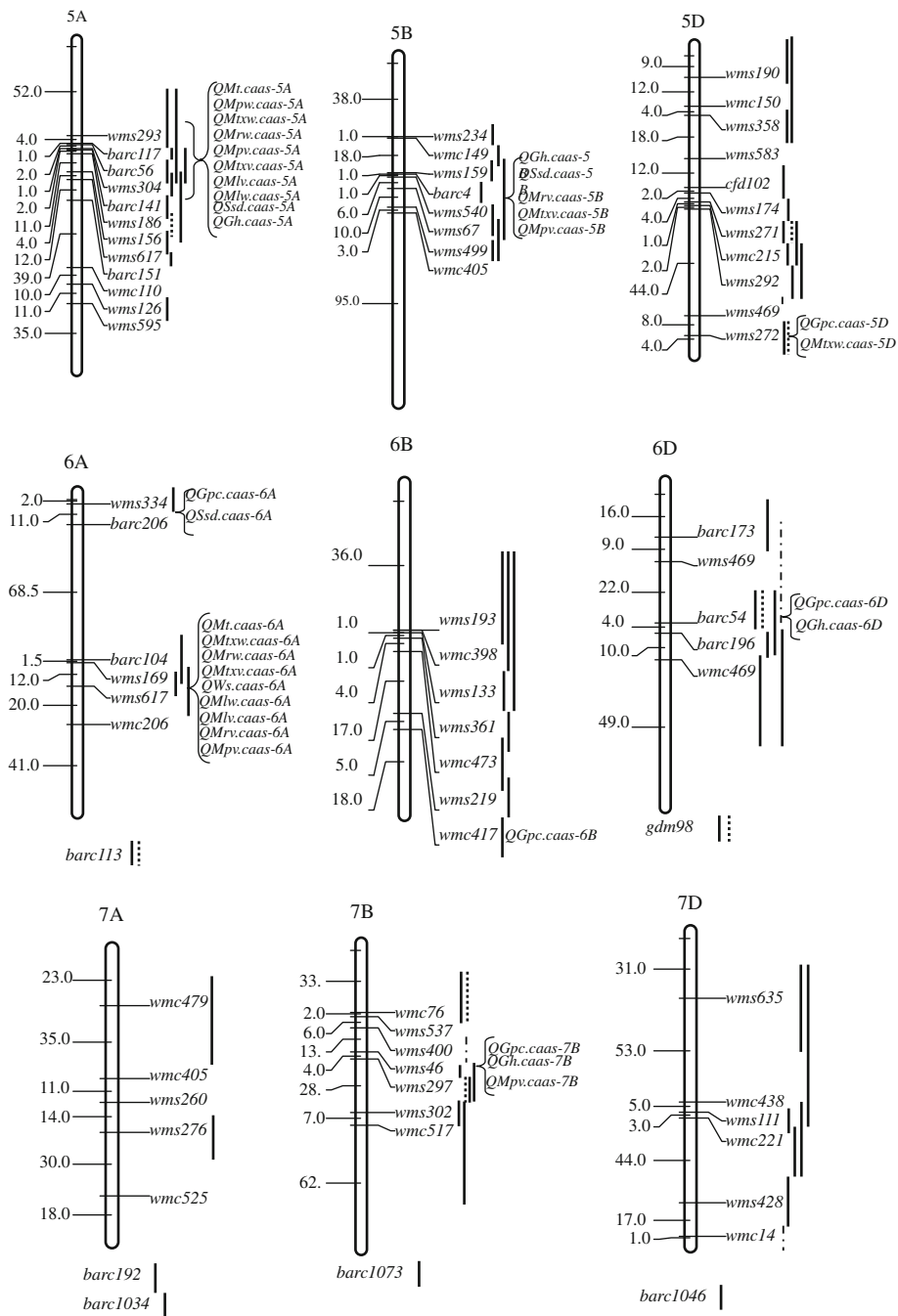
Fig. 1 continued

parameters are detailed in Supplementary Table 1. The SSD correlation between Beijing 2006 and Beijing 2007, Beijing 2006 and Luoyang 2007, Beijing 2007 and Luoyang 2007 were 0.83, 0.72, 0.69 respectively; the GPC correlation between Beijing 2007 and Luoyang 2007 was 0.43; the GH correlation between Beijing 2007 and Luoyang 2007 was 0.57. The heritability of SSD, GPC and GH was 79.3, 41.5 and 54.4%, respectively. The higher correlation and heritability suggest that higher and

Table 1 Correlations between quality parameters and yield parameters

	SSD	GPC	GH	MLV	MLW	MRV	MRW	MTxV	MPTi	MPV	MPW	MTxW	WS	MT
GPC	0.01													
GH	0.00	0.60**												
MLV	0.67**	0.28	0.20											
MLW	0.64**	0.29*	0.12	0.75**										
MRV	0.80**	0.29*	0.07	0.82**	0.80**									
MRW	0.54**	0.11	−0.11	0.63**	0.57**	0.74**								
MTxV	0.79**	0.24	−0.01	0.80**	0.78**	0.98**	0.79**							
MPTi	0.55**	0.07	−0.03	0.58**	0.29*	0.48**	0.47**	0.51**						
MPV	0.62**	0.38**	0.11	0.64**	0.78**	0.85**	0.43**	0.82**	0.12					
MPW	0.54**	0.24	0.16	0.50**	0.54**	0.68**	0.43**	0.66**	0.06	0.69**				
MTxW	0.54**	0.07	−0.12	0.60**	0.51**	0.70**	0.93**	0.75**	0.48**	0.42**	0.34*			
WS	−0.13	0.15	0.19	−0.01	0.17	−0.03	−0.38**	−0.10	−0.56**	−0.41**	0.19	−0.37**		
MT	0.60**	0.06	−0.07	0.68**	0.50**	0.69**	0.91**	0.73**	0.72**	0.27	0.30*	0.87**	−0.57**	
GNS	−0.51**	0.22	0.26	−0.25	−0.18	−0.29	−0.02	−0.27	−0.03	−0.36*	−0.18	−0.13	−0.10	0.03
SNS	−0.46**	0.13	0.11	−0.27	−0.24	−0.31	−0.05	−0.32	−0.03	−0.39*	−0.10	−0.17	−0.07	−0.04
TGW	−0.23	0.25	0.34	−0.41*	−0.41*	−0.49**	−0.62**	−0.49**	−0.11	−0.28	−0.22	−0.52**	0.20	−0.54**

* $P < 0.05$

** $P < 0.01$

reliable QTL for these traits could be detected in the present experiment.

The end-use quality of Laizhou 953 was very poor. Using a recurrent parent characterized by poor end-use quality can facilitate the detection of the high-quality loci from the donor parent. Wide variation was found for all the quality parameters. MRW, MTxW and MT had high values of coefficient of variation (CV of 59.2, 46.0 and 34.0%, respectively). As indicated by the K-S test, for most of the parameters the phenotypic data across the ILs showed normal distribution except for SSD (Beijing 2006), MTxW and MRW. Although neither parents scored highly for any of the parameters, some ILs had outstanding quality scores—notably for SSD, in which the best IL outperformed the recurrent parent by 70.6, 68.9 and 52.1% in Beijing 2006, Beijing 2007 and Luoyang 2007, respectively. Transgressive segregation was also noted for MT, MPW, MPTi, MTxW and WS. Thus, it is apparent that the quality of the recurrent parent can be improved by the introgression of particular *T. carthlicum* and/or *Ae. tauschii* segments.

3.4 Correlation analysis of yield and quality parameters

The correlations between 14 parameters of quality traits and their correlations with three yield parameters are reported in Table 1. GPC was positively correlated with GH, MLW, MRV and MPV, while SSD was positively correlated with all of the mixograph parameters except for WS. WS was negatively correlated with MRW, MPTi, MPV, MTxW and MT, confirming its negative correlation with bread-making quality. The correlations between mixograph parameters were mostly positive. Of the 42 correlation combinations between three yield traits and 14 quality traits, eleven significant correlations were detected, and all of them were negative. They included two correlation combinations between GNS and quality traits (SSD and MPV), two between SNS and SSD and MPV, and seven between TGW and quality traits, MLV, MLW, MRV, MRW, MTxV, MTxW, and MT. The correlation values were from −0.36 (between GNS and MPV) to −0.62 (between TGW and MRW). No significant correlation between yield traits and GPC and HD were detected in the present study.

3.5 QTL for quality parameters

A total of 116 QTL for 14 quality parameters were detected using one-way ANOVA analysis with four glutenin and 170 SSR loci (Fig. 1; Tables 3, 4). Except for the *Glu-B3* locus, the effect of the other three glutenin loci, *Glu-A1, Glu-A3* and *Glu-D3*, on quality parameters were not detected, which showed that the alleles from Am3 and Laizhou 953 in these loci had no significant differences in quality parameters. Ten SSD QTL were detected across the three environments (Table 2), in which nine were mapped to chromosomes 1A, 1B, 1D, 2B, 2D, 4B, 5A, 5B and 6A, and one linked to *barc1031* could not be located to a specific chromosome. *QSsd.caas-1D* was found in two of the three environments, while the other nine QTL were detected in all three environments. The Am3 alleles at all ten SSD QTL had a positive effect on the trait, with *A* (additive effect) and *A%* (additivity percentage) ranging from 1.2 to 4.0 ml and from 6.3 to 21.9%, respectively. Thus, the alleles from Am3 potentially increased the SSD of ILs to 43.8% (from single environment). *QSsd.caas-4B* and *QSsd.caas-2D* both had a large effect on SSD, with the Am3 allele increasing SSD by 31.2 and 24.2% (the average of three environments), respectively. The QTL linked to *wmc128* on chromosome 1B had an *A%* of 13.7%. Because this SSR locus maps to chromosome arm 1BS and the recurrent parent Laizhou 953 carries the 1BL.1RS translocation, this QTL probably reflects the negative effect of 1BL.1RS translocation. Thus, *QSsd.caas-4B* is probably the largest contributor to SSD, followed by *QSsd.caas-2D*, *QSsd.caas-6A* and *QSsd.caas-5A*.

QTL analysis for GPC and GH was conducted on harvests from two of the three environments (not Beijing2006, see Table 3). Nine QTL for GPC were detected on chromosomes 1A, 2D, 3A, 4B, 5D, 6A, 6B, 6D and 7B. The alleles of Am3 exerted a positive effect at six of these QTL, with *A* varying from 0.3 to 0.9%, and *A%* from 2.2 to 11.5%. The largest QTL was *QGpc.caas-6A*, with an *A%* of 11.5%. For GH the two parents Am3 and Laizhou 953 belong to the same class (medium hard) of grain hardness. Consequently minor QTL were expected. Six QTL for GH were mapped to chromosomes 1A, 1D, 4B, 5A, 5B and 6D, with *A* ranging from 1.7 to 3.9. The Am3 allele was associated with an increase in GH at three of the six QTL, and with a decrease at the other three loci.

Table 2 Putative QTL for SSD detected in the IL population

Locus	Linked marker	Source	Beijing 2006			Luoyang 2007			Beijing 2007			Candidate gene/ corresponding QTL[d]
			P	Additive effect (A)[b]	A%[c]	P	Additive effect (A)	A%	P	Additive effect (A)	A%	
QSsd.caas-1A	barc148	Am3	4E–05	1.8	8.9	8E–06	1.3	6.8	0.0001	1.7	9.1	
QSsd.caas-1B	wmc128	Am3	8E–06	2.0	10.1	7E–15	2.9	16.0	6E–11	2.7	15.2	
QSsd.caas-1D	wmc222	Am3	–	–	–	1E–05	1.2	6.3	0.03	1.3	6.8	
QSsd.caas-2B	wms374	Am3	2E–05	1.9	9.4	1E–06	2.1	11.2	4E–05	2.0	10.9	
QSsd.caas-2D	barc159	Am3	1E–08	2.2	11.5	4E–12	2.4	13.5	3E–07	2.0	11.2	
QSsd.caas-4B	wms495/wms513	Am3	8E–07	2.3	11.5	3E–09	2.5	13.5	2E–10	4.0	21.9	
QSsd.caas-5A	wms186	Am3	5E–12	2.7	14.8	1E–05	1.9	10.9	0.0001	1.6	9.3	psr145xSsd[1]
QSsd.caas-5B	Barc4	Am3	0.008	1.9	9.2	4E–06	1.8	9.5	0.002	1.8	9.6	
QSsd.caas-6A	wms334	Am3	0.0004	2.3	11.1	1E–05	1.7	8.8	4E–05	2.9	15.3	
QSsd.caas-x[a]	barc1031	Am3	0.03	1.7	8.3	0.005	1.7	8.3	0.003	1.9	10.2	

[a] QSsd.caas-x denotes that the QTL was not located to a specific chromosome

[b] A positive additive effect indicates that the favorable allele was derived from the donor Am3, and a negative one from the recurrent parent Laizhou 953

[c] A% = Additivity percentage

[d] Candidate genes or corresponding QTLs published in: [1] Blanco et al. (1998)

Table 3 Putative QTL for GPC and GH detected in the IL population

Trait	Locus	Linked marker	Source	Beijing 2007			Luoyang 2007			Candidate gene/ corresponding QTL[c]
				P	Additive effect (A)[a]	$A\%$[b]	P	Additive effect (A)	$A\%$	
GPC	QGpc.caas-1A	wms136	Am3	0.0000	0.6	4.4				
	QGpc.caas-2D	barc159	Am3				0.002	0.7	5.1	
	QGpc.caas-4B	wms513	Am3	0.002	0.8	5.7				QGpc.Z86-4B.a[1] QPro.mgb-4B[2]
	QGpc.caas-5D	wms272	L953	0.004	−0.4	−2.9				
	QGpc.caas-6A	wms334	Am3	0.002	0.6	11.5				
	QGpc.caas-6B	wmc417	L953	0.04	−0.9	−6.5				
	QGpc.caas-6D	barc54	L953	0.02	−0.4	−2.9				
	QGpc.caas-7B	wms46	Am3				0.02	0.3	2.2	QGpc.crc-7B[3] QPro.mgb-7B[2]
	QGpc.caas-3A	wms155	Am3				0.05	0.3	2.2	
GH	QGh.caas-5A	wms304	Am3	0.0002	3.9	6				Psr120axKernel hardness[4] psr133xgrain texture[5] GSP-A1[6] QG h.caas-5A[7]
	QGh.caas-6D	barc54	L953	0.01	−2.4	−3.5	0.02	−2.0	−2.7	
	QGh.caas-4B	wms513	Am3	0.04	2.3	3.3	0.04	1.7	2.3	
	QGh.caas-5B	barc4	L953	0.05	−2.2	−3.2				
	QGh.caas-1A	wmc59	L953				0.01	−3.2	−4.3	
	QGh.caas-1D	wmc222	Am3				0.02	2.0	2.7	

[a] A positive additive effect indicates that the favorable allele was derived from the donor Am3, and a negative one from the recurrent parent Laizhou 953 (L953)

[b] $A\%$ = Additivity percentage

[c] Candidate genes or corresponding QTL published in: [1] Kunert et al. (2007), [2] Blanco et al. (2002), [3] Huang et al. (2006), [4] Zanetti et al. (2001), [5] Turner et al. (2004), [6] Tranquilli et al. (2002), [7] Li et al. (2009)

QGh.caas-4B and QGh.caas-6D were detected in both environments of Beijing2007 and Luoyang 2007.

In all, 91 QTL for mixograph parameters were detected on chromosomes 1A, 1B, 1D, 2B, 2D, 3A, 4A, 4B, 5A, 5B, 5D, 6A and 7B (Table 4), with $A\%$ ranging from 2.8% (for MPW) to 51.7% (for MRW). The Am3 alleles at all these loci were favorable for bread-making quality. Chromosome 1A was associated with 15 QTL and chromosome 2D with ten QTL. Of the six MT QTL on chromosomes 1B, 2D, 4B, 4A, 5A and 6A, the two with higher $A\%$ values were QMt.caas-4A (32.6%) and QMt.caas-6A (22.7%). Two QTL for WS, QWs.caas-4A and QWs.caas-6A, had $A\%$ values of 14.5 and 14.2%, respectively, with the positive alleles derived from Laizhou 953; thus, here too the Am3 alleles were favorable for bread-making quality, because of the negative correlation between WS and bread-making quality. The $A\%$ of the nine QTL for MTxW ranged from 17.6 to 48.6%. Of them, the most effective QTL was QMtxw.caas-4A (48.6%), followed by QMtxw.caas-6A (35.3%) and QMtxw.caas-1B (35.0%). For MPTi, QMpti.caas-4A and QMpti.caas-2D had $A\%$ of 17.5 and 7.5%, respectively. Among the ten MPW QTL, QMpw.caas-1A.2 ($A\%$ of 18.9%) and QMpw.caas-3A (13.9%) were the most important. The nine QTL for MRW were located on chromosomes 1A, 1B, 2B, 2D, 3A, 4A, 4B, 5A and 6A, with the 4A locus having the largest effect (51.7%), followed by those on 1B (48.9%), 6A (37.5%) and 4B (35.8%). Eight, 11, 9 and 12 QTL were detected for MLV, MLW, MRV and MTxV, respectively. The ranges in $A\%$ for these loci were 5.3–9.0, 9.6–19.6, 5.6–11.9 and 4.7–12.5%, respectively.

Table 4 Putative QTL for mixograph parameters detected in the IL population using the mixed sample of Luoyang 2007 and Beijing 2007

Trait	QTL	Linked marker	P	Additive effect (A)	A%[a]
MT	QMt.caas-1B	wmc128	0.001	0.40	19.2
	QMt.caas-2D	barc159	0.007	0.30	13.7
	QMt.caas-4B	wms495	0.048	0.40	18.2
	QMt.caas-4A	barc1047	7.5E−05	0.75	32.6
	QMt.caas-5A	wms293	0.04	0.30	13.1
	QMt.caas-6A	barc104	0.002	0.50	22.7
WS	QWs.caas-4A	barc1047	0.002	−2.10	−14.5
	QWs.caas-6A	barc104	0.003	−2.05	−14.2
MTxW	QMtxw.caas-1B	wmc128	6.0E−06	1.10	35.0
	QMtxw.caas-1D	wmc222	0.02	0.90	26.5
	QMtxw.caas-2D	barc159	0.01	0.70	21.9
	QMtxw.caas-4B	wms495	0.008	0.90	27.3
	QMtxw.caas-5D	wms272	0.01	0.70	17.6
	QMtxw.caas-3A	wms155	0.0003	0.90	28.2
	QMtxw.caas-4A	barc1047	3.E−07	1.70	48.6
	QMtxw.caas-5A	wms293	0.02	0.75	22.1
	QMtxw.caas-6A	barc104	0.0004	1.20	35.3
MPW	QMpw.caas-1A.1	barc148	0.02	1.90	9.6
	QMpw.caas-1A.2	wms136	0.001	3.60	18.9
	QMpw.caas-1A.3	wmc59	0.03	1.50	7.5
	QMpw.caas-1B	wmc128	0.0001	2.00	10.7
	QMpw.caas-2B	wms374	0.01	1.60	8.5
	QMpw.caas-1D	wmc222	0.03	0.60	2.8
	QMpw.caas-2D	barc159	0.048	1.30	6.7
	QMpw.caas-4B	wms495	0.002	1.70	9.6
	QMpw.caas-3A	wms155	0.01	2.55	13.9
	QMpw.caas-5A	wms304	0.003	2.00	11.5
MPTi	QMpt.caas-2D	barc159	0.02	0.10	7.5
	QMpt.caas-4A	barc1047	0.008	0.35	17.5
MRW	QMrw.caas-1A	wmc59	0.048	1.40	23.3
	QMrw.caas-1B	wmc128	1.6E−05	2.25	48.9
	QMrw.caas-2B	wms374	0.04	1.35	24.5
	QMrw.caas-2D	barc159	0.01	1.50	30.0
	QMrw.caas-4B	wms495	0.03	1.90	35.8
	QMrw.caas-3A	wms155	0.03	1.50	28.8
	QMrw.caas-4A	barc1047	0.0001	3.00	51.7
	QMrw.caas-5A	wms293	0.01	1.60	28.6
	QMrw.caas-6A	barc104	0.004	2.10	37.5
MPV	QMpv.caas-1A.1	barc148	2.0E−05	3.00	6.7
	QMpv.caas-1A.2	wms136	0.002	3.90	8.6
	QMpv.caas-1A.3	wmc59	0.0004	2.60	5.7
	QMpv.caas-1B	wmc128	2.1E−11	3.30	7.6
	QMpv.caas-1D	wmc222	0.0006	2.00	4.4

Table 4 continued

Trait	QTL	Linked marker	P	Additive effect (A)	$A\%$[a]
	QMpv.caas-2B	wms374	0.0005	2.20	4.9
	QMpv.caas-2D	barc159	0.0002	2.30	5.1
	QMpv.caas-4B	wms495	4.7E−05	2.20	4.9
	QMpv.caas-5B	barc4	0.001	2.30	5.0
	QMpv.caas-3A	wms155	0.002	2.65	5.9
	QMpv.caas-5A	wms293	0.006	2.75	3.9
	QMpv.caas-6A	barc104	0.047	1.50	3.3
	QMpv.caas-7B	wms46	0.04	1.30	2.9
MTxV	QMtxv.caas-1A.1	wms136	0.003	0.45	12.5
	QMtxv.caas-1A.2	wmc59	0.004	2.10	6.6
	QMtxv.caas-1B	wmc128	2.6E−11	3.20	10.7
	QMtxv.caas-1D	wmc222	0.002	2.00	6.4
	QMtxv.caas-2B	wms374	0.0006	2.05	6.6
	QMtxv.caas-2D	barc159	0.0001	2.20	7.2
	QMtxv.caas-4B	wms495	2.7E−05	2.55	8.4
	QMtxv.caas-5B	barc4	0.02	1.65	5.2
	QMtxv.caas-3A	wms155	0.001	2.75	8.9
	QMtxv.caas-4A	barc1047	0.03	1.50	4.7
	QMtxv.caas-5A	wms293	0.003	1.90	6.1
	QMtxv.caas-6A	barc104	0.006	2.10	6.5
MRV	QMrv.caas-1A.1	barc148	0.01	2.00	5.6
	QMrv.caas-1A.2	wmc59	0.001	2.85	7.9
	QMrv.caas-1B	wmc128	6.5E−13	4.00	11.9
	QMrv.caas-1D	wmc222	0.009	2.05	5.8
	QMrv.caas-2B	wms374	6.8E−05	2.80	8.0
	QMrv.caas-2D	barc159	7.9E−06	2.85	8.3
	QMrv.caas-4B	wms495	2.0E−05	3.00	8.7
	QMrv.caas-5B	barc4	0.02	2.00	5.6
	QMrv.caas-6A	barc104	0.003	2.70	7.4
MLW	QMlw.caas-1A.1	barc148	0.002	2.75	11.7
	QMlw.caas-1A.2	wms136	0.03	3.85	16.0
	QMlw.caas-1A.3	wmc59	0.006	3.00	12.4
	QMlw.caas-1B	wmc128	5.9E−08	4.15	19.6
	QMlw.caas-1D	wmc222	0.01	2.25	9.6
	QMlw.caas-2B	wms374	0.002	2.95	12.8
	QMlw.caas-2D	barc159	0.0002	2.60	11.5
	QMlw.caas-4B	wms495	0.001	3.65	16.2
	QMlw.caas-3A	wms155	0.02	2.50	11.0
	QMlw.caas-5A	wms293	0.01	2.25	9.8
	QMlw.caas-6A	barc104	0.04	2.30	9.7
MLV	QMlv.caas-1A	wmc59	0.03	2.10	5.6
	QMlv.caas-1B	wmc128	3.4E−06	3.25	9.0
	QMlv.caas-1D	wmc222	0.04	2.10	5.6
	QMlv.caas-2B	wms374	0.02	2.00	5.3

Table 4 continued

Trait	QTL	Linked marker	P	Additive effect (A)	$A\%$[a]
	QMlv.caas-2D	barc159	2.6E−05	2.30	6.2
	QMlv.caas-4B	wms495	0.02	2.75	7.4
	QMlv.caas-5A	wms293	0.01	2.20	5.9
	QMlv.caas-6A	barc104	0.03	2.30	5.9

[a] $A\%$ = Additivity percentage

Except for the QTL linked to barc1031, all QTL were located on 18 loci of 15 chromosomes, and among the 18 loci, 17 were pleiotropic, influencing no less than two parameters. Among them, seven loci showed significant effects on multiple bread-making quality parameters. The 1BL. 1RS translocation with Glu-B3j (null) allele, a well-known region having a large negative effect on quality, was involved in 10 quality parameters including SSD, MT, MTxW, MPW, MRW, MLV, MRV, WLW, MTXV and MPV (Fig. 1). In addition, barc159 (2D), wms155 (3A), barc1047 (4A), wms495 (4B), wms293 (5A) and barc104 (6A) were associated with 12, 7, 6, 12, 10 and 9 quality parameters, respectively. The effects of the QTL linked to these six loci were similar to those of the 1BL.1RS translocation. For example, barc1047 (4A) locus showed large effects on the important quality parameters MT, WS, MTxW and MPTi, with $A\%$ values of 32.6, 14.5, 48.6 and 17.5%, respectively; barc104 (6A) locus showed large effects on the important quality parameters SSD, MT, WS and MTxW, with $A\%$ values of 11.7 (mean), 22.7, 14.2 and 35.3%, respectively; wms495 (4B) locus had large effects on SSD, MT and MTxW, with $A\%$ values of 15.6 (mean), 18.2 and 27.3%, respectively.

4 Discussion

4.1 Construction of the ILs and their genome coverage

ILs have been developed and used in various crop species, including tomato, rice, barley and soybean, but have not yet been widely exploited in wheat. Previously, Liu et al. (2006) and Pestsova et al. (2006) constructed ILs and described the use of

DNA-based markers to characterize the position and length of the introgressed segments. The Am3 ILs described in the present study were obtained after five backcrosses, when the expected proportion of the recurrent parent's genome in the ILs is 98.4%. The observed level varied from 87.0 to 99.7% (96.1% on average), which was very close to the expected proportion. About 59% of the donor genome was represented among the ILs, a notably higher proportion than the 37.7% estimated to be present in the set of BC4 ILs selected from the same cross by Liu et al. (2006). The reason may be that the ILs in Liu et al. (2006) were selected randomly, whereas the ILs in the present study were also selected on the basis that the phenotype differed from that of the recurrent parent. Therefore, a higher proportion of the Am3 genome was obtained in the ILs of this study. Combining the 97 ILs in our previous study (Liu et al. 2006) with the present set of ILs provides a population of 179 lines, covering >70% of the Am3 genome. To achieve a 100% coverage of Am3 genome, it will be necessary to screen the uncharacterized ILs with the molecular markers mapped on the regions not represented in this collection. The mean genetic length of the introgressed segments was 12.9 cm, which is somewhat less than the estimated mean segment length of 15.4 cm among ILs in Liu et al. (2006). This probably reflects the effect of an additional cycle of backcrossing, since this gives an opportunity to reduce the number of introgressed segments by reassortment, and their mean size by recombination. Although the proportions of recurrent parent genome were higher than 96% in the ILs, each IL contained an average of 7.6 introgressed segments. Because the wheat genome is comparatively larger than that of other crops it is necessary to backcross more times or use marker-assisted selection to develop single fragment introgression lines.

4.2 The favorable and novel major QTL clusters for bread-making quality detected in synthetic wheat

The previous study for bread-making quality mainly focused on glutenin subunits. In the present study, we detected six novel major QTL clusters favorable for bread-making quality in an IL population, located on chromosomes 2D, 3A, 4A, 4B, 5A and 6A. The QTL cluster responsible for 12 quality parameter QTL on chromosome 2D was mapped on the region of markers barc59 and barc159. Kuchel et al. (2006) detected a total of 37 QTL for 14 bread-making quality traits by using a doubled haploid population. Of the 37 QTL, one for water absorption was mapped on the gwm539-cfd44 interval, which was about 10 cM from barc59; another QTL for water absorption and flour protein content was mapped near wms484 which was about 60 cM from barc159. Because no QTL for other dough rheological traits was detected near barc59 and barc159, the QTL cluster detected in the present study differs from those previously reported. Chromosome 3A is an important chromosome for bread-making quality. We detected a QTL cluster consisting of seven QTL located near wms155. Kuchel et al. (2006) mapped two QTL for bread volume and crumb score near gwm666 which was about 30 cm from wms155. Groos et al. (2007) mapped a cluster of four QTL for loaf volume, bread score, dough score and GPC near wms369 on 3AS, about 60 cM from wms155. A cluster consisting of five QTL was mapped on chromosome 4A near barc1047. No QTL for bread-making quality had previously been mapped on 4A. The QTL cluster on 4B wms495 affected 12 quality traits. Although Kunert et al. (2007) reported a QTL for loaf volume that was mapped between wms113 and wms495, which was similar to our results; however, they did not report effects of this region on GPC and SSD. Blanco et al. (2002) reported a major QTL for GPC on chromosome 4B which explained up to 37% variation of the protein content. However, we did not know the relation of our QTL cluster with their QTL because they mapped the QTL on a large region. On chromosome 5A, Blanco et al. (2002) detected a QTL for GPC near wms186. A QTL for SSD was also located in this region by Blanco et al. (1998). The GH QTL on chromosome 5A ($A\% = 6\%$) was mapped close to the major gene Gsp-A1 for GH (Tranquilli et al. 2002). The GH QTL detected in our study has a similar location to those reported by Turner et al. (2004), Li et al. (2009) and Zanetti et al. (2001) in which the locus was not a significant QTL but had a consistent effect for GH. In the present study, we detected a QTL cluster near barc56 which was close to wms186. This cluster consisted of 10 QTL including a QTL for SSD and GH. The QTL cluster consisted of nine QTL and was mapped near barc104 on chromosome 6A. No QTL for bread-making quality in this region had been reported previously. Kuchel et al. (2006) detected a QTL for GPC near barc107 which was mapped close to the centromere of chromosome 6A and about 30 cM from barc104.

Based on map location and/or target traits, all the six QTL clusters were different from the QTL for bread-making quality reported previously. The main reason for the high number of QTL revealed by our study should be attributed to the population employed. Most populations employed for QTL mapping in previous studies were derived from common wheat crosses. In the present study, the IL population was derived from a cross between common wheat and a synthetic wheat Am3. Am3 was derived from *T. carthlicum,* the wild or semi-wild ancestor of the A and B genomes, and *Ae. tauschii,* the wild ancestor of the D genome. Compared to common wheat, the wild ancestor species are more polymorphic. Interestingly, all the favorable alleles of the six major QTL clusters detected in the present study were from synthetic wheat Am3, indicating a high frequency of favorable allele for bread-making quality in wild species of wheat. More importantly, the wild species have been rarely used in wheat improvement; therefore, they represent a valuable gene pool for wheat quality improvement. The detection of novel loci for wheat bread-making quality is also important for finding additional alleles that are superior to the alleles presently used in breeding programs.

Negative correlation between yield traits and bread-making quality were reported previously (Kibite and Evans 1984; Yagd et al. 2007). Although, negative correlation between yield traits was also detected in the present study, of the 42 correlation combinations, only 11 combinations were significant. No significant correlations were found between yield traits and GPC, GH and WS, which were major parameters of quality. For the significant correlations

detected, R^2 values were low, ranging from 0.13 to 0.38. All these results suggest that the favorable alleles for quality detected from Am3 have no or very weak negative effects on yield components. In fact, most quality QTL detected here were separate from the yield QTL detected in the same population. Wang et al. (2008) reported that seven major QTL for GNS were detected in this population, of which only two, *Qgns.caas-2B* and *Qgns.caas-4B*, were found in the same region with the QTL cluster detected here; Liao et al. (2008) reported that four major QTL for TGW were detected in this population, and only one of them, *Qtgw.caas-4B,* were mapped in the same region with the QTL cluster here.

All 6 major QTL were present in clusters of 6–12 QTL. There are probably three reasons leading to the detection of QTL clusters. One is that the QTL clusters which were detected here were governed by genes which have pleiotropic effects on bread-making quality. A second reason is probably due to the strong correlations of the quality parameters which were measured (see Table 1). Among the 91 correlations between the 14 quality parameters tested, 61 (67%) were significant. In particular, for the 55 correlation combinations between the 11 mixograph parameters, 47 (85%) were significant. Kuchel et al. (2006) also found close correlations between quality traits. The third reason may be caused by the co-expression of gene clusters. In plant genomes, gene clusters have been reported for disease resistance (Graham et al. 2002; Hankuil et al. 2007). Other studies have revealed a clustered gene expression in eukaryotic genomes (Ren et al. 2005) or localized expression domains (Birnbaum et al. 2003). It is likely that additional gene and expression clusters will be revealed in wheat as the whole-genome sequencing and gene expression studies progress.

Three loci detected in the present study were linked to some protein loci identified by Merlino et al. (2009). The QTL linked to *barc148* on chromosome 1A was close to the spot *agl 1227* identified as legumin-like protein which was related to nutrient reservoir activity. The QTL linked to *wms293*, *wms304* and *barc117* on chromosome 5A was close to the spot *agl 1626* identified as a putative uncharacterized protein. The QTL linked to *wms46* on chromosome 7B was close to the spot *agl 190* which was identified as putative glycyl-tRNA synthetase which is involved in translation. This showed that some quality loci linked to

regions encoding some proteins and that the quantity of the protein influenced the quality.

In the present study, all the technological tests used to assess quality of the ILs are indirect tests;they reveal only one or a few characteristics of the dough quality. To assess the true end-use quality of the ILs, it will be needed to perform a final direct test (such as bread-making test, biscuit test or noodle test). The analysis of HMW-GS, LMW-GS, GH and the mixograph parameters allowed assessment of a valuable part only of the total genetic component of bread-making quality (Oury et al. 2010). Consequently the positive effects of the QTL revealed mostly from Am3 using indirect tests need to be further confirmed using final direct tests.

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