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Mapping of main and epistatic effect QTLs associated to grain protein and gluten strength using a RIL population of durum wheat

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Abstract Quality, specifically protein content and gluten strength are among the main objectives of a durum wheat breeding program. The aim of this work was to validate quantitative trait loci (QTLs) associated with grain protein content (GPC) and gluten strength measured by SDS sedimentation volume (SV) and to find additional QTLs expressed in Argentinean environments. Also, epistatic QTL and QTL x environmental interactions were analyzed. A mapping population of 93 RILs derived from the cross UC1113 x Kofa showing extreme values in gluten quality was used. Phenotypic data were collected along six environments (three locations, two years). Main effect QTLs associated with GPC were found in equivalent positions in two environments on chromosomes 3BS (R^2=21.0-21.6%) and 7BL (R^2=12.1-13%), and in one environment on chromosomes 1BS, 2AL, 2BS, 3BL, 4AL, 5AS, 5BL and 7AS. The most important and stable QTL affecting SV was located on chromosome 1BL (*Glu-B1*) consistently detected over the six environments (R^2=20.9-54.2%). Additional QTLs were found in three environments on chromosomes 6AL (R^2=6.4-12.5%), and in two environments on chromosomes 6BL (R^2=11.5-12.1%),

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7AS (R^2=8.2-10.2%) and 4BS (R^2=11–16.4%). In addition, pleiotropic effects were found affecting grain yield, test weight, thousand-kernel- weight and days to heading in some of these QTLs. Epistatic QTLs and QTL x environment interactions were found for both quality traits, mostly for GPC. The flanking markers of the QTLs detected in this work could be efficient tools to select superior genotypes for the mentioned traits.

Keywords Durum wheat · Gluten strength · Grain protein content · Molecular markers · Quantitative trait loci (QTLs)

Abbreviations

GPC	Grain protein content
SV	SDS sedimentation volume
RIL	Recombinant inbred line
QTL	Quantitative trait locus
GY	Grain yield
TKW	Thousand kernel weight
TW	Test weight

Introduction

Durum wheat (*Triticum turgidum* L. ssp. *durum*) is mainly used to produce pasta because its grains are the only ones, among the cereals, able to produce semolina. The aptitude of semolina for pasta production is conferred by the particular characteristics of its endosperm storage proteins that comprise the gluten matrix. A strong gluten and high protein content are conducive to the production of dough with excellent rheological properties for pasta making. Gliadin and glutenin are the main endosperm storage proteins found in mature seeds of wheat. Gluten strength is affected by grain protein content (GPC) and the characteristics of these proteins (Payne et al. 1984; D'Egidio et al. 1990). Two kinds of glutenins, designated as high or low molecular weight glutenin subunits (HMWGs and LMWGs, respectively), are present in wheat endosperm. While the association between HMWGs and gluten strength is not considered to be as strong as the correlation observed in the context of breadmaking quality in bread wheat (Payne et al. 1984; Pogna et al. 1990), the strong association of LMWGs with pasta quality has been widely reported (Boggini and Pogna 1989; Peña et al. 1994; Pogna et al. 1990; Carrillo et al. 1991; Ruiz and Carrillo 1995a). Additionally, reports have been published about the relationship between gliadins and pasta quality in durum wheat (Pogna et al. 1984, 1990; Carrillo et al. 1991; Ruiz and Carrillo 1995a; Lerner et al. 2004; Martínez et al. 2005).

Protein content is a trait with a strong environmental component while gluten strength tends to be more heritable. High gluten quality is one of the most important goals in pasta wheat breeding programs. Gluten strength is traditionally measured by rheological methods. However, these methods are difficult to apply during the early stages of breeding programs or in genetic mapping studies due to the small quantity of grains available, the high number of genotypes to be evaluated and the elevated cost and time consumption the methods imply. In this context, the SDS sedimentation volume (SV) appears to be amongst the most valuable methods of predicting gluten strength since it shows useful correlations with rheological methods and shows intermediate to high heritability (Clarke et al. 2000).

Both, GPC and gluten strength are complex heritable traits and their dissection into Mendelian factors offers a useful tool for manipulating them using marker-assisted-selection (MAS) in durum wheat breeding programs.

Regarding the genetic control of the endosperm storage proteins, the *Gli-1* and *Gli-2* loci encoding gliadin components have been located on the short arm of the homoeologous chromosome groups 1 and 6, respectively. Joppa et al. (1983) found the *Gli-B1* locus coding for the γ-gliadins bands (γ-45/γ-42) associated with gluten strength. Alternatively, the loci *Glu-1* and *Glu-3,* encoding for glutenins, have been reported to have an important role in gluten strength and were located on the group 1 chromosomes (Pogna et al. 1990). Payne et al. (1984) found a positive correlation between the *Glu-B3* locus and gluten strength measured by the SDS sedimentation technique. In bread wheat, the HMWGs are encoded by the homoeologous *Glu-1* loci (*Glu-A1*, *Glu-B1* and *Glu-D1*) located on the long arms of the group 1 chromosomes (Payne 1987) and the LMWGs are encoded by the *Glu-3* loci (*Glu-A3*, *Glu-B3* and *Glu-D3*) located on the short arms of these chromosomes and tightly linked to the *Gli-1* loci (Lafiandra et al. 2007). Allelic variation is present at each *Glu-1* locus and differential effects of allelic subunits on quality have been repeatedly reported (Payne 1987; Gianibelli et al. 2001; Shewry et al. 2003). However, the effect of the *Glu-B1* locus in some populations of durum wheat can be low or null when the alleles at the parental lines show similar effects (Blanco et al. 1995; Elouafi et al. 2000; Li et al. 2009). Also some alleles present at *Glu-B3* locus can decrease the differences between the *Glu-B1* alleles (Martínez et al. 2005).

The genetic bases of GPC have also been widely studied. The locus *Gpc-B1* on chromosome 6BS has been reported as affecting GPC (Olmos et al. 2003). This locus was more precisely delimited by Distelfeld et al. (2006) and a candidate gene coding for a transcription factor regulating senescence was subsequently cloned (Uauy et al. 2006). Quantative trait loci (QTLs) contributing to the

variation of grain protein content were mapped in all chromosomes using hexaploid and tetraploid wheat mapping populations (Blanco et al. 2000, 2002, 2006; Distelfeld et al. 2006; Joppa and Cantrell 1990; Mann et al. 2009; Olmos et al. 2003; Suprayogi et al. 2009; Uauy et al. 2006; Zhang et al. 2008). In addition, QTLs for flour protein content (Campbell et al. 2001; McCartney et al. 2006; Zhao et al. 2010) or others affecting SV (Elouafi et al. 2000; Kerfal et al. 2010; Li et al. 2009; Patil et al. 2009; Zhang et al. 2008) have also been detected.

The aim of this work was to validate QTLs associated with GPC and gluten strength measured by SV using a mapping population previously evaluated in the USA and to find additional QTLs expressed in Argentinean environments. In addition, epistatic QTLs and QTL x environment interactions were studied in order to gain a better understanding of the genetic bases of these quality traits in durum wheat. These QTLs and its flanking markers would be useful tools to assist durum wheat breeding Argentinean programs.

Methods and materials

Plant material

The mapping population consisted of 93 F_9 recombinant inbred lines (RILs) obtained by single seed descent from the cross between the line UC1113 and the variety Kofa. UC1113 is a breeding line from the UC Davis wheat breeding program with excellent agronomic performance and intermediate pasta quality parameters (W=123-149) (Zhang et al. 2008). Kofa is a durum variety developed by the company West-Bred that has optimal semolina and pasta color, high protein content and strong gluten (W= 290-330). We used eight Argentinean durum wheat varieties as checks in all the experiments (Buck Platino, Buck Topacio, Buck Esmeralda, Buck Cristal, Buck Ambar, Bonaerense INTA Facon, Bonaerense INTA Carilo and Bonaerense INTA Cumenay).

Field trials

The 93 RILs, the parental lines and the eight Argentinean check varieties were sown during two consecutive years (2006 and 2007) at three locations in Argentina (Cabildo [CA], Barrow [BW] and Balcarce [BC]). The field trials were sown following a randomized complete block design (RCBD) with three replications using experimental plots of 3 m^2 in size. A seed density of 150 seeds per square meter average was used. Each year x location combination was considered as environment in the statistics analysis. Agronomical management of fertilization with nitrogen and phosphorous was performed in two applications, at presowing or sowing and tillering, according to local practices and doses for each experimental field (Supplemental material, Table S4). In order to maintain optimum performance of genotypes herbicides and fungicides were used when necessary.

Phenotypic traits

Grain protein content (GPC) expressed in percentage was determined in each plot using Near-Infrared Transmission (NIRT) (Infratec 1226, Tecator, Suecia) according to IRAM procedure 15.879 and based upon 12% moisture content. Whole wheat flour was obtained by milling whole grains with an UDY experimental cyclonic mill (UDY Corporation) with a 1 mm sieve. The SV test was performed according to the technique described by Dick and Quick (1983) using 1 g of whole wheat flour. Quality traits were determined in the three replications by each genotype in each environment. Thousand kernel weight (TKW) was obtained from the mean weight of two 100 seed samples. Test weight (TW) was performed and was expressed in kg hl^{-1}. Grain yield (GY) of each plot was measured from the entire plot and was expressed in kg ha^{-1}. We used these three parameters (TKW, TW and GY) to check the correlation with quality traits. Days to heading was calculated as the number of days between seedling emergence and the day when >50% of the ears of each RIL had emerged from the flag leaf.

Statistical analysis

Standard statistical analyses were carried out using the Microsoft Office Excel 2003 package and SAS software version 9.0 (SAS Institute Inc., Cary, NC, 1990). Analysis of variance (ANOVA) was conducted for every environment separately and a combined ANOVA was performed over all environments. The normality of residuals was analyzed by the Shapiro-Wilk test at 5% significance level. To conduct the joint analysis over environments, variance homogeneity was tested according to the criteria proposed by Cruz and Ragazzi (1997), in which variances are considered as homogeneous when the ratio between the larger and the smaller residual mean square is smaller than 7. Population parameters such as the heritability and the genotypic, phenotypic, environmental and interaction variances were estimated by the GENES program (Cruz 1997).

Genetic map and QTL analysis

QTL mapping was performed using the linkage map of durum wheat reported by Zhang et al. (2008). The total

length of the map was 2,140 cM (giving a mean chromosome length of 153 cM), based on 269 markers including molecular (230 SSR, 23 SNP, 10 RFLP and 3 STS), morphological (*Bla*) and protein markers (*Glu-B1*and *Gli-A2* loci). Following the nomenclature used in the linkage map (Zhang et al. 2008), the X preceding the marker name generally used to indicate marker type (McIntosh et al. 2003) was omitted from text and tables. Windows QTL Cartographer version 2.5 (Wang et al. 2004) was used to conduct composite interval mapping (CIM) with a 0.5 cM walking speed and a 10 cM window size. The threshold LOD score was calculated for each trait and environment performing 1000 permutations at $p<0.10$ (suggestive) and $p<0.05$ (significant) (Churchill and Doerge 1994) (ranges from Table S2: SV $p<0.10$[2.78-3.29], $p<0.05$[3.11-3.70]; GPC $p<0.10$[2.76-2.96], $p<0.05$ [3.11-3.66]). The confidence intervals were indicated as the two-LOD drop off support intervals that confer a 95% confidence region (Van Ooijen 1992). QTL mapping was performed for every environment separately and for the average of the six environments (Mean QTL) for each trait. Interactions were identified with the software QTLNetwork version 2.0 (http://ibi.zju.edu.cn/software/qtlnetwork/) based on the mixed linear model (Wang et al. 1999). Single-locus and two-locus QTL analyses were performed to examine the main and epistatic effects (QQ) and QTL x environment interactions (QE and QQE). Single factor ANOVA was performed to search for overlapping QTL. The markers closely linked to the SV and GPC QTL identified by CIM were used to verify their effect on DH, TW, TKW and GY. QTLs for GPC and SV were denoted by Gpc and Sv, respectively, in the text and tables, following the rules for QTLs proposed by McIntosh et al. (2003).

Results

Quality traits

The RIL population, the two parental lines and the eight check varieties were evaluated for GPC and SV. The RILs showed transgressive bi-directional segregation for both traits. The phenotypic results - GPC and SV (mean, variances and heritability) - obtained in different years and locations from Argentina are shown in Table 1. The GPC data were normally distributed in five out of six environments, although the SV values were normal only in two environments. The check varieties values for both traits are shown in Table S1 (supplemental material).

The parental lines showed statistically significant differences in GPC only in three of the six environments considered, with the variety Kofa giving higher values than UC1113. However, the RILs had more extreme values of GPC than the parental lines in all the environments. The transgressive lines presented mostly positive transgressive segregation with higher GPC values than the variety Kofa. The ANOVA allowed us to detect highly significant differences between the RILs in the six environments, with very low experimental error (CV range=2.6% - 4.5%). The genotypic variance was much higher than the environmental one, resulting in high values of heritability in each environment (Table 1). On the other hand, for the SV test several lines showed negative transgressive segregation, even though most of the RILs were within the range of the parental lines in four out of six of the environments (CA 2006, BC 2006, BW 2007, and BC 2007). Only in the two remaining environments a few lines showed positive transgressive segregation. Nevertheless, the parental lines

Table 1 Grain protein content (GPC) and SDS sedimentation volume (SV) from a RILs population derived from the cross UC1113 x Kofa in six environments of Argentina

Trait	Environment [a]	UC1113	Kofa	RIL mean (range)	CVe% [b]	σ_p^2 [c]	σ_e^2 [d]	σ_G^2 [e]	h^2% [f]
SV	CA 2006	44.8	72.2***	52.1 (37.7-74.7)	4.76	45.98	2.05	43.93	95.54
	BW 2006	48.6	73.8***	57.1 (36.0-83.3)	4.73	74.21	2.43	71.78	96.72
	BC 2006	45.8	74.1***	56.0 (42.3-70.3)	4.46	42.81	2.07	40.74	95.16
	CA 2007	52.3	89.3***	66.2 (43.0-95.0)	5.3	134.46	4.18	130.28	96.89
	BW 2007	55.0	90.3***	61.5 (40.0-92.0)	6.88	106.16	6.19	99.97	94.17
	BC 2007	55.7	87.7***	61.5 (40.0-90.0)	4.79	106.48	3.14	103.34	97.05
GPC	CA 2006	17.5	17.6	18.1 (16.3-19.7)	2.86	0.52	0.09	0.43	82.85
	BW 2006	15.0	15.3	15.5 (14.2-16.9)	2.91	0.23	0.07	0.16	70.48
	BC 2006	13.1	14.2**	14.2 (13.0-15.8)	2.82	0.35	0.05	0.30	84.75
	CA 2007	15.0	15. 7	16.2 (13.0-18.8)	4.53	0.73	0.18	0.55	75.38
	BW 2007	14.7	15.8**	15.6 (14.4-17.5)	2.59	0.24	0.05	0.18	77.20
	BC 2007	14.3	15.9**	15.3 (13.3-17.6)	3.10	0.44	0.08	0.36	82.82

[a] CA=Cabildo, BW=Barrow, BC=Balcarce. [b] CVe%=experimental variation coefficient. [c] σ_p^2 =phenotypic variance. [d] σ_e^2 =environmental variance. [e] σ_G^2 =genotypic variance. [f] h^2 =broad-sense heritability percent. **, *** Significantly different of UC1113 at $p<0.01$ and $p<0.001$ respectively

had very well differentiated extreme values. The ANOVA showed highly significant differences in SV values between the RILs for all the environments, with acceptable low CV % values, ranging between 4.5%-6.9%. The broad-sense heritability for the trait in each environment was very high (Table 1).

For both traits, the homogeneity of variances in all the environments was acceptable according to the criteria cited by Cruz and Ragazzi (1997), so the combined ANOVA was performed. We found that the genotype x environment interaction for both traits was also highly significant. The Pearson's simple correlations among environments ranged from 0.20 to 0.52 for GPC, except between the environments CA 2006 and BC 2007, where there was not significant correlation. The SV test showed correlation values among environments ranging from 0.35 to 0.74 (Supplemental material, Table S3). Based on the results of the combined ANOVA, the environmental effect on GPC was much higher than on SV. The major difference between the highest transgressive RIL and the parental variety Kofa (high GPC) was of 2.63% in CA 2007, whereas the lowest difference was found in BW 2007 (1.17%). Both traits, GPC and SV test, were not correlated considering the complete data set. We also investigated the association between GPC and yield parameters and we found that it was negatively and highly significantly correlated with GY (r= −0.35), TKW (r= −0.57) and TW (r= −0.57). In contrast, SV was not affected by these parameters.

QTL analysis

QTLs for grain protein content (GPC)

A total of nine significant ($p<0.05$) and one suggestive ($p<0.10$) QTLs were detected by CIM analysis for GPC explaining from 9.3% to 21.6% of the phenotypic variance (Table 2). The QTL analysis in the individual environments allowed the identification of genomic regions associated with GPC on the following chromosome arms 1BS, 2AL, 2BS, 2BL, 3BS, 4AL, 5AS, 5BL, 7AS and 7BL. For this trait, both parental lines contributed with positive alleles, although the majority of them were contributed by the line UC1113.

Two QTLs (*QGpc.cerz-3BS* and *QGpc.cerz-7BL*) were expressed in two out of the six individual environments and in the QTL analysis on the average of the six environments. These QTLs showed a very stable peak position. The highest effect was detected for the *QGpc.cerz-3BS*, located on chromosome 3BS, which explained 21.6%, 21.0% and 16.1% of the phenotypic variance in the individual environments BC 2006, CA 2007 and on the average of the six environments, respectively. This QTL had also been found in previous studies performed in Cabildo (CA) in 2004 (Conti et al. 2008) as having a significant effect and explaining 15.5% of the phenotypic variation. The QTL, *QGpc.cerz-7BL*, located on chromosome 7BL, showed a stable position between the SSRs *cfa2040* and *barc1073*.

Table 2 Main effect QTLs for grain protein content (GPC) mapped in a RILs population derived from the cross UC1113 x Kofa in six environments of Argentina

Chr. arm [a]	QTLs [b]	Flanking markers	LOD [c]	Aditive effect (%)	R^2 (%)[d]	Peak position (cM)	2-LOD support interval	Positive alelle	Environment [e]
1BS	*QGpc.cerz-1BS*	*gwm273-wmc626*	4.6*	0.18	13.3	35.1	20.3-41.2	Kofa	BW 2006
2AL	*QGpc.cerz-2AL*	*cfd50-gdm93*	3.2 s	−0.2	14.1	150.0	123.5-162.5	UC1113	BW 2007
2BS	*QGpc.cerz-2BS*	*wmc597-BM140538_39*	5.8*	−0.32	20.8	24.2	17.3-34.7	UC1113	BC 2007
3BS	*QGpc.cerz-3BS*	*barc147-gwm493*	7.4*	−0.29	21.6	13.0	9.8-17.5	UC1113	BC 2006
3BS	*QGpc.cerz-3BS*	*barc147-gwm493*	5.6*	−0.39	21.0	12.3	4.5-20.5	UC1113	CA 2007
3BS	*QGpc.cerz-3BS*	*barc147-gwm493*	4.9*	−0.2	16.1	13.0	8.3-19.5	UC1113	Mean
3BL	*QGpc.cerz-3BL*	*gwm66-cfa2134*	3.5*	−0.23	9.5	116.3	71.9-136.9	UC1113	CA 2006
3BL	*QGpc.cerz-3BL*	*cfa2134-BQ159467_233*	3.3*	−0.16	9.3	117.3	87.9-130.8	UC1113	Mean
4AL	*QGpc.cerz-4AL*	*dupw4-barc170*	5.7*	−0.3	16.6	44.2	35.6-54.3	UC1113	CA 2006
5AS	*QGpc.cerz-5AS*	*barc101-barc117*	4.8*	0.23	21.0	29.5	12.5-40.5	Kofa	BW 2007
5BL	*QGpc.cerz-5BL*	*gwm499-BE495277_339*	3.9*	−0.26	14.6	72.5	56.5-87.8	UC1113	BC 2007
7AS	*QGpc.cerz-7AS*	*wmc168-barc219*	3.2*	0.25	12.7	30.1	14.5-42.6	Kofa	BC 2007
7BL	*QGpc.cerz-7BL*	*cfa2040 -barc1073*	4.1*	0.18	12.1	184.6	170.9-191.0	Kofa	BW 2006
7BL	*QGpc.cerz-7BL*	*cfa2040 -barc1073*	4.2*	0.2	13.0	184.6	177.9-191.0	Kofa	BW 2007
7BL	*QGpc.cerz-7BL*	*barc1073-barc340*	4.3*	0.21	15.6	185.6	178.9-190.1	Kofa	Mean

[a] Chr.=chromosome. [b] Gpc=grain protein content, *cerz*=Centro de Recursos Naturales de la Zona Semiárida. [c] s and * threshold LOD at $p<0.10$ (suggestive) and $p<0.05$ (significant), respectively. [d] R^2 =% Phenotypic variance explained for the QTL. [e] CA=Cabildo, BW=Barrow, BC=Balcarce. Mean=pooled data of the six environments

This QTL explained 12.1%, 13.0% and 15.6% of the variation in the environments BW 2006, BW 2007 and in the QTL analysis on the average data (combined six environments), respectively. The parental line UC1113 contributed with the positive allele for *QGpc.cerz-3BS*, whereas Kofa carried the positive allele for *QGpc.cerz-7BL*.

The QTL, *QGpc.cerz-4AL*, was mapped on chromosome 4AL and explained 16.6% of the phenotypic variance in CA 2006. Another QTL, *QGpc.cerz-5AS*, was found significant in BW 2007 on the chromosome arm 5AS, accounting for 21.0% of the phenotypic variance in this environment. A minor effect QTL (*QGpc.cerz-3BL*) was mapped on chromosome arm 3BL in CA 2006 and in the average of the six environments with their positive allele carried by UC1113.

In this study, seven out of 10 QTLs detected were only present in one environment (*QGpc.cerz-1BS, QGpc.cerz-2AL, QGpc.cerz-2BS, QGpc.cerz-4AL, QGpc.cerz-5AS, QGpc.cerz-5BL* and *QGpc.cerz-7AS*). The QTL, *QGpc.cerz-1BS*, located on chromosome arm 1BS explained 13.3% of the phenotypic variation in BW 2006. The *QGpc.cerz-2AL* was associated with GPC in BW 2007. We found three QTLs affecting GPC in BC 2007 (*QGpc.cerz-2BS*, *QGpc.cerz-5BL* and *QGpc.cerz-7AS*), but they were only detected in this environment, where the *QGpc.cerz-2BS* had the most important effect on GPC (R^2= 20.8%).

QTLs for SDS sedimentation volume

Eleven QTLs were mapped by CIM for SV, explaining from 4.9 to 54.2% of the phenotypic variation. They were distributed on chromosome arms 1AS, 1AL, 1BL, 3BS, 3BL, 4AL, 4BS, 6AL, 6BL, 7AS and 7AL (Table 3). The most important QTLs mapped in this work were located on chromosome arms 1BL, 6AL, 6BL and 7AS, with positive alleles contributed by the parental line Kofa.

The main QTL affecting SV, *QSv.cerz-1BL*, was found to be closely linked to the HMWG locus *Glu-B1* on chromosome arm 1BL. This QTL was consistently detected in the six environments and explained the highest percentage of the variance in all of them, ranging between 20.9% and 54.2% (LOD=6.7 - 17.6).

A significant QTL, *QSv.cerz-6AL*, was mapped on chromosome arm 6AL in three environments (CA 2006, BC 2006 and BC 2007). Although not significant or suggestive, according to the permutation test, a LOD value of 2.9 was observed at the same position in the mean QTL detection. Another important significant QTL, *QSv.cerz-6BL*, was mapped on chromosome arm 6BL in two environments and in the average of the six environments (Table 3). The QTL mapped on chromosome arm 7AS appeared in two environments, but was only significant in the mean of the six environments, in which it explained 15.2% of the phenotypic variation. The *QSv.cerz-3BL* and *QSv.cerz-4BS* QTLs were detected only in two environments.

Pleiotropic QTLs with yield and yield related traits

To explore the possibility that both SV and GPC QTLs were mapped in a pleiotropic region that also affected grain yield, yield related traits (TKW, TW) or growth traits such as days to heading, which affect the agronomic performance, a one-way ANOVA with the locus in the peak of the QTLs detected by CIM was conducted (Table 6).

A significant effect of the *gwm493* marker, linked to *QGpc.cerz-3BS*, on GY in four out of the six environments and for the mean data of the six environments was detected. This marker also had a significant effect on TKW and TW in one and two environments, respectively. The positive allele for these traits carried by Kofa also affected protein content, showing a decrease. In the same way, the microsatellite *barc117*, linked to *QGpc.cerz-5AS* showed a significant effect on TKW in BW 2007 and the mean data. But in a different way, the *BE495277_339* allele from UC1113 closely linked to *QGpc.cerz-5BL*, was associated with a simultaneous increase in GPC, TW and TKW in three and four data sets. The presence of this allele decreased the GY in CA 2007. In addition, an association with GY was found with the linked SSR markers *bar113* (*QSv.cerz-6AL*), whereas the *barc219* allele from Kofa, linked to *QSv.cerz-7AS*, also was associated to a decrease the TW in four environments.

Epistatic effects and QTL x environment interactions

The results of QE interactions for both quality traits are shown in Table 4. For SDS sedimentation volume only the *QSv.cerz-7AL* was involved in QE interaction. Nevertheless, three (*QGpc.cerz-2BS*, *QGpc.cerz-3BS* and *QGpc.cerz-4AL*) out of nine of the significant main effect QTLs detected for GPC showed QE interaction. Most of the QE interaction was detected in the environments that presented extreme rainfall conditions (CA 2006 and BC 2007), with the lowest and highest precipitation values, respectively (Table S5). Also, these locations showed the major differences in mean and maximum temperatures across the growing season (Supplementary material, Table S5). The QTL, *QGpc.cerz-3BS*, had the highest number of environmental interactions. QTLs with QQ and QQE interactions effects for both quality traits are shown in Table 5. A total of five digenic epistatic QTLs were detected for GPC and two QQ interactions for SV. The *QSv.cerz-1BL*, that presented the most important effect on SV, showed an epistatic effect with the *QSv.cerz-5BL* that did not show a main effect. Only one pair of epistatic QTLs (*QGpc.cerz-*

Table 3 Main effect QTLs for SDS sedimentation volume mapped in a RILs population obtained from the cross UC1113 x Kofa in six environments of Argentina

Chr. arm [a]	QTLs [b]	Flanking markers	LOD [c]	Aditive effect (%)	R^2 (%)[d]	Peak position (cM)	2-LOD support interval	Positive alelle	Environment [e]
1AS	*QSv.cerz-1AS*	*Bla-wmc95*	3.3*	−2.01	8.6	0.0	0-18.5	UC1113	CA 2006
1AL	*QSv.cerz-1AL*	*BM140362_603-wmc312*	3.0 s	1.47	4.9	87.0	77.4-91.6	Kofa	BC 2006
1AL	*QSv.cerz-1AL*	*BM140362_603-wmc312*	3.3 s	1.84	5.8	88.0	76.2-112.6	Kofa	Mean
1BL	*QSv.cerz-1BL*	*Glu-B1-cfa2129*	11.0*	3.92	31.0	82.6	75.3-89.3	Kofa	CA 2006
1BL	*QSv.cerz-1BL*	*barc181-Glu-B1*	7.4*	4.65	27.1	80.3	70.3-92.8	Kofa	BW 2006
1BL	*QSv.cerz-1BL*	*barc181-Glu-B1*	15.4*	4.78	51.8	78.8	70.3-82.6	Kofa	BC 2006
1BL	*QSv.cerz-1BL*	*barc181-Glu-B1*	7.4*	6.93	34.7	80.3	71.3-94.3	Kofa	CA 2007
1BL	*QSv.cerz-1BL*	*cfa2129-psr162*	12.6*	7.75	54.2	90.8	84.8-96.8	Kofa	BW 2007
1BL	*QSv.cerz-1BL*	*Glu-B1-cfa2129*	6.7*	4.88	20.9	82.6	74.8-92.8	Kofa	BC 2007
1BL	*QSv.cerz-1BL*	*barc181-Glu-B1*	17.6*	5.19	46.2	81.8	74.8-84.1	Kofa	Mean
3BS	*QSv.cerz-3BS*	*cfd79-ksm45*	4.0*	4.17	14.7	30.0	22.0-43.4	Kofa	BC 2007
3BL	*QSv.cerz-3BL*	*BQ159467_233-barc164*	3.2*	−2.22	9.9	128.8	119.8-154.9	UC1113	CA 2006
3BL	*QSv.cerz-3BL*	*gwm66-cfa2134*	4.3*	−1.98	8.4	116.3	109.5-136.9	UC1113	BC 2006
4AL	*QSv.cerz-4AL*	*dupw4-barc170*	4.1*	−2.06	7.3	46.2	32.6-57.3	UC1113	Mean
4BS	*QSv.cerz-4BS*	*ksm62-gwm113*	4.2*	2.34	11.0	30.9	13.2-39.7	Kofa	CA 2006
4BS	*QSv.cerz-4BS*	*ksm62-gwm113*	7.2*	2.69	16.4	29.9	25.5-34.4	Kofa	BC 2006
6AL	*QSv.cerz-6AL*	*barc113-wmc553*	3.9*	2.25	10.5	59.9	52.7-68.8	Kofa	CA 2006
6AL	*QSv.cerz-6AL*	*barc116-barc113*	3.4*	1.67	6.4	57.4	49.2-67.1	Kofa	BC 2006
6AL	*QSv.cerz-6AL*	*barc113-wmc553*	3.8*	3.98	12.5	65.9	58.9-71.8	Kofa	BC 2007
6BL	*QSv.cerz-6BL*	*gwm219-wmc621*	4.5*	3.7	12.1	127.5	115.5-136.7	Kofa	BW 2007
6BL	*QSv.cerz-6BL*	*gwm219-wmc621*	3.2 s	3.61	11.5	119.5	98.9-131.0	Kofa	BC 2007
6BL	*QSv.cerz-6BL*	*gwm219-wmc621*	4.7*	2.35	9.6	117.5	106.9-129.0	Kofa	Mean
7AS	*QSv.cerz-7AS*	*gwm635-barc70*	3.0 s	2.01	8.2	9.5	0-31.6	Kofa	CA 2006
7AS	*QSv.cerz-7AS*	*barc70-wmc168*	3.4 s	3.8	10.2	16.0	2.0-39.6	Kofa	CA 2007
7AS	*QSv.cerz-7AS*	*barc70-wmc168*	7.3*	3.01	15.2	16.0	6.5-24.0	Kofa	Mean
7AL	*QSv.cerz-7AL*	*wmc603-wmc488*	4.7*	5.65	22.2	112.1	96.4-123.1	Kofa	CA 2007

[a] Chr.=chromosome. [b] Sv=SDS sedimentation volume, *cerz*=Centro de Recursos Naturales de la Zona Semiárida. [c] s and * threshold LOD at $p<0.10$ (suggestive) and $p<0.05$ (significant), respectively. [d] R^2 =% Phenotypic variance explained for the QTL. [e] CA=Cabildo, BW=Barrow, BC=Balcarce. Mean=pooled data of the six environments

2BS and *QGpc.cerz-3BL*) also showed environmental interactions for GPC.

Discussion

Phenotypic data

Kofa showed numerically higher GPC than UC1113 in all the environments considered, but the differences were statistically significant only in three out of the six mentioned environments (Table 1). These results were unexpected, according to previous knowledge that we had about these varieties. A possible explanation may be that these materials were not previously tested in these environments and the genotype behavior is different than in the US. On the other hand, problems due to erroneous seed mixing was ruled out based upon the results of molecular markers for a study on lipoxygenase genes using the same plant materials.

The transgressive bi-directional segregation for GPC was mainly positive and would allow the selection of genotypes having favorable allele combinations for GPC. For SV, the parental lines showed significant differences in all the environments considered, ranging between 20 and 30 mm, but for this trait the transgressive bi-directional segregation was mainly negative. This agrees well with the results of the QTL mapping in which the line UC1113 contributed with very few positive alleles to increase the SV values. It is possible that the RILs do not have better allele combinations than Kofa, since the SV values were similar or lower than the ones obtained for this variety.

Table 4 QTL x environment interactions for SDS sedimentation volume (SV) and grain protein content (GPC) in the UC1113 x Kofa mapping population of durum wheat

Trait	QTL[a]	Flanking markers	Additive effect	QTL x environment interactions [b]
SV	*QSv.cerz-7AL*	*wmc603 - wmc488*	5.65	−1.97** (CA 2007)
GPC	*QGpc.cerz-2BS*	*wmc597 - BM140538_39*	−0.32	−0.09*(CA 2006), 0.12**(BC 2007)
	QGpc.cerz-3BS	*barc147 - gwm493*	0.50	0.10*(BC 2006), 0.16**(CA 2007), -0.12**(BC 2007)
	QGpc.cerz-4AL	*dupw4 -barc170*	0.43	0.15**(CA 2006), -0.13**(BC 2007)

[a] GPC/Gpc=grain protein content, SV/Sv=SDS sedimentation volume, *cerz*=Centro de Recursos Naturales de la Zona Semiárida. [b] *P<0.05; **P<0.01, respectively. CA=Cabildo, BC=Balcarce

Genotype was the main source of variation for both evaluated traits, indicating that the environmental variance, although present, was relatively lower and allowed the expression of the genotypic differences, resulting in high heritability values. Heritability values for GPC ranged from 70.5% to 84.8%, being more variable between years in Cabildo and Barrow. Our results showed moderate to high heritability values for GPC, similar to those reported in several publications (Blanco et al. 2002; Huang et al. 2006). For SV the heritability ranged from 94.2% to 97.1%. These results were in agreement with those reported by Clarke et al. (2000) and were higher than those reported by Huang et al. (2006) and Patil et al. (2009). The genotype–environment interaction was highly significant for GPC and SV, showing that these traits require selection in multiple environments. Possibly, it was mostly due the high differences observed between locations and years in rainfall conditions (Supplemental material, Table S5). Also, the application of nitrogen and phosphorous was different between locations, taking into account the local agronomical practices. For that reason, the use of molecular markers linked to QTL would simplify the selection process in breeding programs.

QTL analysis

Grain protein content

The presence of QTLs influencing GPC in nine different chromosomes of the UC1113 x Kofa mapping population agrees well with previous reports in cultivated and wild wheat (Joppa and Cantrell 1990; Zanetti et al. 2001; Blanco et al. 2002). The most significant QTLs detected in this work on chromosomes 3BS and 7BL (*QGpc.cerz-3BS* and *QGpc.cerz-7BL*) were previously mapped by Zhang et al. (2008) using the same RIL population evaluated in California (USA). The *QGpc.cerz-3BS* was detected only in one environment from California, whereas the effect of this QTL in Argentinean environments was higher, although with moderate values, explained the highest percentage of phenotypic variation in two environments (BC 2006 and CA 2007) and in the QTL analysis using the average data of the six environments. This also agrees with a QTL on 3B recently reported by Zhao et al. (2010) using a common wheat population. However, the closest marker to this QTL also showed a significant effect on GY, TKW and TW in the Argentinean environments (Table 6). The

Table 5 Epistatic QTLs and QTL x QTL x environment interaction for the durum wheat quality traits SDS sedimentation volume and grain protein content

Trait[a]	QTL_i[b]	Flanking $markers_i$	Peak $position_i$	QTL_j[b]	Flanking $markers_j$	Peak $position_j$	Q_i x Q_j epistatic effect [c]	Q_i x Q_j x E interaction [c]
SV	*QSv.cerz-1BL*	*GluB1-cfa2129b*	83.60	*QSv.cerz-5BL*	*gwm497- gwm118*	180.2	0.97	–
	QSv.cerz-1BL.2	*barc80-ksm176*	145.40	*QSv.cerz-5BL*	*gwm497- gwm118*	180.2	2.13	–
GPC	*QGpc.cerz-2BS*	*cfa2201-gwm429*	17.30	*QGpc.cerz-3BL*	*cfa2134-BQ159467_233*	97.20	0.08	−0.10*(CA 2006), 0.12**(BC 2007)
	QGpc.cerz-3BS	*wmc43-gwm285*	60.40	*QGpc.cerz-5BL*	*wmc149-barc74*	15.10	0.15	–
	QGpc.cerz-4AL	*wmc262-barc343*	103.10	*QGpc.cerz-7BL*	*wmc396-barc278*	106.30	−0.11	–
	QGpc.cerz-5BL	*wmc149-barc74*	15.10	*QGpc.cerz-7AS*	*BE471272_393-wmc596*	99.70	0.09	–
	QGpc.cerz-5BL	*barc74-gwm371*	47.20	*QGpc.cerz-7AS*	*BE471272_393-wmc596*	99.70	0.16	–

[a, b] GPC/Gpc=grain protein content, SV/Sv=SDS sedimentation volume. [b] Bold=QTLs with significant main effect. [c] CA=Cabildo, BC=Balcarce. Q_i=QTL_i, Q_j=QTL_j, E=environment

Table 6 Single factor ANOVA with the locus in the peak of the QTLs associated with SV and GPC detected by CIM used to find putative overlapping QTLs associated with days to heading (DH), test weight (TW), thousand kernel weight (TKW) and grain yield (GY)

Trait [a]	QTL (allele) [b]	Peak marker	Overlapping	F test [d]						
			QTL (allele) [b,c]	CA 2006	BW 2006	BC 2006	CA 2007	BW 2007	BC 2007	Average
GPC	*QGpc.cerz-1BS* (K)	*wmc626*	GY (U)	ns	4.01*	ns	ns	5.2*	ns	5.88*
	QGpc.cerz-2BS (U)	*BM140538_39*	DH (K)	–	16.38***	–	6.27**	–	ns	7.67**
			TKW (K)	ns	ns	4.03*	ns	ns	ns	ns
			GY (U)	10.22**	8.46**	ns	ns	ns	ns	ns
	QGpc.cerz-3BS (U)	*gwm493*	TW (K)	ns	ns	37.98***	ns	ns	5.03*	ns
			TKW (K)	ns	ns	33.03***	ns	ns	ns	ns
			GY (K)	ns	5.69*	51.66***	25.29***	6.68*	ns	25.6***
	QGpc.cerz-4AL (U) / *QSv.cerz-4AL* (U)	*barc170*	DH (U)	–	ns	–	ns	–	4.3*	ns
			TW (K)	5.83*	ns	ns	ns	ns	ns	ns
			GY	4.3* (K)	ns	ns	ns	ns	4.23*(U)	ns
	QGpc.cerz-5AS (K)	*barc117*	TKW (U)	ns	ns	ns	ns	4.34*	ns	6.9*
	QGpc.cerz-5BL (U)	*BE495277_339*	TW (U)	9.8**	ns	4.92**	ns	ns	ns	7.74**
			TKW (U)	11.16**	ns	4.09*	ns	5.83*	ns	8.24**
			GY (K)	ns	ns	ns	5.13*	ns	ns	ns
SV	*QSv.cerz-1BL* (K)	*Glu-B1*	TW (U)	ns	11.22**	ns	4.44*	ns	ns	ns
			GY (U)	7.74**	19.39***	ns	ns	ns	ns	4.78*
	QSv.cerz-4BS (K)	*gwm113*	GY (U)	ns	ns	ns	ns	ns	8.44**	ns
	QSv.cerz-3BS(K)	cfd79	DH (U)	–	4.60*	–	10.63***	–	ns	8.25**
			TW (K)	ns	ns	11.45**	ns	ns	ns	ns
			TKW (K)	ns	ns	21.22***	ns	ns	ns	4.44*
			GY (K)	6.68*	4.96*	19.91***	11.99***	ns	ns	9.19**
	QSv.cerz-6AL (K)	*bar113*	DH (K)	–	5.74*	–	7.48**	–	6.77*	8.67**
			TW (U)	ns	ns	4.00*	ns	ns	ns	ns
			GY (U)	4.16*	ns	8.80**	14.15***	ns	ns	4.10*
	QSv.cerz-7AS (K)	*barc219*	TW (U)	ns	10.17**	6.79*	4.91*	4.92*	ns	10.59**

[a] SV = SDS sedimentation volume, GPC = grain protein content. [b] U = UC1113, K = Kofa. [c] DH = Days to heading, TW = Test weight, TKW=1000-kernel weight, GY = Grain yield. [d] *, **, *** significant values at $p<0.05$, $p<0.01$ and $p<0.001$. ns=not significant. CA = Cabildo, BW = Barrow, BC = Balcarce. Only significant associations were shown in the table

positive allele for *QGpc.cerz-3BS* was carried by the UC1113 line, but this allele decreased the GY, TKW and TW. These results may interfere with the use of the 3BS QTL in MAS and it will be necessary to characterize the pleiotropic effect of this QTL in different populations or cultivar collections.

In contrast, *QGpc.cerz-7BL* did not show a pleiotropic effect with GY or yield related QTLs and could be a good target to help in the Argentinean breeding programs using MAS. The close negative relationship between grain yield and GPC is well known, and an independent gene to increase GPC is an important goal. Zhang et al. (2008) found this QTL in USA environments using the same mapping population. Our analysis allowed us to validate this QTL in a stable position on the SSR *barc1073* in Argentinean environments. The RILs carrying the Kofa allele for this marker have shown higher GPC. Blanco et al. (2006) and Campbell et al. (2001) in durum wheat and Huang et al. (2006) in bread wheat also reported a QTL located on chromosome 7BL associated with flour protein content. Suprayogi et al. (2009) also found a QTL for GPC on the distal region of 7BL in a similar position to that found in our work, based on the common marker *wmc311*.

The *QGpc.cerz-5AS* QTL was also reported by Zhang et al. (2008). This QTL was more relevant in California, but our analysis showed the *QGpc.cerz-5AS* only significant in BW 2007, in which it explained the highest percentage of variance. Mann et al. (2009) also found a QTL on 5A in common wheat, but in a more distal position of the telomeric region. However, the positive allele from Kofa for *QGpc.cerz-5AS* also showed a decrease in the TKW in BW 2007 and the mean data (Table 6) and could limit the

usefulness of this QTL in MAS, although validation in different genetic backgrounds is needed.

A QTL on 7AS was also reported by Suprayogi et al. (2009) at 10.3 cM apart from the marker *barc219*. In our study, the *QGpc.cerz-7AS* QTL was flanked by the microsatellite *barc219*. Blanco et al. (2002) in durum wheat and Prasad et al. (2003) and Groos et al. (2003) in common wheat also reported a QTL for GPC on 7AS. Kofa carried the positive allele for *QGpc.cerz-7AS* that did not show pleiotropic effects on GY, TKW, TW or DH. Another QTL, the *QGpc.cerz-4AL*, that showed environmental interaction in two environments (Table 4), was previously reported by Kunert et al. (2007) in hexaploid wheat. This QTL and our QTL (*QGpc.cerz-4AL*) were flanked by a common SSR marker (*barc170*). This microsatellite showed to be significant associated with GY, but with the opposite allele in the two environments detected, indicating a possible spurious association with GY. Although *QGpc.cerz-4AL* did not show a main effect in BC 2007, this QTL showed environmental interaction in this environment, may be due to the high rainfall conditions (supplemental material, Table S5).

The *QGpc.cerz-2BS* QTL linked to the *BM140538_39* marker was also reported by Suprayogi et al. (2009), in a region similar to the one reported in this work. Even though the UC1113 allele was associated with a simultaneous increase of the GPC and GY in two environments (CA 2006 and BW 2006), we found a significant reduction of the heading date caused by this allele in three data set, which could prejudice their application in MAS. An additional QTL was also mapped on chromosome arm 3BL. Previous works also reported a QTL associated with GPC on chromosome 3B (Joppa and Cantrell 1990; Li et al. 2009) and specifically on the long arm (Blanco et al. 2000).

SDS sedimentation volume

The most important QTLs for SV found in this work are in agreement with those cited by other authors on chromosome arms 1BL, 6AL, 6BL and 7AS (Elouafi et al. 2000; Kerfal et al. 2010; Patil et al. 2009; McCartney et al. 2006; Zhang et al. 2008). The position of the *QSv.cerz-1BL* QTL located on chromosome 1BL coincided with the protein marker *Glu-B1* on the map. This result confirms the positive influence of HMWGs over gluten strength. In a previous work, we found the *Glu-B1* allele carried by Kofa (allele d, subunits 6+8) strongly associated with higher SV values, while the parental line UC1113 (allele b, subunits 7+8) showed poor values (V.A. Conti 2007, PhD Thesis, Universidad Nacional del Sur, Argentina). The *QSv.cerz-1BL* was the main QTL affecting SV across the environments (R^2=20.92 - 54.18 %) and the positive allele was contributed by the higher parental Kofa. This QTL explained a higher percentage of variance in Argentina compared to Californian environments (Zhang et al. 2008). This locus also showed an epistatic effect with the *QSv.cerz-5BL* QTL, which did not have a main effect. However, the *QSv.cerz-1BL* flanked by the *Glu-B1* locus did not show environmental interactions (QE and QQE), which agrees well with the strong genetic effect detected across all the environments. Huang et al. (2006) and McCartney et al. (2006) found the *Glu-B1* locus associated with SV, using common wheat populations. Alternatively, Li et al. (2009) reported the homoeologous loci *Glu-A1* and *Glu-D1* strongly associated with this trait, also in common wheat. Recently, Patil et al. (2009) found a QTL linked to the *Glu-B1* locus associated with SV in durum wheat. In contrast, Elouafi et al. (2000) and Blanco et al. (2000) did not find any effect of the *Glu-B1* locus on gluten strength and they suggested that this had been probably due to the similar effect of the alleles carried by the parental lines in these durum wheat populations.

The present work allowed the identification of previously undetected QTLs on chromosomes 3BS, 3BL, 4AL, 4BS, 6AL, 7AS and 7AL using the UC1113 x Kofa mapping population, in addition to those already detected by Zhang et al. (2008). However, the effect of the QTL reported on 5AL was not validated using Argentinean environments, while *QSv.cerz-1AL* was only detected as suggestive ($p<0.10$) in our analysis. The 7AS QTL was recently reported by Kerfal et al. (2010) as being closely linked to the *gwm635* marker. This agrees well with our results because this microsatellite flanked the confidence interval of the *QSv.cerz-7AS* in the UC1113 x Kofa linkage map.

On the other hand, the QTLs *QSv.cerz-3BL* and *QSv.cerz-4AL* showed pleiotropic effects on GPC, with small differences in the QTL peak position. The marker on the peak of *QSv.cerz-4AL* has also been associated with GY and TW, as was discussed for GPC (Table 6). Four additional QTLs affecting SV, *QSv.cerz-3BS*, *QSv.cerz-4BS*, *QSv.cerz-6AL* and *QSv.cerz-1BL*, were associated with pleiotropic effects on GY, while the favorable allele of the peak marker of *QSv.cerz-7AS* showed a decrease in the TW. The *cfd79* allele from Kofa, linked to *QSv.cerz-3BS*, was associated with an increase in the gluten strength and also with GY, TKW and TW, but caused a small decrease in days to heading (1 day). The *QSv.cerz-4BS* marked by *gwm113* was significantly associated with GY in BC 2007 with opposite allele compared to SV. While, the Kofa allele of *barc113*, linked to *QSv.cerz-6AL*, increased the SV values and the DH, but it was associated with lowest GY values in three environments and in the average data set. It is necessary to consider these effects before using the QTLs in MAS, although some pleiotropic effects were lower.

In this study, QTLs with QQ interactions were found for both quality traits showing the complexity of these parameters. QE interactions were also found in this work, mainly affecting GPC, which confirm the major influence of the environment in the expression of this quality trait. These mapping results suggest that other additional genes affecting SV and GPC are present in the UC1113 x Kofa genetic background and the evaluation in Argentinean environments allowed these genes to be expressed. The highest effect detected in some QTLs in relation with the work of Zhang et al. (2008) could indicate that they may be better adapted to Argentina. The QTL, *QGpc.cerz-7BL*, is an interesting target loci to increase the GPC in Argentinean breeding programs; the *Glu-B1* locus also showed a strong effect, but the interaction with Glu-B3 alleles or their effect on different genetic backgrounds should be confirmed.

The contribution of new information coming from the evaluation in different environments and using different plant populations will combine to understand the genetic bases of these complex and quantitative traits and will furthermore help to select molecular markers to be used in MAS of durum wheat.

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References

Blanco A, and De Giovanni C (1995) Triticum dicoccoides for qualitative improvement of durum wheat: Associations of protein loci to grain traits in recombinant inbred lines. p. 149–159. In N. di Fonzo et al. (ed.) Durum wheat quality in the Mediterranean region.CIHEAM/ICARDA/CIMMYT,Zaragoza, Spain. 17–19Nov. 1993. Mediterranean Agronomic Institute, Chania, Greece

Blanco A, Simeone R, Laddomada B, Pascualone A, Troccoli A, Di Fonzo N (2000) Variation for grain protein content and identification of QTLs by molecular markers in tetraploid wheats. En: Durum wheat improvement in the Mediterranean region: New challenges. pp. 455–461. Royo C, Nachit, MM, DiFonzo N, y Arauz, JL. (eds). International Centre for Advanced Mediterranean Agronomic Studies (CIHEAM), Zaragoza

Blanco A, Pasqualone A, Troccoli A, Di Fonzo N, Simeone R (2002) Detection of grain protein content QTLs across environments in tetraploid wheats. Plant Mol Biol 48:615–623

Blanco A, Simeone R, Gadaleta A (2006) Detection of QTLs for grain protein content in durum wheat. Theor Appl Genet 112:1195–1204

Boggini G, Pogna NE (1989) The breedmaking quality and storage proteins composition of italian durum wheat. J Cereal Sci 9:131–138

Campbell KG, Finney PL, Bergman CJ, Gualberto DG, Anderson JA, Giroux MJ, Siritunga D, Zhu J, Gendre F, Roué C, Vérel A, Sorrells ME (2001) Quantitative trait loci associated whit milling and baking quality in a soft x hard wheat cross. Crop Sci 41:1275–1285

Carrillo JM, Vázquez JF, Ruiz M, Albuquerque MM (1991) Relationships between gluten strength and protein components in spanish durum wheat landraces. pp. 268–276. En: Gluten Proteins 1990. W. Bushuk y R. Tkachuk (eds.). Am. Assoc. Cereal Chem. St. Paul, MN

Churchill GA, Doerge RW (1994) Empirical threshold values for quantitative trait mapping. Genetics 138:963–971

Clarke JM, Clarke FR, Ames NP, McCaig TN, Knox RE (2000) Evaluation of predictors of quality for use in early generation selection. In: Royo C, Nachit MM, Di Fonzo N, Araus JL (eds) Durum Wheat Improvement In The Mediterranean Region: New Chalenges. International Centre for Advanced Mediterranean Agronomic Studies (CIHEAM), Zaragoza, pp 439–446

Conti V, Cervigni G, Miranda R, Wehrhahne L, Jensen C, Bariffi J, Echenique V (2008) Utilidad de marcadores moleculares asociados a fuerza de gluten en la selección asistida de trigo candeal. VII National Wheat Conference. 2–4 July. La Pampa, Argentina. http://rian.inta.gov.ar/trabajoscongresotrigo2008/

Cruz CD (1997) Programa Genes: aplicativo computacional em genética e estatística. p. 442. Viçosa: Editora UFV

Cruz CD and Regazzi AJ (1997) Modelos biométricos aplicados ao melhoramento genético. 2ª edición. Editora UFV, Universidade Federal de Viçosa. Brasil

D'Egidio MG, Marian BM, Nardi S, Novaro P, Cubadda R (1990) Chemical and technological variables and their relationships: a predictive equation for pasta cooking quality. Cereal Chem 67:275–281

Dick JW, Quick JS (1983) A modified screening test for rapid estimation of gluten strength in early generation durum wheat breeding lines. AACC. Vol. 60, Nº 4

Distelfeld A, Uauy C, Fahima T, Dubcovsky J (2006) Physical map of the wheat high-grain protein content gene Gpc-B1 and development of a high-throughput molecular marker. New Phytol 169:753–763

Elouafi I, Nachit MM, Elsaleh A, Asbati A, Mather DE (2000) QTL-mapping of genomic regions controlling gluten strength in durum (Triticum turgidum L. var. durum). En: Durum wheat improvement in the Mediterranean region: New challenges. Options mediterranéennes 40: 455–461. Royo, C, Nachit, MM, DiFonzo, N. y Arauz, JL (eds) International Centre for Advanced Mediterranean Agronomic Studies (CIHEAM), Zaragoza

Gianibelli MC, Larroque OR, MacRitchie F, Wrigley CW (2001) Biochemical, genetic, and molecular characterization of wheat endosperm proteins. Cereal Chem 78:635–646

Groos C, Robert N, Bervas E, Charmet G (2003) Genetic analysis of grain protein-content, grain yield and thousand-kernel weight in bread wheat. Theor Appl Genet 106:1032–1040

Huang XQ, Cloutier S, Lycar L, Radovanovic N, Humphreys DG, Noll JS, Somers DJ, Brown PD (2006) Molecular detection of QTL for agronomic and quality traits in a doubled haploid population derived from two Canadian wheats (Triticum aestivum L.). Theor Appl Genet 113:753–766

Joppa LR, Cantrell RG (1990) Chromosomal location of genes for grain protein in content of wild tetraploid wheat. Crop Sci 30:1059–1064

Joppa LR, Khan K, Williams ND (1983) Chromosomal location of genes for gliadin polypeptides in durum wheat Triticum turgidum. Theor Appl Genet 64:289–293

Kerfal S, Giraldo P, Rodríguez-Quijano M, Vázquez JF, Adams K, Lukow OM, Röder MS, Somers DJ, Carrillo JM (2010) Mapping quantitative trait loci (QTLs) associated with dough quality in a soft x hard bread wheat progeny. J Cereal Sci 52:46–52

Kunert A, Naz AA, Dedeck O, Pillen K, Leon J (2007) AB-QTL analysis in winter wheat: I. Synthetic hexaploid wheat (T. turgidum ssp. dicoccoides · T. tauschii) as a source of favourable alleles for milling and baking quality traits. Theor Appl Genet 115:683–695

Lafiandra D, Sanguineti MC, Maccaferri M. and DeAmbrogio E (2007) Molecular markers and qtl analysis for grain quality improvement in wheat. Chapter 2. R.K. Varshney and R. Tuberosa (eds.), Genomics Assisted Crop Improvement:Vol. 2: Genomics Applications in Crops, 25–50

Lerner SE, Cogliatti M, Ponzio NR, Seghezzo ML, Molfese ER, Rogers WJ (2004) Genetic variation for grain protein components and industrial quality of durum wheat cultivars sown in Argentina. J Cereal Sci 40:161–166

Li Y, Song Y, Zhou R, Branlard G, Jia J (2009) Detection of QTLs for bread-making quality in wheat using a recombinant inbred line population. Plant Breed 128:235–243

Mann G, Diffey S, Cullis B, Azanza F, Martin D, Kelly A, McIntyre L, Schmidt A, Ma W, Nath Z, Kutty I, Leyne EP, Rampling L, Quail KJ, Morell MK (2009) Genetic control of wheat quality: interactions between chromosomal regions determining protein content and composition, dough rheology, and sponge and dough baking properties. Theor Appl Genet 118:1519–1537

Martínez MC, Ruiz M, Carrillo JM (2005) Effects of different prolamin alleles on durum wheat quality properties. J Cereal Sci 41:123–131

McCartney CA, Somers DJ, Lukow O, Ames N, Noll J, Cloutier S, Humphreys DG, McCallum BD (2006) QTL analysis of quality traits in the spring wheat cross RL4452 x AC Domain. Plant Breed 125:565–575

Mcintosh RA, Yamazaki Y, Devos KM, Dubcovsky J, Rogers WJ, Appels R (2003) Catalogue of gene symbols for wheat. In: International Wheat Genetics Symposium. (10º, 1–6 September, 2003, Instituto Sperimentale per la Cerealicoltura, Rome, Paestum, Italy). 2003, vol. 4, 77 p

Olmos S, Distelfeld A, Chicaiza O, Schlatter AR, Fahima T, Echenique V, Dubcovsky J (2003) Precise mapping of a locus affecting grain protein content in durum wheat. Theor Appl Genet 107:1243–1251

Patil RM, Oak MD, Tamhankar SA, Rao VS (2009) Molecular mapping of QTLs for gluten strength as measured by sedimentation volume and mixograph in durum wheat (*Triticum turgidum* L. ssp *durum*). J Cereal Sci 49:378–386

Payne PI (1987) Genetics of wheat storage proteins and the effect of allelic variation on bread-making quality. Annu Rev Plant Physiol 38:141–153

Payne PI, Holt LM, Jackson EA, Law CN (1984) Wheat storage proteins: their genetics and their potential for manipulation by plant breeding. Philos Trans R Soc Lond 304:359–371

Peña RJ, Zarco-Hernandez J, Amaya-Celis A, Mujeed-Kazi A (1994) Relationships between chromosome 1B-encoded glutenin subunit compositions and bread-making quality characteristics of some durum wheat (Triticum turgidum) cultivars. J Cereal Sci 19:243–249

Pogna NE, Dal Belin Peruffo A, Mellini F (1984) Genetic aspects of gliadin bands 40 and 43.5 associated with gluten strength. Genet Agrar 39:101–108

Pogna NE, Autran JC, Mellini F, Lafiandra D, Feillet P (1990) Chromosome 1B-encoded gliadins and glutenin subunits in durum wheat: genetics and relationship to gluten strength. J Cereal Sci 11:15–34

Prasad M, Kumar N, Kulwal PL, Röder MS, Balyan HS, Dhaliwal HS, Gupta PK (2003) QTL analysis for grain protein content using SSR markers and validation studies using NILs in bread wheat. Theor Appl Genet 106:659–667

Ruiz M, Carrillo JM (1995) Separate effects on gluten strength of Gli-1 and Glu-3 prolamin genes on chromosomes 1A and 1B in durum wheat. J Cereal Sci 21:137–144

Shewry PR, Halford NG, Lafiandra D (2003) Genetics of wheat gluten proteins. Adv Genet 49:111–184

Suprayogi Y, Pozniak CJ, Clarke FR, Clarke JM, Knox RE, Singh AK (2009) Identification and validation of quantitative trait loci for grain protein concentration in adapted Canadian durum wheat populations. Theor Appl Genet 119:437–448

Uauy C, Distelfeld A, Fahima T, Blechl A, Dubcovsky J (2006) A NAC gene regulating senescence improves grain protein, zinc, and iron content in wheat. Science 314:1298–1301

Van Ooijen JW (1992) Accuracy of mapping quantitative trait loci in autogamous species. Theor Appl Genet 84:803–811

Wang DL, Zhu J, Li ZK, Paterson AH (1999) Mapping QTLs with epistatic effects and QTL x environment interactions by mixed linear model approaches. Theor Appl Genet 99:1255–1264

Wang S, Basten CJ, Zeng Z (2004) Windows QTL cartographer. V2.0 Program in statistical genetics. North Carolina State University, North Carolina. http://www.statgen.ncsu.edu/qtlcart/WQTLCart.htm

Zanetti S, Winzeler M, Feuillet C, Keller B, Messmer M (2001) Genetic analysis of bread-making quality in wheat and spelt. Plant Breed 120:13–19

Zhang W, Chao S, Manthey F, Chicaiza O, Brevis JC, Echenique V, Dubcovsky J (2008) QTL analysis of pasta quality using a composite microsatellite and SNP map of durum wheat. Theor Appl Genet 117:1361–1377

Zhao L, Zhang KP, Zhi-ying Deng BL, Qu HL, Tian JC (2010) A comparison of grain protein content QTLs and flour protein content QTLs across environments in cultivated wheat. Euphytica 174:325–335