Euphytica (2017) 213:277
https://doi.org/10.1007/s10681-017-2058-2

QTL mapping and analysis of epistatic interactions for grain yield and yield-related traits in *Triticum turgidum* L. var. *durum*

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Received: 11 November 2016 / Accepted: 31 October 2017 / Published online: 16 November 2017

Abstract A quantitative trait loci (QTL) analysis of grain yield and yield-related traits was performed on 93 durum wheat recombinant inbred lines derived from the cross UC1113 × Kofa. The mapping population and parental lines were analyzed considering 19 traits assessed in different Argentine environments, namely grain yield, heading date, flowering time, plant height, biomass per plant, and spikelet number per ear, among others. A total of 224 QTL with logarithm of odds ratio (LOD) $\geq$ 3 and 47 additional QTL with LOD $>$ 2.0 were detected. These QTL were clustered in 35 regions with overlapping QTL, and 12 genomic regions were associated with only one phenotypic trait. The regions with the highest number of multi-trait and stable QTL were 3BS.1, 3BS.2, 2BS.1, 1BL.1, 3AL.1, 1AS, and 4AL.3. The effects of epistatic QTL and QTL × environment interactions were also analyzed. QTL putatively located at major gene loci (*Rht*, *Vrn*, *Eps*, and *Ppd*) as well as additional major/minor QTL involved in the complex genetic basis of yield-related traits expressed in Argentine environments were identified. Interestingly, the 3AL.1 region was found to increase yield without altering grain quality or crop phenology.

Keywords Durum wheat · Heading date · Quantitative trait locus · Yield components

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10681-017-2058-2) contains supplementary material, which is available to authorized users.

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Abbreviations

QTL	Quantitative trait locus
RIL	Recombinant inbred line
Rht	Reduced height
MAS	Marker assisted selection
NDVI	Normalized difference vegetation index
Ppd	Photoperiod
Vrn	Vernalization
Eps	Earliness per se
SNP	Single nucleotide polymorphism
SSR	Simple sequence repeat
RFLP	Restriction fragment length polymorphism
STS	Sequence-tagged site
CA	Cabildo

BW	Barrow
BC	Balcarce
Hd	Heading date
Flt	Flowering time
Ssm	Number of spikes per square meter
Yld	Grain yield
Tgw	Thousand grain weight
Ph	Plant height
PdL	Peduncle length
Bpp	Biomass per plant
Snp	Number of spikes per plant
Gne	Grain number per ear
Gnp	Grain number per plant
Sne	Spikelet number per ear
Fse	Number of fertile spikelets per ear
Gwe	Grain weight per ear
Gwp	Grain weight per plant
Gnfs	Grain number per fertile spikelet
Gnts	Grain number per total spikelets
Hi	Harvest index
Sf	Spike fertility
QQ	Epistatic interaction
QE	QTL × environment interaction
LOD	Logarithm of odds ratio
Ypc	Yellow pigment content
Fb	Flour yellow color (b CIELAB)
Gpc	Grain protein content
Sv	Sedimentation volume (SDS test)

Introduction

Durum wheat (*Triticum turgidum* L. var. *durum*) is the crop of preference for premium pasta production worldwide. Yield is the most important trait to many members of the wheat production chain, particularly farmers, distributors, and exporters. As grain yield is a complex trait that normally shows relatively low heritability, it is difficult to obtain high genetic gains in yield during the breeding process.

Durum wheat cultivation area in Argentina reached nearly half a million hectares in the early 1970s but decreased rapidly in the subsequent decades and stabilized at up to ~ 57,000 ha in the period 2001–2011 (http://www.siia.gob.ar/sst_pcias/estima/estima.php). Durum wheat is planted mainly in the southern sector of Buenos Aires province, Argentina. The main reason why durum cultivation decreased was the low average durum wheat yield compared to that of bread wheat and the lower profit margin compared to other agricultural systems although durum was priced higher than bread wheat in Argentina.

Breeding strategies for yield improvement focused mainly on biomass partitioning (harvest index) towards the spike through the pleiotropic effects of genes introduced during the "green revolution" (*Rht*) (Abbate et al. 1995; Royo et al. 2007). The most common methods to improve wheat yield were through understanding how yield components could be manipulated and could contribute individually to yield potential (Slafer 2007), and through better adaptation to environmental stresses (Tuberosa 2012). In the past 2 decades, new biotechnological techniques helped accelerate improvements in wheat yield via marker assisted selection (MAS) based on quantitative trait locus (QTL) mapping and on specific genes.

QTL analysis of yield components and morpho-phenological traits as well as of overall yield offers the possibility of detecting direct and indirect genetic effects on yield-related traits. Epistatic interactions of yield-related genes/QTL as well as QTL × environment interactions should also be taken into account to better understand the complex genetic basis of wheat yield. Previous studies, particularly on bread wheat, were conducted to identify either QTL or genomic regions with effects on different yield components (Quarrie et al. 2006; Kuchel et al. 2007; Kumar et al. 2007; Hai et al. 2008; Wang et al. 2011; Wu et al. 2012; Rustgi et al. 2013).

Relatively few studies on durum wheat (Maccaferri et al. 2008; Diab et al. 2008; Peleg et al. 2009; Golabadi et al. 2011; Blanco et al. 2012; Patil et al. 2013; Dura et al. 2013, 2014; Graziani et al. 2014) have reported the presence of QTL associated with yield, yield components, and pheno-physiological parameters in all chromosomes. These studies highlight the importance of a major QTL located on chromosome 3BS with effects on yield, plant height, heading date (Maccaferri et al. 2008), canopy reflectance (NDVI index), leaf greenness (SPAD units), peduncle length (Graziani et al. 2014), thousand-kernel weight (Blanco et al. 2012; Graziani et al. 2014), and kernel number/spike and spike weight (Marza et al. 2006). Other key QTL were reported on chromosome 2BL (Maccaferri et al. 2008; Graziani et al. 2014). In addition, QTL on chromosomes 2AS,

2BS and 4BS were associated with thousand-kernel weight, test weight, spikelets per spike, and grain yield (Patil et al. 2013). A high-density consensus map constructed based on SNP and other additional integrated markers has allowed localization of QTL positions more precisely for different traits and was also useful as a framework map to complement linkage disequilibrium analysis and genome-wide association mapping (Maccaferri et al. 2014, 2015).

The aim of this work was to identify the main genomic regions associated with variation in grain yield, yield components, and morpho-phenological related traits using a durum wheat RIL population. To explore the complexity of these traits, we also investigated the existence of pleiotropic effects, QTL × QTL, and QTL × environment interactions in the durum wheat genome.

Materials and methods

Plant material

A durum mapping population consisting of 93 F_9 recombinant inbred lines (RIL) derived from a cross between UC1113 and variety Kofa was used (Zhang et al. 2008). Kofa is a Desert Durum® variety with intermediate yield and high quality, selected from a population designated ''DICOCCUM ALPHA POP-85 S-1'' by the West-Bred Company. UC1113, is a CIMMYT-derived line (KIFS//RSS/BD1419/3/MEXIS-CP/4/WAHAS/5/YAV79) selected by the Wheat Breeding Program of the University of California (Davis). Eight local commercial varieties were used as controls (Buck Platino, Buck Topacio, Buck Esmeralda, Buck Cristal, Buck Ambar, Bonaerense INTA Facón, Bonaerense INTA Cariló, and Bonaerense INTA Cumenay).

Experimental design and planting

Six field trials were carried out over 2 years (2006 and 2007) at different locations in the southern sector of Buenos Aires province. RIL, parental lines (UC1113 and Kofa), and controls were all grown in Cabildo [CA] (39°36′S 61°64′W), Barrow [BW] (38°20′S 60°13W) and Balcarce [BC] (37°45′S 58°18′W), following a gradient of water availability from Cabildo to Balcarce. Rainfalls in Cabildo, Barrow, and Balcarce in the periods from July to December were 280.6, 397.7, and 328.9 mm in 2006, and 248.4, 286.9, and 381.7 mm in 2007. The agronomic management and rainfall conditions are described in detail in Supplementary Tables S4 and S5 of Conti et al. (2011).

Field trials were organized in a randomized complete block design with three replications (plots were 3 m^2 with 3 rows of 5 m spaced 0.20 m apart). Planting dates ranged from July to August and harvest dates were in December and January. An additional experiment was carried out at Marcos Juárez [MJ] (32°42′S 62°07′W), but only two phenological traits (heading and flowering times) were considered because a severe drought period caused crop loss.

Yield and yield-related trait measurements

The following data were recorded: (1) heading date (Hd), growth (GS) stage 55 (Zadoks et al. 1974); (2) flowering time (Flt), GS 65; (3) number of spikes per square meter (Ssm) calculated from the number of spikes in a 2 m row section located in the middle of the plot; (4) grain yield (Yld, kg/ha), weight of clean grains from the entire machine-harvested plot, and (5) thousand grain weight (Tgw, g) calculated as the average weight of two 100 grain samples from each plot.

At harvest time, ten plants from the middle row of each plot (replicate × genotype × environment) were collected for analysis of yield-related traits. Average values by plot were also calculated. The following traits were analyzed per plant: (6) plant height (Ph), calculated as the distance from the edge of separation of the stem from the root to the tip of the spike (cm); (7) peduncle length (PdL), measured as the distance from the last internode to the base of the spike and calculated as the average of all tillers per plant (cm); (8) biomass per plant (Bpp, g), obtained as the aerial dry weight of the entire plant; (9) number of spikes per plant (Snp); (10) grain number per ear (Gne); (11) grain number per plant (Gnp), calculated as the sum of the number of grains from all ears per plant; (12) spikelet number per ear (Sne) expressed as the average number of spikelets/ear, obtained by counting the number of spikelets in all ears/plant; (13) number of fertile spikelets per ear (Fse) obtained in the same way as Sne but considering only the number of fertile spikelets; (14) grain weight per ear (Gwe, g),

obtained by weighing the grains from each ear of the plant and averaged; (15) grain weight per plant (Gwp, g), obtained as the sum of the weight of grains from all ears per plant; (16) grain number per fertile spikelet (Gnfs), calculated as the average ratio of Gne/Fse; (17) grain number per spikelet (Gnts), calculated as the average ratio of Gne/Sne; (18) harvest index (Hi), calculated as the ratio between grain weight per plant (Gwp) and total above-ground biomass per plant (Bpp), and (19) spike fertility (Sf) calculated as ratio Fse/Sne (%).

Genetic map

The genetic map used in this study consisted of 269 markers, including 230 SSRs, 23 SNPs, 10 RFLPs, three STSs, two proteins, and one morphological marker, arranged on 14 linkage groups covering a total length of 2140 cM with an average 153 cM per chromosome (Zhang et al. 2008).

Statistical analysis

The descriptive statistics (Table 1) of untransformed variables by environment was obtained using PROC MEANS. Normality of residuals was assessed by modified Shapiro–Wilk test in Infostat software (Di Rienzo et al. 2016). The LSMEANS for all traits by environment were calculated following PROC MIXED procedure. Pearson's correlation coefficients (r) of LSMEANS were estimated for RILs ($n = 93$) by the PROC CORR procedure implemented in SAS 9.0 software (SAS 9.2 Procedures Guide 2010). For ANOVA within each environment, genotype was considered a fixed effect and replication was considered a random effect. Broad sense heritability (h^2) was calculated using the mean square values obtained from PROC MIXED procedure in each environment as $h^2 = \sigma_g^2/\sigma_p^2$, where genotypic $\left(\sigma_g^2\right)$ and phenotypic $\left(\sigma_p^2\right)$ variances were calculated as $\sigma_g^2 = (MS_{RIL} - MS_e)/r$ and $\sigma_p^2 = \left(\sigma_g^2 + \sigma_e^2\right)$, respectively. MS_{RIL} and MS_e are the mean sums of square for genotype and residual error, respectively, and r is the number of replications.

The criterion proposed by Cruz and Regazzi (1997) to join environments in a combined ANOVA over all environments was used. Residual mean squares (RMSs) from ANOVA of each individual environment were compared and variance was considered homogeneous when the ratio between the larger and the smaller RMS was lower than 7. Combined analysis of variance (ANOVA) was carried out using a mixed lineal model with PROC MIXED procedure in SAS and considering genotype as a fixed effect and environments and interactions as random effects.

QTL mapping

Arithmetic means by environment were used to map QTL. For the combined QTL analyses, mean values across environments were calculated. QTL were mapped using the CIM method with software Windows QTL Cartographer v.2.5 (Wang et al. 2005). Model 6 was implemented with a walking speed of 0.5 cM and a window size of 10 cM to exclude closely linked control markers using a forward and backward regression method. A LOD threshold value of three was used to consider a QTL to be significant. A confidence interval of 95% was calculated as the two-LOD drop from the maximum peak value (Van Ooijen 1992). QTL with LOD values between 2.0 and 3.0 that were mapped either on or closest (into the two-LOD interval) to significant QTL for the same or another trait were considered to be "suggestive" and were included in the results.

QTL were indicated as forming a cluster when they co-localized based on overlapping confidence intervals. In addition, we tested if some QTL could be putatively pleiotropic using the Multiple-trait CIM (MCIM) method (Jiang and Zeng 1995). To run the MCIM, we considered the main clusters detected in this work involving correlated traits. However, to test the hypothesis of pleiotropy, the QTL, which had been observed in a previous study from our group, to affect quality traits on a RIL mapping population, were also taken into account. Parameter settings and threshold values were the same as those for CIM analyses.

An analysis of epistatic (QQ) and environmental (QE and QQE) interaction was carried out with a mixed linear model (Wang et al. 1999) using software QTLNetwork v.2.0 (Yang et al. 2007) (http://ibi.zju.edu.cn/software/qtlnetwork/). The parameter set to select marker intervals was a walk speed of 0.5 cM. A window size of 10 cM was used to consider other

marker intervals as cofactors. The critical threshold value of F-statistics was determined by the 1000 permutation test at a significance level of 0.05 (Doerge and Churchill 1996). QTL were indicated following the nomenclature suggested by McIntosh et al. (2003), the letter × preceding DNA marker names was omitted as in a previously published genetic map (Zhang et al. 2008).

Results

Analyses of phenotypic traits

The modified Shapiro–Wilk test showed that most of the phenotypic data sets [79/110] were normally distributed (Table S1). Ten traits [Ph, PdL, Yld, Snp, Gnp, Gwe, Gwp, Gnfs, Gnts, and Tgw] were found to be normally distributed in five environments, three

Table 1 Phenotypic variation and heritability (h^2_B) of yield-related traits in RIL, parental lines, and controls

Trait [a]	Env. [b]	N	RIL min.	RIL mean	RIL max.	SD	CV	SE	h^2_B	Kofa	UC1113	Buck Platino	Buck Topacio	Buck Esmeralda	BonINTA Facon	BonINTA Carilo	BonINTA Cumenay	Buck Cristal	Buck Ambar
Hd	CA 2006	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	BW 2006	279	59.0	64.7	71.0	2.3	3.6	0.1	0.87	62.3	64.3	71.3	72.0	67.3	68.3	72.3	68.0	69.0	70.3
	BC 2006	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	MJ 2006	279	62.0	66.4	71.0	2.8	4.2	0.2	0.67	64.0	67.3	69.0	70.0	69.7	67.7	68.0	69.3	69.7	70.3
	CA 2007	279	67.0	73.6	77.0	2.0	2.7	0.1	0.85	70.7	74.7	75.0	75.0	75.0	75.0	75.0	75.0	75.0	75.0
	BW 2007	279	59.0	64.7	73.0	2.4	3.8	0.1	0.78	62.0	64.3	76.3	78.0	70.3	73.0	80.0	73.0	73.0	75.7
	BC 2007	271	66.0	71.0	76.0	2.0	2.8	0.1	0.36	69.3	72.0	80.0	80.0	75.7	75.0	76.0	76.3	75.0	80.0
Flt	CA 2006	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	BW 2006	279	67.0	70.6	77.0	1.5	2.2	0.1	0.8	69.0	70.7	75.7	76.3	72.3	73.0	78.3	73.0	73.0	75.0
	BC 2006	279	71.0	73.5	81.0	1.6	2.2	0.1	0.9	71.0	73.0	79.0	80.7	75.0	76.0	80.0	75.0	75.7	78.7
	MJ 2006	279	69.0	73.2	80.0	2.5	3.5	0.2	0.4	71.0	73.7	76.0	76.0	76.7	75.3	74.3	75.7	76.0	76.3
	CA 2007	279	73.0	78.0	82.0	2.3	3.0	0.1	0.7	74.7	78.7	91.0	93.0	86.0	83.0	91.0	85.3	82.7	90.3
	BW 2007	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	BC 2007	200	75.0	80.9	86.0	2.8	3.5	0.2	0.5	75.3	80.5	.	.	.	.	.	.	.	.
Ph	CA 2006	251	50.5	72.2	90.0	6.4	8.9	0.4	0.69	73.9	72.8	79.6	68.8	80.8	75.6	72.8	78.8	77.8	75.8
	BW 2006	278	55.5	73.7	90.1	6.6	9.0	0.4	0.85	84.5	77.2	82.5	69.4	81.9	71.8	69.6	80.5	78.1	76.8
	BC 2006	279	51.2	74.9	91.3	6.8	9.1	0.4	0.81	81.9	74.8	85.2	83.1	85.0	76.9	76.4	83.2	80.7	81.3
	CA 2007	272	49.4	68.8	83.7	5.7	8.3	0.3	0.75	70.3	74.1	81.6	80.5	82.2	78.6	77.7	77.9	72.2	84.0
	BW 2007	278	56.6	77.8	92.0	5.9	7.6	0.4	0.79	81.4	75.3	87.1	81.1	94.3	77.0	81.6	78.3	86.0	86.3
	BC 2007	269	63.7	78.6	94.3	6.2	7.9	0.4	0.84	81.7	79.6	94.8	88.1	99.5	81.0	85.3	88.5	86.0	91.6
PdL	CA 2006	251	17.2	26.0	41.5	3.8	14.8	0.24	0.44	26.6	25.3	27.3	21.0	28.7	26.3	20.5	30.0	27.0	25.8
	BW 2006	278	15.9	23.3	33.1	3.0	13.1	0.18	0.81	27.5	22.9	24.2	20.4	25.9	20.0	18.3	26.4	25.3	23.2
	BC 2006	279	19.3	26.4	34.9	2.7	10.2	0.16	0.72	30.0	28.7	30.6	27.1	30.6	26.7	22.9	28.8	28.3	28.1
	CA 2007	272	17.9	25.1	36.8	2.8	11.3	0.2	0.72	26.5	26.7	25.2	23.1	28.1	26.0	21.5	25.2	25.4	28.0
	BW 2007	278	20.6	30.2	38.1	3.0	9.9	0.2	0.78	33.8	29.1	28.9	32.0	38.6	27.3	26.0	26.6	36.2	31.1
	BC 2007	269	22.6	31.7	43.1	3.3	10.4	0.2	0.86	33.8	32.5	33.7	31.4	31.0	33.3	30.0	31.9	33.0	33.4
Yld	CA 2006	267	1115.0	2293.3	3524.3	402.0	17.5	24.6	0.51	1911.9	1980.8	1977.4	1963.9	2298.8	1980.9	1785.4	1836.9	1845.7	1770.2
	BW 2006	279	1003.7	2406.2	4716.7	683.3	28.4	40.9	0.44	2999.8	3099.8	3005.4	2800.0	3172.2	2145.6	2983.3	2755.6	2727.7	2433.9
	BC 2006	279	987.7	2747.8	5005.0	731.2	26.6	43.8	0.65	3545.9	3786.1	3919.0	2783.0	4608.3	3144.7	2664.8	3682.8	3432.0	3664.0
	CA 2007	279	964.0	2562.8	3663.3	478.3	18.7	28.6	0.70	2515.6	3161.1	2087.8	2176.7	2792.2	1937.8	2324.4	2255.6	2402.2	2060.0
	BW 2007	279	2406.3	4080.4	6896.7	735.9	18.0	44.1	0.18	3956.6	4444.4	4017.9	3872.3	3750.7	3244.8	4549.2	3868.1	4386.2	3726.6
	BC 2007	270	1661.3	3055.0	4937.0	675.2	22.1	41.1	0.52	2640.3	3674.7	4621.0	5210.9	4914.7	3876.8	4447.1	4222.8	4007.9	4877.6
Bpp	CA 2006	251	1.77	4.34	13.00	1.88	43.4	0.12	0.01	7.14	6.85	.	.	.	.	.	.	.	.
	BW 2006	278	2.94	10.58	23.86	3.23	30.6	0.19	0.46	14.47	10.15	12.13	14.82	12.54	11.75	8.47	11.45	8.31	8.85
	BC 2006	279	3.09	8.66	20.30	3.01	34.8	0.18	0.12	6.69	3.77	11.12	13.74	9.47	7.06	8.14	9.20	8.51	7.86
	CA 2007	272	3.91	7.80	13.23	1.67	21.5	0.10	0.22	8.38	7.76	7.29	8.44	9.74	11.32	9.29	7.46	8.74	8.38
	BW 2007	278	4.13	9.88	21.61	2.54	25.7	0.15	0.19	10.72	9.89	8.98	12.11	12.47	11.32	13.41	10.68	11.68	7.65
	BC 2007	269	3.68	9.97	19.47	2.62	26.3	0.16	0.25	9.22	7.52	9.62	13.22	12.24	12.25	10.94	10.80	12.26	11.16
Ssm	CA 2006	267	78.0	288.3	578.0	79.8	27.7	4.9	0.22	250.1	259.3	199.1	286.1	249.1	263.9	248.1	270.4	239.8	324.1
	BW 2006	276	97.0	239.5	444.4	54.1	22.6	3.3	0.39	263.9	256.5	290.7	235.2	277.8	180.6	284.3	224.1	217.6	185.2
	BC 2006	279	91.0	211.1	367.0	45.5	21.5	2.7	0.10	254.6	252.8	247.2	216.7	254.6	218.5	236.1	211.1	214.8	195.4
	CA 2007	279	155.0	282.7	495.0	54.3	19.2	3.2	0.27	261.7	245.0	273.3	272.5	252.5	326.7	265.0	241.7	320.8	253.3
	BW 2007	279	130.0	246.8	365.0	47.3	19.2	2.8	0.24	260.0	229.2	221.7	245.8	258.3	215.0	283.3	231.7	280.0	187.5
	BC 2007	270	172.5	291.7	502.5	46.4	15.9	2.8	0.09	285.8	176.7	180.0	285.8	305.0	240.8	248.3	292.5	312.5	259.2
Snp	CA 2006	251	1.0	1.7	4.7	0.7	41.8	0.0	0.02	2.6	2.6	.	.	.	.	.	.	.	.
	BW 2006	278	1.0	2.5	4.3	0.5	21.4	0.0	0.41	4.1	3.1	3.3	3.0	4.0	4.0	3.0	3.0	2.7	2.5
	BC 2006	279	1.0	1.9	3.0	0.4	18.3	0.0	0.06	2.2	1.2	2.7	2.9	2.6	2.1	2.3	2.3	2.2	2.4
	CA 2007	272	1.4	2.1	3.6	0.3	13.2	0.0	0.06	3.1	2.8	2.7	2.8	3.3	3.9	3.4	2.6	3.4	3.0
	BW 2007	278	1.4	2.2	3.7	0.3	16.0	0.0	0.01	3.3	3.0	2.7	3.5	3.7	3.6	4.2	3.0	3.6	2.3
	BC 2007	269	1.3	2.3	3.9	0.4	16.5	0.0	0.11	3.3	2.1	2.7	3.2	4.6	3.6	3.2	2.5	3.7	3.0
Gne	CA 2006	251	16.2	29.2	40.0	4.3	14.9	0.27	0.16	30.6	33.1	25.9	32.1	28.4	26.9	28.3	24.5	23.2	20.5
	BW 2006	278	19.9	31.9	43.8	3.8	11.9	0.23	0.60	33.8	32.6	34.6	36.2	34.1	29.6	30.8	30.4	30.4	31.8
	BC 2006	279	20.1	33.9	46.7	4.5	13.2	0.3	0.46	29.7	31.3	35.8	45.1	38.2	36.5	37.1	33.0	37.1	29.5
	CA 2007	272	14.5	30.1	39.5	3.9	13.0	0.2	0.54	30.0	34.5	27.0	29.3	27.6	30.7	28.9	26.6	29.0	27.8
	BW 2007	278	20.6	29.7	52.6	3.7	12.4	0.2	0.37	28.8	35.0	29.5	35.5	33.3	33.4	34.9	30.8	31.2	32.8
	BC 2007	269	6.5	18.3	32.9	4.3	23.4	0.3	0.34	13.2	17.0	23.0	35.5	25.2	25.3	24.0	21.2	21.6	22.9
Gnp	CA 2006	251	19.8	49.7	153.3	21.3	42.9	1.3	0.03	83.4	84.3	.	.	.	.	.	.	.	.
	BW 2006	278	32.1	78.5	158.0	19.7	25.1	1.2	0.46	143.0	98.1	117.4	108.1	135.5	117.9	92.3	91.2	81.4	80.4
	BC 2006	279	26.6	64.5	111.2	15.3	23.7	0.9	0.22	64.1	38.4	98.4	132.1	96.7	73.3	86.8	75.3	77.8	71.6
	CA 2007	272	25.4	63.8	98.5	11.8	18.5	0.7	0.31	93.3	95.5	69.9	82.6	98.6	117.7	98.6	69.5	97.8	84.3
	BW 2007	278	35.2	64.9	124.1	13.8	21.2	0.8	0.16	93.8	102.7	78.1	124.5	124.7	121.1	147.6	91.8	112.6	76.2
	BC 2007	269	10.4	43.0	96.3	13.6	31.6	0.8	0.25	44.7	41.1	58.4	112.5	115.4	95.2	75.2	53.8	76.3	71.1
Sne	CA 2006	251	10.1	13.5	21.1	1.4	10.1	0.09	0.32	14.7	14.8	13.8	16.3	13.9	15.0	16.7	11.9	19.8	13.3
	BW 2006	278	14.1	17.0	19.2	0.9	5.0	0.05	0.72	17.6	16.3	18.5	18.6	17.8	17.8	20.0	16.4	17.2	18.4
	BC 2006	279	11.0	15.3	18.4	1.3	8.4	0.1	0.48	14.2	12.9	17.3	18.9	17.0	16.8	18.1	14.8	17.2	16.7
	CA 2007	272	12.1	15.3	18.3	0.9	5.8	0.1	0.63	15.1	15.3	18.0	17.7	17.4	17.2	19.3	15.6	16.7	17.5
	BW 2007	278	14.1	16.3	18.6	0.7	4.3	0.0	0.79	16.4	16.3	18.8	18.9	18.0	17.5	19.7	17.6	17.9	18.8
	BC 2007	269	12.5	15.8	18.2	0.8	5.1	0.0	0.50	15.4	15.2	18.0	19.4	17.8	16.9	19.0	16.4	17.4	18.2
Fse	CA 2006	251	8.5	12.8	21.1	1.5	11.7	0.1	0.26	14.1	14.1	12.8	15.2	13.2	14.2	14.8	11.6	13.5	11.9
	BW 2006	278	10.8	15.5	20.6	1.1	7.2	0.1	0.47	16.3	14.2	16.4	16.4	15.6	15.2	16.8	14.7	15.3	15.9
	BC 2006	279	7.4	13.9	16.6	1.5	11.1	0.1	0.49	13.0	12.3	15.8	17.8	15.4	15.4	16.5	13.5	15.6	14.4
	CA 2007	272	5.8	13.5	16.4	1.3	9.6	0.1	0.61	13.6	14.2	14.0	15.0	13.9	14.7	15.5	13.3	14.4	14.6
	BW 2007	278	10.1	13.4	19.5	1.2	9.2	0.1	0.33	13.5	14.0	13.8	16.0	14.6	14.7	16.2	14.5	13.5	15.6
	BC 2007	269	4.1	9.4	15.7	1.7	18.2	0.1	0.30	7.5	9.2	10.7	15.7	12.1	12.4	12.4	10.3	10.8	11.1

Table 1 continued

Trait [a]	Env.[b]	N	RIL min.	RIL mean	RIL max.	SD	CV	SE	h^2_B	Kofa	UC1113	Buck Platino	Buck Topacio	Buck Esmeralda	BonINTA Facon	BonINTA Carilo	BonINTA Cumenay	Buck Cristal	Buck Ambar
Gwe	CA 2006	251	0.45	0.89	1.69	0.20	23.1	0.01	0.08	0.98	0.95	0.78	0.87	0.69	0.74	0.65	0.81	0.68	0.50
	BW 2006	278	0.64	1.19	1.79	0.20	16.7	0.01	0.44	1.43	1.31	1.37	1.31	1.29	1.03	1.00	1.36	1.19	1.21
	BC 2006	279	0.76	1.49	2.18	0.26	17.4	0.02	0.50	1.32	1.47	1.69	1.97	1.83	1.62	1.50	1.65	1.72	1.42
	CA 2007	272	0.48	0.95	1.51	0.16	17.0	0.01	0.40	1.08	1.07	0.73	0.74	0.80	0.86	0.79	0.89	0.85	0.77
	BW 2007	278	0.81	1.22	1.66	0.17	13.6	0.01	0.25	1.26	1.35	1.15	1.15	1.07	1.18	1.22	1.23	1.20	1.17
	BC 2007	269	0.30	0.96	1.76	0.24	24.6	0.01	0.32	0.70	0.88	1.26	1.57	1.40	1.27	1.16	1.22	1.08	1.30
Gwp	CA 2006	251	0.5	1.5	4.5	0.6	43.6	0.0	0.16	2.5	2.3	.	.	.	.	.	.	.	.
	BW 2006	278	1.1	3.9	9.2	1.3	32.5	0.1	0.43	6.1	3.9	4.6	4.0	5.1	3.8	3.0	4.1	3.2	3.1
	BC 2006	279	1.2	3.7	8.8	1.2	33.5	0.1	0.20	2.9	1.8	4.6	5.7	4.8	3.3	3.4	3.7	3.7	3.5
	CA 2007	272	1.0	2.8	4.8	0.7	24.4	0.0	0.29	3.3	3.0	1.9	2.1	3.1	3.3	2.7	2.3	2.8	2.3
	BW 2007	278	1.6	3.7	8.6	1.0	27.2	0.1	0.13	4.2	4.0	3.1	4.1	4.0	4.3	5.2	3.8	4.3	2.7
	BC 2007	269	0.6	2.9	7.0	1.1	36.1	0.1	0.28	2.4	2.1	3.2	5.0	6.4	4.8	3.6	3.0	4.0	4.0
Gnfs	CA 2006	251	1.7	2.3	3.1	0.2	10.8	0.0	0.27	2.2	2.4	2.0	2.1	2.2	1.9	1.9	2.1	1.7	1.7
	BW 2006	278	1.4	2.1	2.6	0.2	8.5	0.0	0.68	2.1	2.3	2.1	2.2	2.2	2.0	1.8	2.1	2.0	2.0
	BC 2006	279	1.7	2.4	2.9	0.2	8.1	0.0	0.59	2.3	2.5	2.3	2.5	2.5	2.4	2.2	2.5	2.4	2.0
	CA 2007	272	1.7	2.2	2.6	0.2	7.5	0.0	0.48	2.2	2.4	1.9	2.0	2.0	2.1	1.9	2.0	2.0	1.9
	BW 2007	278	1.8	2.2	3.6	0.2	8.9	0.0	0.22	2.1	2.5	2.1	2.2	2.3	2.3	2.2	2.1	2.3	2.1
	BC 2007	269	1.4	1.9	3.0	0.2	10.5	0.0	0.16	1.8	1.9	2.2	2.3	2.1	2.0	1.9	2.1	2.0	2.1
Gnts	CA 2006	251	1.1	2.2	3.1	0.3	14.5	0.0	0.16	2.1	2.2	1.9	2.0	2.0	1.8	1.7	2.1	1.3	1.5
	BW 2006	278	1.1	1.9	2.4	0.2	11.1	0.0	0.67	1.9	2.0	1.9	1.9	1.9	1.7	1.5	1.9	1.8	1.7
	BC 2006	279	1.5	2.2	2.8	0.2	10.0	0.0	0.54	2.1	2.4	2.1	2.4	2.3	2.2	2.1	2.2	2.2	1.8
	CA 2007	272	0.9	2.0	2.4	0.2	11.6	0.0	0.55	2.0	2.3	1.5	1.7	1.6	1.8	1.5	1.7	1.7	1.6
	BW 2007	278	1.3	1.8	3.2	0.2	11.5	0.0	0.31	1.8	2.2	1.6	1.9	1.8	1.9	1.8	1.8	1.7	1.8
	BC 2007	269	0.4	1.2	2.0	0.2	21.5	0.0	0.34	0.9	1.1	1.3	1.8	1.4	1.5	1.3	1.3	1.2	1.3
Hi	CA 2006	251	0.20	0.34	0.53	0.05	13.6	0.00	0.41	0.35	0.34	0.31	0.27	0.28	0.32	0.26	0.29	0.27	0.24
	BW 2006	278	0.21	0.37	0.48	0.04	10.7	0.00	0.45	0.41	0.38	0.38	0.30	0.41	0.33	0.35	0.36	0.38	0.35
	BC 2006	279	0.31	0.44	0.63	0.0	8.1	0.0	0.27	0.44	0.47	0.42	0.42	0.50	0.47	0.43	0.40	0.43	0.44
	CA 2007	272	0.18	0.35	0.44	0.0	10.9	0.0	0.35	0.39	0.38	0.26	0.24	0.31	0.29	0.29	0.31	0.32	0.28
	BW 2007	278	0.28	0.37	0.50	0.0	7.9	0.0	0.16	0.39	0.41	0.34	0.34	0.32	0.38	0.38	0.35	0.37	0.35
	BC 2007	269	0.15	0.29	0.42	0.1	19.0	0.0	0.37	0.26	0.28	0.33	0.38	0.90	0.38	0.34	0.29	0.32	0.36
Sf	CA 2006	251	0.58	0.94	1.00	0.1	6.5	0.00	0.06	0.96	0.95	0.93	0.93	0.95	0.95	0.89	0.97	0.77	0.89
	BW 2006	278	0.62	0.91	0.99	0.0	4.7	0.00	0.53	0.92	0.85	0.90	0.85	0.87	0.85	0.83	0.90	0.87	0.84
	BC 2006	279	0.80	0.93	1.00	0.0	3.5	0.0	0.29	0.91	0.94	0.91	0.94	0.90	0.91	0.90	0.90	0.90	0.85
	CA 2007	272	0.39	0.88	0.97	0.1	7.3	0.0	0.63	0.89	0.93	0.81	0.85	0.80	0.86	0.79	0.85	0.85	0.82
	BW 2007	278	0.60	0.82	0.94	0.1	7.6	0.0	0.19	0.82	0.86	0.73	0.84	0.81	0.83	0.82	0.82	0.74	0.82
	BC 2007	269	0.26	0.59	0.98	0.1	16.6	0.0	0.30	0.49	0.57	0.55	0.79	0.67	0.72	0.64	0.63	0.61	0.62
Tgw	CA 2006	267	23.0	32.0	40.5	2.9	9.2	0.2	0.63	35.0	31.7	32.0	30.0	30.6	30.7	27.7	32.8	33.4	26.4
	BW 2006	279	31.9	41.0	50.6	3.4	8.4	0.2	0.42	45.4	40.6	41.2	41.8	42.2	41.2	38.1	45.0	41.3	41.5
	BC 2006	279	36.3	47.7	56.5	3.4	7.2	0.2	0.74	49.5	47.9	48.4	46.0	50.8	44.9	45.3	52.7	47.2	52.3
	CA 2007	279	29.2	35.0	43.8	3.0	8.6	0.2	0.52	38.5	35.1	30.7	30.3	34.3	30.6	29.9	37.6	34.0	30.4
	BW 2007	279	21.3	44.2	54.7	3.5	8.0	0.2	0.30	46.1	43.0	40.7	34.4	34.1	38.6	37.3	43.7	39.1	39.0
	BC 2007	270	46.4	54.1	63.2	3.0	5.5	0.2	0.62	54.6	54.2	53.4	45.6	57.9	50.2	49.4	58.6	53.2	58.0

[a] *Hd* heading date, *Flt* flowering time, *Ph* plant height, *PdL* peduncle length, *Yld* grain yield, *Bpp* biomass per plant, *Ssm* spike number per square meter, *Snp* spike number per plant, *Gne* grain number per ear, *Gnp* grain number per plant, *Sne* spikelet number per ear, *Fse* number of fertile spikelet per ear, *Gwe* grain weight per ear, *Gwp* grain weight per plant, *Gnfs* grain number per fertile spikelet, *Gnts* grain number per spikelet, *Hi* harvest index, *Sf* spike fertility, *Tgw* thousand grain weight

[b] *Env.* environment, *N* number of samples, *min.* minimum, *max.* maximum, *SD* standard deviation, *CV* coefficient of variation, *SE* standard error, h^2_B broad sense heritability

[Gne, Hi, and Bpp] in four environments and only Ssm was normal in all tested environments. Only the test for Flt was rejected in all environments.

RIL mean values, distribution ranges, standard deviations, broad sense heritabilities (h^2_B), and control average values for all traits analyzed are shown in Table 1. Transgressive segregant genotypes were identified for all traits in each environment.

Analysis of variance

ANOVA revealed highly significant differences among RIL (G) and environments (E) (Table S2h). The main source of variation in all traits was the environment. GxE was highly significant for all traits, indicating that differences among genotypes should be considered for each environment. Based on these results, ANOVA by environment was performed (Table S2a–g), considering genotype as a fixed effect and replication as a random effect. The genotype effect was significant for most traits and environments. Only Bpp (CA 2006, BC 2006), Snp (CA 2006, BC 2006, CA 2007, BW 2007, BC 2007), Ssm (BC 2006, BC 2007), Gwp (BW 2007), Gnp, Sf, and Gnp (CA 2006) showed no significant effects.

Correlation analysis

Correlations of LSMEANs among the 19 traits considered were analyzed for each environment. Higher correlation values for Ph versus PdL, Hd versus Flt, Bpp versus Gwp, Gnp versus Gwp, Gne versus Gnts, Bpp versus Snp, Gne versus Gwe, and Gnts versus Gnfs were detected in all environments (Table S3a–g). Gwe and Gne were significantly positively correlated across all environments with ten (Gne, Ph, Bpp, Fse, Gnp, PdL Gnfs, Gnts, Hi, and Sf) and eight (Gnts, Gwe, Gnp, Sne, Fse, Gwp, Gnfs,

and Sf) different traits, respectively. Grain yield showed positive correlations with Ph, PdL, and Hi across environments but was negatively correlated with Hd and Flt in BW and BC 2006. Yld was significantly positively correlated with Gwp, Gwe, Gnp, and Gnts in five of six environments analyzed. Both crop seasons in Balcarce showed the highest significant correlation values involving Yld, mainly associated with Gwe, Fse, and Gne. In BC 2006, Tgw was highly correlated with Yld ($r = 0.64$), whereas in 2007 Hi showed a high association with Yld ($r = 0.61$). The lowest associations between traits in both years were at Barrow. In BW 2006, Yld was significantly correlated with Ssm ($r = 0.47$), Hi, and Sf. However, in 2007 Yld was slightly associated with grain weight (Gwe, Gwp), grain number (Gne, Gnp), Bpp, and Hi. Yld and Hi were also significantly correlated in Cabildo (2006 and 2007). On the other hand, Flt and Hd were significantly and negatively associated with PdL in all environments and positively correlated with Sne. Only Flt versus Sne in BC 2007 was not significant. Tgw showed the highest number of positive correlations in BC 2006 with 10 traits, and was negatively correlated either with Hd or Flt in three environments (BC 2006, CA 2007, and BW 2007).

Identification of genomic regions associated with yield-related traits

A total of 224 significant QTL (LOD $\geq$ 3) was identified for the 19 traits considered in the present study. Additionally, 47 suggestive QTL (LOD $>$ 2) were located in the same positions, yielding a total of 271 QTL for all traits and environments (Table S4). These results allowed us to identify 47 genomic regions affecting yield across the complete durum genome. Based on QTL with overlapping confidence intervals, it was possible to define 35 QTL clusters (C1–C35) affecting different related traits (Table 2). The remaining 12 genomic regions were involved in genetic control of only one trait. A summary of the number of genomic regions identified per trait and their locations is shown in Table 3.

The number of QTL identified per trait varied from 4 (Snp, Ssm) to 14 (Tgw, Yld) and the percentage of phenotypic variation (R^2) explained by those QTL ranged from 6.3 to 55.1%. The highest LOD score (16.5) obtained in this study corresponds to the 3BS QTL (3BS.1) mapped using plant height data (Cluster 13). This was the most important mapped genomic region affecting a total of 11 traits. Another 20 trait-specific QTL were mapped in three or more environments and could be considered environmentally stable QTL, the most important ones being located on 1AS, 1BL.1, 2BS.1, 3AL.1, 3BS.1, 3BS.2, 4AL.3, 5AL.2, 5AL.3, 6AL.1, and 6BS.1. A subset of these QTL (1AS, 1BL.1, 2BS.1, 3AL.1, 3BS.1, 3BS.2, 4AL.3) affected more than five traits (Table 2). Two additional regions, 4AL.2 and the centromeric QTL 4BS/4BL.1 were mapped for 6 and 7 traits, respectively, but no trait was associated with a stable QTL across environments.

The distribution of QTL between the two genomes of durum wheat was approximately similar, with a somewhat larger contribution of B genome (55%). The contribution of favorable alleles from both parents for the 271 QTL detected was approximately equal, where Kofa contributed with 47.2% of favorable alleles, and UC1113 with 52.8%. The corresponding positions and the QTL confidence intervals are shown in Supplementary Table S4.

As stated above, the genomic regions affecting yield and yield-related traits were grouped in 35 clusters (Table 2). The main clusters are described below and shown in Fig. 1. Additional clusters are shown in Supplementary Figure S1.

Cluster 1 (1AS)

This genomic region affected 5 phenotypic traits (Sne, Flt, Fse, Gne, and Gwe), Sne being the main trait detected. QTL for Sne were detected in six environments and explained 29.1% of variation in the mean data from all environments and more than 20% in four environments. The number of spikelets/ear (Sne) ranged from 10.1 to 21.1 across environments. Fse, the fertile portion of spikelets, was mapped in three environments, but was only a suggestive QTL in the mean data from all environments. Flt was mapped only in the additional environment, Marcos Juárez (LOD $>$ 3).

Cluster 3 (1BL.1)

Eight traits were affected by this region (Yld, Bpp, Fse, Sne, Gnp, Gwp, Gwe, and Tgw). The main association was with grain weight measured at different levels, from plant to spike or individual grains.

Table 2 QTL analyses for yield and yield-related traits in the UC1113 × Kofa RIL population in seven environments in Argentina

Chr. arm (cluster)	QTL [a]	Marker interval	Closest marker	Positive allele	CA 2006 [b]		BW 2006		BC 2006		CA 2007		BW 2007		BC 2007		MJ 2006		Mean	
					LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)
1AS.1	*QSne.cerz-1AS*	*wmc95 - barc148*	*wmc24*	UC1113	3.8	11.9	4.7	20.1	5.2	20.6	5.5	20.1	7.3	22.9	4.0	15.8			8.8	29.1
(cluster 1)	*QFlt.cerz-1AS*	*wmc24 - barc148*	*wmc24*	UC1113													3.5	12.0		
	QFse.cerz-1AS	*wmc95 - barc148*	*wmc95*	UC1113	3.2	14.9	5.6	21.2	(2.5)	8.2			3.3	12.4					(2.1)	8.8
	QGne.cerz-1AS	*Bla - wmc24*	*wmc95*	UC1113			3.1	14.1					(2.7)	13.1						
	QGwe.cerz-1AS	*Bla -wmc95*	*wmc95*	UC1113									3.1	22.0						
1AS.2	*QHi.cerz-1AS*	*barc148 - wg983*	*barc148*	Kofa							3.3	11.4								
1AL	*QGne.cerz-1AL*	*barc213 - cdo393*	*cdo393*	UC1113															3.3	20.1
1BS	*QGwe.cerz-1BS*	*wmc406 - wmc193*	*wmc406*	UC1113							3.0	10.7								
(cluster 2)	*QYld.cerz-1BS*	*wmc193 - barc8*	*wmc193*	UC1113	3.3	9.9														
1BL.1	*QYld.cerz-1BL.1*	*wmc85 - barc302*	*BE443797_436*	UC1113			3.1	13.8											5.1	13.4
(cluster 3)	*QBpp.cerz-1BL.1*	*BE443797_436 - barc302*	*BE443797_436*	UC1113									4.3	15.6					3.8	12.4
	QFse.cerz-1BL.1	*BE443797_436 - barc302*	*BE443797_436*	UC1113	(2.1)	7.5	(2.9)	10.4	(2.2)	6.9									3.3	11.3
	QSne.cerz-1BL.1	*BE443797_436 - barc302*	*BE443797_436*	UC1113	4.0	12.5														
	QGnp.cerz-1BL.1	*BE443797_436-barc302*	*BE443797_436*	UC1113									(2.9)	12.3						
	QGwp.cerz-1BL.1	*BE443797_436-barc302*	*BE443797_436*	UC1113															4.2	15.0
	QGwe.cerz-1BL.1	*wmc85 - BE500714_237*	*wmc85*	UC1113															4.7	18.2
	QTgw.cerz-1BL.1	*wmc626 - wmc85*	*wmc85*	UC1113			3.8	12.9												
1BL.2	*QFse.cerz-1BL.3*	*psr162 - wg241*	*psr162*	Kofa									4.3	47.4						
(cluster 4)	*QBpp.cerz-1BL.3*	*psr162 - wg241*	*psr162*	Kofa							3.1	10.9								
	QYld.cerz-1BL.3	*psr162 - wg241*	*wg241*	UC1113							3.2	9.9								
	QTgw.cerz-1BL.3	*psr162 - ksm176*	*wg241*	UC1113	3.1	14.7							3.9	19.1					4.4	13.5
2AS	*QTgw.cerz-2AS*	*gwm122 - barc309*	*barc309*	Kofa											3.2	13.7				
(cluster 5)	*QBpp.cerz-2AS*	*gwm296 - wmc296*	*wmc296*	Kofa	3.0	11.6														
	QSnp.cerz-2AS	*gwm122 - barc309*	*gwm122*	Kofa	3.6	13.1														
	QHi.cerz-2AS	*gwm296 - wmc296*	*wmc296*	Kofa									4.3	23.4						
2AL.1	*QPdL.cerz-2AL.1*	*wmc401 - gwm328*	*gwm328*	Kofa					(2.7)	7.2										
(cluster 6)	*QGnfs.cerz-2AL.1*	*wmc401 - gwm328*	*wmc401*	Kofa					3.7	10.6										
	QGnts.cerz-2AL.1	*gwm71 - wmc401*	*gwm71*	Kofa					3.7	10.5										
2AL.2	*QSnp.cerz-2AL.2*	*cfd50-gwm526*	*gwm526*	Kofa			3.1	12.0												
2BS.1	*QYld.cerz-2BS.1*	*cfa2201 - gwm429*		UC1113	7.1	23.0	(2.6)	9.0												
(cluster 7)	*QHd.cerz-2BS.1*	*wmc154 - cfa2201*	*cfa2201*	Kofa			10.0	31.9			3.8	20.8			(2.7)	12.0			4.5	16.7
	QFlt.cerz-2BS.1	*wmc154 - cfa2201*	*cfa2201*	Kofa			4.0	18.1	4.7	17.1									6.1	21.3
	QPdL.cerz-2BS.1	*wmc154 - cfa2201*	*cfa2201*	UC1113	5.5	20.6	5.0	15.7					(2.9)	9.4					4.2	10.4
	QGnfs.cerz-2BS.1	*wmc154 - cfa2201*	*cfa2201*	UC1113	3.1	13.2					3.6	14.9								
	QGnts.cerz-2BS.1	*wmc154 - cfa2201*	*cfa2201*	UC1113	4.0	17.9														
	QHi.cerz-2BS.1	*cfa2201 - gwm429*	*cfa2201*	UC1113	5.4	18.4														
	QSne.cerz-2BS.1	*wmc154 - gwm429*	*cfa2201*	Kofa	4.6	15.5	3.1	15.8	7.1	21.8			4.9	19.5					8.4	32.1
2BS.2	*QYld.cerz-2BS.2*	*BM140538_39 - cnl158*	*BM140538_39*	UC1113			3.7	12.6												
(cluster 8)	*QFlt.cerz-2BS.2*	*cnl158 - wmc35*	*cnl158*	Kofa							3.9	14.9								
2BL	*QTgw.cerz-2BL*	*wmc361 - barc159*	*barc159*	Kofa							4.8	17.3								
(cluster 9)	*QPh.cerz.2BL*	*wmc361 - barc159*	*wmc361*	UC1113			5.1	13.4												
	QGnp.cerz-2BL	*wmc361 - barc159*	*barc159*	UC1113															3.0	11.7
	QGwp.cerz-2BL	*wmc361 - barc159*	*barc159*	UC1113											(2.7)	9.0				
	QPdL.cerz-2BL	*wmc361 - barc159*	*wmc361*	UC1113			3.8	9.5												
	QSf.cerz-2BL	*wmc361 - barc159*	*barc159*	UC1113															3.3	12.6
3AS.1	*QGnfs.cerz-3AS.1*	*wmc532 - gwm369*	*wmc532*	UC1113											3.2	14.2				
3AS.2	*QHi.cerz-3AS.2*	*wmc505 - barc356*	*wmc505*	UC1113							3.3	11.3								
(cluster 10)	*QSsm.cerz-3AS.2*	*wmc505 - barc356*	*wmc505*	Kofa	4.0	17.3														
3AL.1	*QGne.cerz-3AL.1*	*ksm28 -wmc428*	*ksm28*	UC1113	3.5	16.3			(2.4)	10.1									3.9	16.3
(cluster 11)	*QSf.cerz-3AL.1*	*ksm28 -wmc428*	*ksm28*	UC1113			3.9	12.6	(2.5)	10.5										
	QGnts.cerz-3AL.1	*ksm28 -wmc428*	*ksm28*	UC1113			3.0	9.0	(2.6)	8.7										
	QHi.cerz-3AL.1	*ksm28 -wmc428*	*ksm28*	UC1113			(2.5)	11.6					6.5	29.8					3.5	13.1
	QYld.cerz-3AL.1	*ksm28 - BF293500_113*	*wmc428*	UC1113			3.9	11.1			5.4	15.0	(2.9)	13.0					6.9	18.0
3AL.2	*QBpp.cerz-3AL.2*	*BF293500_113-cfa2193*	*cfa2193*	Kofa							4.7	24.2								
(cluster 12)	*QSnp.cerz-3AL.2*	*BF293500_113-cfa2193*	*cfa2193*	Kofa							4.0	15.7								
3BS.1	*QPh.cerz.3BS.1*	*barc147 - gwm493*	*gwm493*	Kofa	9.1	30.5			10.9	34.2	13.1	41.4	10.2	32.3	12.7	40.3			16.5	45.0
(cluster 13)	*QPdL.cerz-3BS.1*	*barc147 - gwm493*	*gwm493*	Kofa	5.1	15.9	5.1	15.7	12.0	36.0	11.6	34.9	4.7	14.3	8.7	27.0			14.3	40.7
	QYld.cerz-3BS.1	*gwm493 - cfd79*	*gwm493201*	Kofa					10.7	38.0	11.2	35.5	(2.0)	7.0					8.1	20.7
	QTgw.cerz-3BS.1	*barc147 - gwm493*	*gwm493*	Kofa					5.7	15.3										
	QBpp.cerz-3BS.1	*gwm493 - cfd79*	*gwm493*	Kofa							3.2	10.0								
	QSf.cerz-3BS.1	*gwm493 - cfd79*	*gwm493*	Kofa			3.5	12.5												
	QGne.cerz-3BS.1	*gwm493 - cfd79*	*gwm493*	Kofa			3.2	11.2			6.0	20.3								
	QGnp.cerz-3BS.1	*gwm493 - cfd79*	*gwm493*	Kofa							4.5	16.5								
	QGwe.cerz-3BS.1	*gwm493 - cfd79*	*gwm493*	Kofa			4.4	18.7	5.1	18.3									3.1	10.3
	QGnfs.cerz-3BS.1	*barc147 - gwm493*	*gwm493*	Kofa					6.4	20.7	6.8	21.1							(2.5)	8.4
	QGnts.cerz-3BS.1	*barc147 - cfd79*	*gwm493*	Kofa			4.3	13.6	6.6	20.8	3.8	12.3							4.8	17.0
3BS.2	*QHd.cerz-3BS.2*	*cfd79 - ksm45*	*cfd79*	UC1113							3.6	13.5	5.8	22.7			3.4	12.0		
(cluster 14)	*QFlt.cerz-3BS.2*	*cfd79 - ksm45*	*ksm45*	UC1113			3.5	13.8	(2.2)	7.4					3.4	14.7			4.6	12.7
	QGnp.cerz-3BS.2	*ksm45 - wmc43*	*ksm45*	UC1113							3.1	15.1								
	QGwp.cerz-3BS.2	*ksm45 - wmc43*	*ksm45*	UC1113							3.6	14.3								
	QPh.cerz.3BS.2	*cfd79 - ksm45*	*cfd79*	Kofa			9.3	29.2	6.0	24.5	5.3	21.1	5.9	23.3	5.3	22.4			7.0	25.3
	QPdL.cerz-3BS.2	*cfd79 - ksm45*	*cfd79*	Kofa	3.3	11.4	7.9	24.5	6.2	23.7	6.8	26.9	5.1	20.9	4.2	17.1			7.2	24.4
	QYld.cerz-3BS.2	*cfd79 - ksm45*	*cfd79*	Kofa					4.9	23.9										
3BL	*QTgw.cerz-3BL*	*gwm247- gwm181*	*gwm247*	UC1113							3.6	11.9								
(cluster 15)	*QSf.cerz-3BL*	*gwm181 - gwm114*	*gwm181*	Kofa			3.9	15.3												
	QGnfs.cerz-3BL	*barc164 - gwm181*	*gwm247*	Kofa			4.2	14.0											3.5	28.3
	QGnts.cerz-3BL	*gwm247- gwm181*	*gwm247*	Kofa	(2.5)	9.9	4.4	13.1												
4AS	*QPh.cerz-4AS*	*gwm192 - LpxA3*	*gwm192*	UC1113					3.1	9.7										
(cluster 16)	*QPdL.cerz-4AS*	*gwm165 - gwm192*	*gwm265*	UC1113							3.4	8.6								
4AL.1	*QYld.cerz-4AL.1*	*wmc617 - dupw4*	*wmc617*	UC1113							(2.7)	6.3								
(cluster 17)	*QSf.cerz-4AL.1*	*wmc617 - dupw4*	*wmc617*	UC1113									3.5	13.8						
4AL.2	*QGnfs.cerz-4AL.2*	*dupw4 - barc170*	*dupw4*	Kofa			3.8	12.4			(2.7)	8.2								
(cluster 18)	*QGnts.cerz-4AL.2*	*dupw4 - barc170*	*dupw4*	Kofa			3.7	11.0												
	QGnp.cerz-4AL.2	*dupw4 - barc170*	*dupw4*	Kofa	4.5	16.6														
	QSnp.cerz-4AL.2	*dupw4 - barc170*	*dupw4*	Kofa	3.7	13.0														
	QYld.cerz-4AL.2	*dupw4 - barc170*	*dupw4*	Kofa	4.9	14.3														
	QHi.cerz-4AL.2	*dupw4 - barc170*	*barc170*	Kofa							4.0	14.4								
4AL.3	*QPh.cerz-4AL.3*	*wmc258 - wmc718*	*wmc258*	UC1113	3.4	11.1					3.4	9.1	3.2	9.6	3.5	15.0			5.9	13.3
(cluster 19)	*QPdL.cerz-4AL.3*	*gwm265 - wmc718*	*wmc258*	UC1113					6.2	15.3									3.6	11.2
	QGne.cerz-4AL.3	*gwm265 - wmc258*	*gwm265*	UC1113											3.3	12.2				
	QGwp.cerz-4AL.3	*wmc258 - wmc718*	*wmc258*	UC1113											3.9	14.0				
	QGwe.cerz-4AL.3	*wmc258 - wmc718*	*wmc258*	UC1113											4.4	14.8				
	QFse.cerz-4AL.3	*gwm265 - wmc258*	*gwm265*	UC1113					(2.6)	8.8					4.2	14.6				
	QBpp.cerz-4AL.3	*wmc258 - wmc718*	*wmc258*	UC1113											3.9	12.9				
4AL.4	*QBpp.cerz-4AL.4*	*barc343 - barc78*	*barc343*	Kofa	3.7	17.4														
(cluster 20)	*QGwp.cerz-4AL.4*	*barc343 - barc78*	*barc343*	Kofa	3.5	14.0														
	QYld.cerz-4AL.4	*barc343 - barc78*	*barc343*	UC1113			4.0	11.2												

Table 2 continued

Chr. arm (cluster)	QTL [a]	Marker interval	Closest marker	Positive allele	CA 2006 [b]		BW 2006		BC 2006		CA 2007		BW 2007		BC 2007		MJ 2006		Mean	
					LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)	LOD	R^2(%)
4BS/4BL.1	*QGne.cerz-4BS*	*ksm62 - gwm113*	*gwm113*	UC1113											4.9	19.8				
(cluster 21)	*QGwe.cerz-4BS*	*ksm62 - gwm113*	*gwm113*	UC1113											(2.8)	10.6				
	QFse.cerz-4BS	*ksm62 - gwm113*	*gwm113*	UC1113											(2.8)	12.4				
	QHi.cerz-4BS	*ksm62 - gwm113*	*gwm113*	UC1113											(2.9)	9.8				
	QGnp.cerz-4BL.1	*gwm540 - gwm495*	*gwm540*	UC1113											3.4	14.7				
	QSsm.cerz-4BL.1	*gwm540 - gwm495*	*gwm540*	Kofa							5.0	19.0								
	QGnts.cerz-4BL.1	*gwm540 - gwm495*	*gwm540*	UC1113											3.8	16.2				
4BL.2	*QYld.cerz-4BL.2*	*cfd39 - wmc47*	*wmc47*	UC1113			3.8	17.6												
5AS.1	*QHd.cerz-5AS.1*	*gwm47 - gwm120*	*gwm47*	UC1113									(2.6)	13.1						
(cluster 22)	*QFlt.cerz-5AS.1*	*wmc350-gwm47*	*wmc350*	UC1113			(2.7)	8.2											3.0	10.5
	QTgw.cerz-5AS.1	*gwm47-gwm120*	*gwm47*	UC1113															4.0	17.5
5AS.2	*QTgw.cerz-5AS.2*	*gwm120-gwm293*	*gwm293*	UC1113					4.2	15.2										
(cluster 23)	*QGwe.cerz-5AS.2*	*gwm120-gwm293*	*gwm293*	UC1113									3.8	22.4						
	QGnts.cerz-5AS.2	*gwm120-gwm293*	*gwm293*	UC1113									3.5	22.9						
5AS.3/5AL.1	*QSne.cerz-AS.3/5AL.1*	*gwm293-barc1182*	*wg341b*	UC1113							2.95s	32.5	3.1	9.4					(2.8)	8.0
5AL.2	*QPh.cerz-5AL.2*	*barc151 - barc355*	*BG607308_101*	UC1113	5.3	15.5			5.1	17.7	4.6	16.9	3.5	20.5					5.5	11.1
(cluster 24)	*QPdL.cerz-5AL.2*	*barc151 - barc355*	*BG607308_101*	UC1113					4.9	14.5	5.7	33.8							3.8	8.1
	QSf.cerz-5AL.2	*BG607308_101 - barc355*	*BG607308_101*	UC1113			(2.8)	8.9												
	QGwp.cerz-5AL.2	*BG607308_101 - barc355*	*BG607308_101*	UC1113															3.0	10.3
5AL.3	*QPh.cerz-5AL.3*	*wmc577 - wmc727*	*gwm179*	Kofa	3.2	8.7							6.4	18.4	3.2	8.4			5.4	11.5
(cluster 25)	*QPdL.cerz-5AL.3*	*gwm179 - wmc727*	*gwm179*	Kofa					6.5	16.3			4.7	15.1	4.0	12.0			6.2	15.6
	QHd.cerz-5AL.3	*gwm179 - wmc727*	*gwm179*	UC1113									(2.7)	9.5						
	QGwe.cerz-5AL.3	*wmc110 - wmc577*	*wmc577*	UC1113							(2.8)	14.2								
5BS	*QYld.cerz-5BS*	*gwm234 - wmc149*	*gwm234*	Kofa							3.6	8.5								
5BL	*QTgw.cerz-5BL*	*BE495277_339-gwm408*	*BE495277_339*	UC1113	3.9	14.7							2.9s	14.8					4.1	13.2
6AL.1	*QSne.cerz-6AL.1*	*barc1165-wmc553*	*barc113*	Kofa			4.9	19.0	3.7	10.5			5.5	18.1					5.6	17.4
(cluster 26)	*QHd.cerz-6AL.1*	*barc113-wmc553*	*barc113*	Kofa			4.5	12.5											6.0	20.8
	QYld.cerz-6AL.1	*barc113-wmc553*	*barc113*	UC1113							(2.6)	6.3								
	QGwp.cerz-6AL.1	*barc113-wmc553*	*barc113*	UC1113					3.2	12.8										
6AL.2	*QSsm.cerz-6AL.2*	*barc104-cfd2*	*barc104*	Kofa											3.9	14.3				
(Cluster 27)	*QGnfs.cerz-6AL.2*	*barc104-cfd2*	*cfd2*	UC1113							5.1	15.1								
6BS.1	*QHd.cerz-6BS.1*	*ksm45-barc14*	*gwm613*	Kofa							3.6	55.1			(2.4)	8.1				
(cluster 28)	*QFlt.cerz-6BS.1*	*ksm45-barc14*	*gwm613*	Kofa													(2.1)	24.5		
6BS.2/6BL.1	*QTgw.cerz-6BS.2/6BL.1*	*barc198-barc354*	*wmc105*	Kofa	3.5	11.4							4.4	15.0					4.2	15.9
6BL.2	*QTgw.cerz-6BL*	*wg341a-gwm219*	*wg341a*	Kofa									3.1	11.7						
(cluster 29)	*QGne.cerz-6BL*	*barc79 - wg341a*	*wg341a*	UC1113							(2.8)	9.9								
	QGnts.cerz-6BL	*barc354-Barc79*	*barc354*	UC1113							3.0	9.4								
7AS.1	*QHi.cerz-7AS.1*	*gwm635-barc70*	*barc70*	UC1113															4.1	16.1
	QSf.cerz-7AS.1	*gwm635-barc70*	*barc70*	UC1113			2.8	12.9												
(cluster 30)	*QHd.cerz-7AS.1*	*gwm635-barc70*	*barc70*	Kofa													3.4	10.1		
7AS.2	*QSne.cerz-7AS.2*	*barc219-barc282*	*barc219*	Kofa							5.0	23.1								
(cluster 31)	*QHd.cerz-7AS.2*	*barc219-barc282*	*barc219*	Kofa									(2.9)	14.4						
7AS.3	*QPdL.cerz-7AS.3*	*BQ170462_176 - barc174*	*barc174*	UC1113			(2.9)	7.1												
(cluster 32)	*QSsm.cerz-7AS.3*	*barc174-barc1034*	*barc174*	UC1113			6.1	24.4												
	QGne.cerz-7AS.3	*barc174-barc1034*	*barc174*	Kofa							3.0	9.8								
	QHi.cerz-7AS.3	*barc174-barc1034*	*barc1034*	UC1113									(2.8)	13.7						
7AS.4	*QGnfs.cerz-7AS.2*	*BE471272_393-wmc596*	*BE471272_393*	UC1113															3.1	10.8
7BS	*QTgw.cerz-7BS*	*barc279 - gwm537*	*barc279*	UC1113							3.0	11.6								
(cluster 33)	*QYld.cerz-7BS*	*barc1005 - wmc606*	*wmc606*	Kofa	3.9	12.2														
7BL.1	*QTgw.cerz-7BL.1*	*gwm333-BF474379_496*	*gwm333*	UC1113	3.0	12.0														
7BL.2	*QGnfs.cerz-7BL.2*	*barc278-BE498985_42*	*BE498985_42*	UC1113					3.5	13.3										
(cluster 34)	*QGnts.cerz-7BL.2*	*barc278-BE498985_42*	*BE498985_42*	UC1113					3.3	11.5										
	QTgw.cerz-7BL.2	*wmc195-wmc311*	*wmc195*	Kofa							4.1	39.7								
7BL.3	*QHd.cerz-7BL.3*	*wmc311-wmc276*	*wmc276*	Kofa									(2.3)	10.3						
(cluster 35)	*QFlt.cerz-7BL.3*	*wmc311-wmc276*	*wmc276*	Kofa													3.8	23.6		
	QGnfs.cerz-7BL.3	*barc1073-barc340*	*barc1073*	UC1113							4.4	12.7								
	QSne.cerz-7BL.3	*barc1073-barc340*	*barc1073*	Kofa							4.3	14.3								
	QHd.cerz-7BL.3	*barc1073-barc340*	*barc1073*	Kofa													5.5	18.2		
	QFlt.cerz-7BL.3	*barc1073-barc340*	*barc1073*	Kofa			(2.6)	6.4											3.3	10.9

[a] *cerz* CERZOS-CONICET

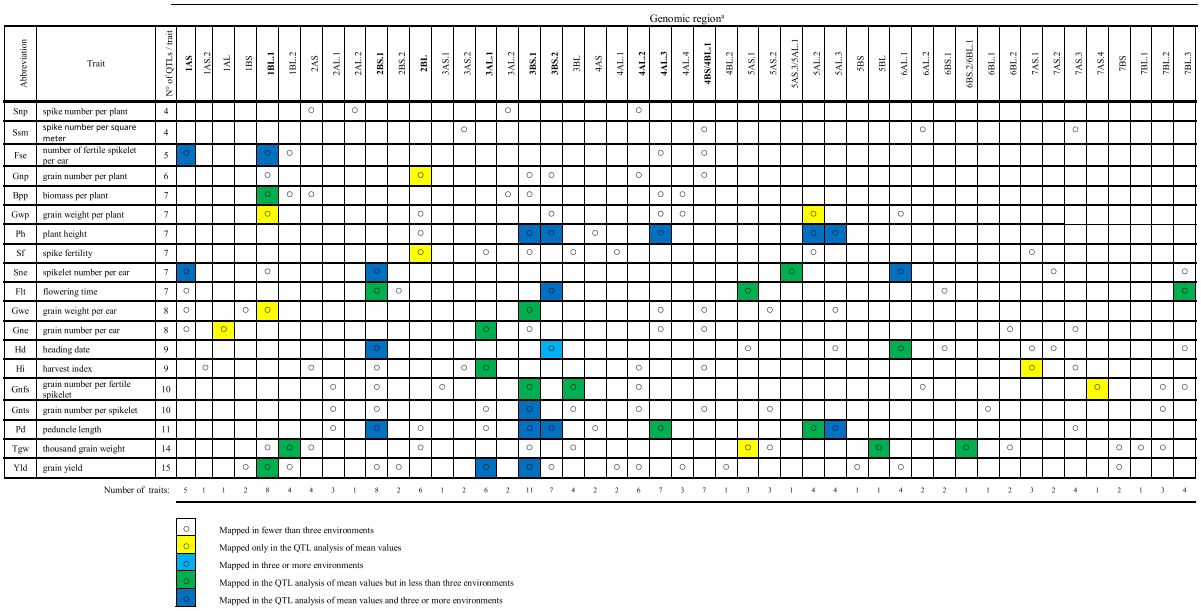
[b] *CA* Cabildo, *BW* Barrow, *BC* Balcarce, *MJ* Marcos Juárez, *Mean* Mean value of three (Flt), five (Hd) or six environments, *LOD* logarithm of the odds score, R^2 percentage of variance explained by QTL

This region explained between 10 and 18% of the phenotypic variation observed in the traits involved. Five of these traits (Yld, Bpp, Fse, Gwp, and Gwe) were mapped using the mean data for the six environments although Gwp and Gwe were not mapped in any individual environment. Most of the QTL from this cluster were mapped in Barrow data from both sampling years. Fse was detected as suggestive in three locations in 2006.

Cluster 7 (2BS.1)

The 2BS.1 genomic region was second in importance after 3BS.1 in terms of QTL stability and number of traits. It was associated with eight traits (Sne, Hd, PdL, Flt, Yld, Gnfs, Hi, and Gnts). Sne, the main trait affected by this cluster, was mapped in four environments with R^2 values ranging from 15 to 22% and explaining 32% of variance in the mean data of the six environments. Hd and PdL were mapped in three

Table 3 QTL analyses for 19 traits, co-localization, and stability among environments. (Color figure online)



[a]Bold indicates a QTL with main effect on more than five traits

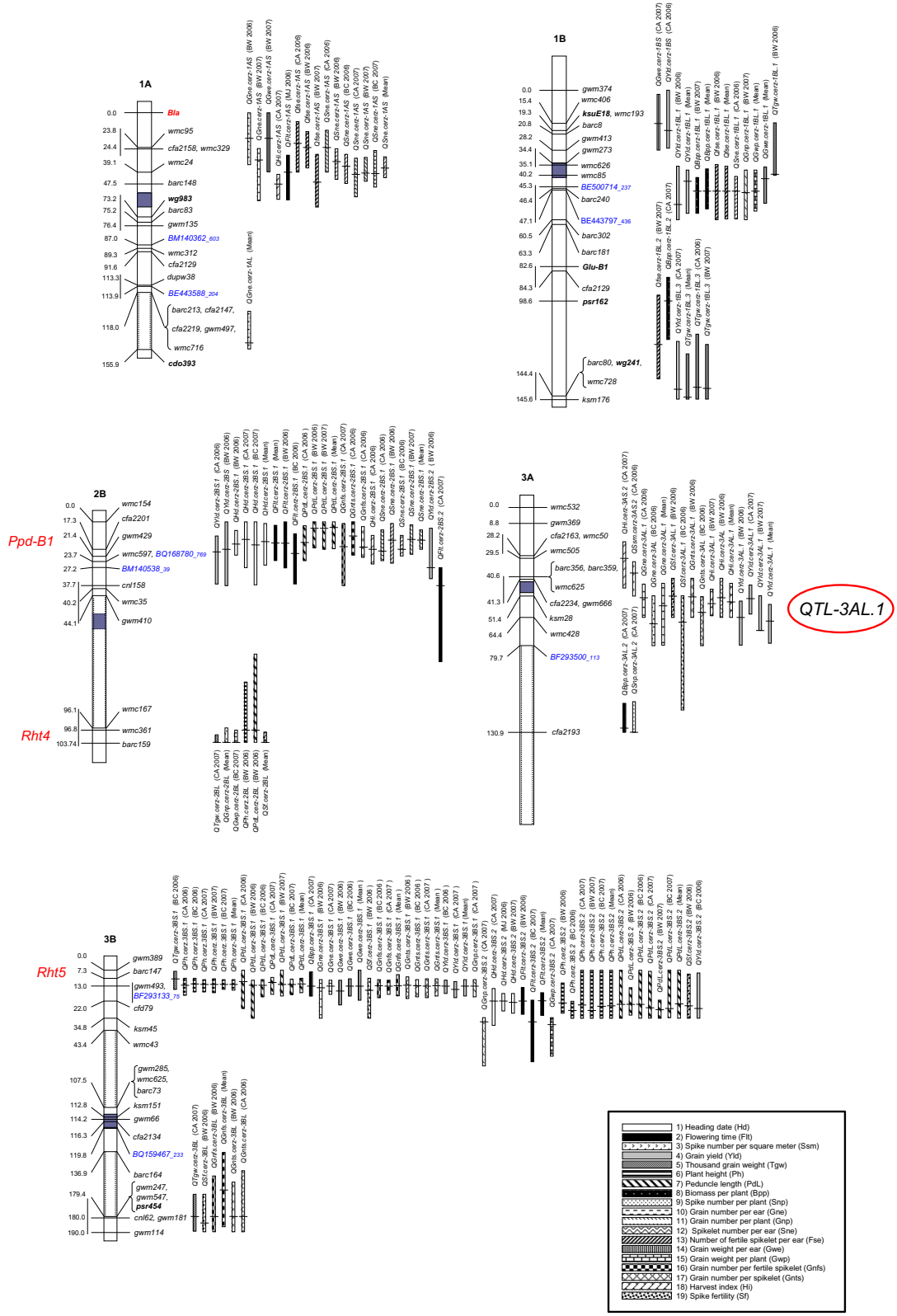
environments and Yld, Flt, and Gnfs, in two. A delay in the heading/flowering stages was caused by the Kofa allele, which was also associated with a high Sne, whereas the UC1113 allele was responsible for higher yield and increasing Gnfs, Gnts, Hi, and PdL. Three of the traits (Sne, Hd, and PdL) controlled by this region could be considered as stable QTL, and their effects were also significantly detected using the means of the environment dataset. Most of the QTL in 2BS.1 cluster were mapped in CA 2006 and BW 2006.

Cluster 11 (3AL.1)

This cluster had a significant influence on 5 traits (Yld, Hi, Gne, Sf, and Gnts) and the QTL for Yld, which was detected in 3 of 6 environments as well as the mean data, showed the highest stability. Taking into account R^2 values, it was the second most important QTL for Yld, after *QYld.cerz-3BS.1*, explaining 11–18% of the variation. This region was one of three identified as affecting yield in the mean data. Gne, Hi, and Yld QTL were each mapped in two to three environments and in the mean analysis. For Hi, 30% of phenotypic variation was explained by this QTL in BW 2007. The positive allele for all traits mapped in this region was provided by UC1113.

Cluster 13 (3BS.1)

This was the main genomic region controlling the traits tested in this work, with effects on 11 traits (Ph, PdL, Yld, Tgw, Bpp, Sf, Gne, Gnp, Gwe, Gnfs, and Gnts). The 3BS.1 region was mapped mainly in CA 2007, BC 2006, and BW 2006, affecting 8, 7, and 6 traits in each environment, respectively. It explained most of the variation for Ph, PdL, and Yld, accounting for 45, 40, and 20%, respectively, of the variation in the mean data for all environments. The QTL mapped for Ph and PdL in the 3BS.1 region in five and six environments, respectively, showed the highest stability. This region was significantly associated with Yld only in two environments and the mean data. However, it explained 35–38% of variation, corresponding to the highest R^2 value for Yld. Effects on three additional traits (Gnts, Gwe, and Gnfs) were detected in this cluster in individual environments (3, 2, and 2, respectively) and in the mean data for all environments, with R^2 values of 10–21%. The remaining traits (Tgw, Bpp, Sf, Gne, and Gnp) were mapped on this cluster only in one environment. The favorable allele for the 3BS.1 QTL cluster was from Kofa.


1A
1B
2B
3A
3B
Ppd-B1
Rht4
Rht5
QTL-3AL.1
1) Heading date (Hd)
2) Flowering time (Flt)
3) Spike number per square meter (Ssm)
4) Grain yield (Yld)
5) Thousand grain weight (Tgw)
6) Plant height (Ph)
7) Peduncle length (PdL)
8) Biomass per plant (Bpp)
9) Spike number per plant (Snp)
10) Grain number per ear (Gne)
11) Grain number per plant (Gnp)
12) Spikelet number per ear (Sne)
13) Number of fertile spikelet per ear (Fse)
14) Grain weight per ear (Gwe)
15) Grain weight per plant (Gwp)
16) Grain number per fertile spikelet (Gnfs)
17) Grain number per spikelet (Gnts)
18) Harvest index (Hi)
19) Spike fertility (Sf)

◀**Fig. 1** QTL associated with yield and yield-related traits mapped on chromosomes 1A, 1B, 2B, 3A, and 3B using UC1113 × Kofa RIL mapping population. Bars represent QTL confidence intervals with 2-LOD drop offs; QTL and environment are indicated at the top. Centromeres are indicated by grey squares. Peak positions are indicated by horizontal lines within QTL bars. Major genes *Ppd-B1*, *Rht4*, and *Rht5* are indicated on the map according to the positions reported by Hanocq et al. (2004), Mohler et al. (2004) and Ellis et al. (2005). New QTL for yield-related traits (QTL-3AL.1) are also indicated. The genetic linkage map was adapted from Zhang et al. (2008)

Cluster 14 (3BS.2)

A second QTL (3BS.2) mapped on 3BS was associated with Hd, Flt, Gnp, Gwp, Ph, Pd, and Yld. For Hd, Flt, Gnp, and Gwp; the favorable allele was provided by UC1113, while for PdL, Ph, and Yld, the favorable allele was provided by Kofa, as for the 3BS.1 QTL. The LOD confidence intervals for these linked QTL (3BS.1 and 3BS.2) controlling PdL in BW 2007 and Ph in BC 2006 were not overlapping. In CA 2007, both QTL affected Gnp with opposite alleles, and the corresponding two-LOD confidence intervals were separated by 15 cM. 3BS.2 was the main genomic region mapped for flowering time in the mean analysis ($R^2 = 16\%$). Flt and Hd were mapped in two and three environments (with LOD > 3), respectively (Table 1).

QTL with effects on single traits

Twelve QTL with single-trait effects were mapped using our RIL population (Table 2). Three QTL (*QSne.cerz-5AS.3/5AL.1*, *QTgw.cerz-5BL*, and *QTgw.cerz-6BS.2/6BL.*1) were identified in various environments and the mean data. The *QSne.cerz-5AS.3/5AL.1* QTL was located in the centromeric region of chromosome 5A and was significantly associated with Sne in BW 2007. It was mapped in CA 2007 and was considered as suggestive in the mean analysis. Another two QTL were associated with Tgw, one of which was mapped on 5BL (*QTgw.cerz-5BL*) and the other one in the centromeric region of 6B (*QTgw.cerz-6BS.2/6BL.1*). *QTgw.cerz-5BL* explained 13–14% of the phenotypic variation in CA 2006, BW 2007, and the mean data. The strongest LOD value for this region occurred in the mean QTL analysis. The second QTL for Tgw (*QTgw.cerz-6BS.2/6BL.1*) was mapped in the same two environments and the mean across environments, where it explained 16% of variation. The other nine single-effect QTL were not consistent among environments.

QTL with epistatic and environmental effects

The environmental interaction effect on the QTL mapped for all traits was explored and 12 of them (Hi, Hd, Sne, Ssm, Bpp, Yld, Tgw, Gne, Gwe, Gnfs, Gnts, and Sf) showed QE effects (Table 4). The main traits with QE interactions were Hi and Hd, with three and two different QTL involved, respectively. The main clusters with QE interactions were 3BS.1 and 2BS.1, which were also the main QTL affecting yield-related traits in our study. The 3BS.1 QTL had the highest number (13) of environmental interactions. Two of the six traits showing QE interaction in 3BS.1, Yld and Gnfs, involved the highest number (3) of environments. Taking into account the environments involved in QE interactions, Balcarce had the majority of interactions in both crop seasons, followed by CA 2006.

Epistatic interactions between QTL (with and without the main effects) were analyzed. Seventeen of the 19 traits analyzed showed QQ effects with at least one interaction. The maximum number of interactions was detected for Sne (four epistatic interactions), followed by Flt and Hd with three QQ interactions. Nine of the 14 remaining traits were involved in two QQ interactions (Tgw, Ph, PdL, Gnfs, Gnts, Snp, Gnp, Gwp, and Bpp) and 5 traits (Yld, Ssm, HI, Fse, and Gwe) showed only one interaction. The epistatic interactions associated with Sne, Gwe, Gnts, Ssm, Snp, Gnp, Gwp, and Bpp traits also had QQE effects (Table 5). The majority of QQ interactions identified per trait involved no main effect QTL.

Multiple trait mapping (MCIM) to test pleiotropy

We next aimed to distinguish genetic linkage from pleiotropy in the different clusters by MCIM. Our previous results from mapping quality traits using the same population coincided with several of the clusters identified in the present work (Table S5). MCIM was used to formally test pleiotropy in the main clusters detected, considering all traits involved in each cluster, the traits mapped using mean values and the 2 or 3 main traits involved, separately or together with the quality traits analyzed in this population. Both negative and positive significant correlations were

Table 4 QTL × environment interactions detected in the RIL population

Chr. arm (cluster)[a]	QTL[b]	Marker interval	CA 2006[c]		BW 2006		BC 2006		CA 2007		BW 2007		BC 2007	
			AE effect[d]	p value	AE effect	p value	AE effect	p value	AE effect	p value	AE effect	p value	AE effect	p value
2BS.1 (C7)	*QHd.cerz-2BS.1*	*wmc154–cfa2201*			− 0.64	**								
	QHi.cerz-2BS.1	*cfa2201–gwm429*	0.01	**									− 0.01	**
	QSne.cerz-2BS.1	*wmc154–gwm429*					− 0.14	**						
3AS.2 (C10)	*QSsm.cerz-3AS.2*	*wmc505–barc356*	− 11.75	**	7.39	*								
3AL.2 (C12)	*QBpp.cerz-3AL.2*	*BF293500_113-cfa2193*	0.35	*										
3BS.1 (C13)	*QYld.cerz-3BS.1*	*gwm493–cfd79*	85.80	*			− 202.51	***					93.99	*
	QTgw.cerz-3BS.1	*barc147–gwm493*	0.45	*			− 1.07	***						
	QGne.cerz-3BS.1	*gwm493–cfd79*							− 0.53	*			0.64	*
	QGwe.cerz-3BS.1	*gwm493–cfd79*					− 0.04	***					0.03	*
	QGnfs.cerz-3BS.1	*barc147–gwm493*					− 0.03	*			0.03	*	0.04	**
	QGnts.cerz-3BS.1	*barc147–cfd79*											0.04	**
4AL.1 (C17)	*QSf.cerz-4AL.1*	*wmc617–dupw4*			− 0.01	*							0.02	***
4AL.2 (C18)	*QHi.cerz-4AL.2*	*dupw4–barc170*											0.01	***
7AS.1 (C30)	*QHi.cerz-7AS.1*	*gwm635–barc70*			− 0.01	*							0.01	**
7BL.3(C35)	*QHd.cerz-7BL.3*	*barc1073–barc340*											0.29	*

[a] *Chr* Chromosome, *C* cluster

[b] *1, 2, 3,* indicate different QTL positions on the same chromosome arm, *Hd* heading date, *Hi* harvest index, *Sne* spikelet number per ear, *Ssm* spike number per square meter, *Bpp* biomass per plant, *Yld* grain yield, *Tgw* thousand grain weight, *Gne* grain number per ear, *Gwe* grain weight per ear, *Gnfs* grain number per fertile spikelet, *Gnts* grain number per spikelet, *Sf* spike fertility

[c] *CA* Cabildo, *BW* Barrow, *BC* Balcarce. *, **, ***significant at p = 0.05, p = 0.01, and p = 0.001, respectively

[d] *AE* Additive × environment

Table 5 Epistatic and QTL × QTL × environment interactions detected for all traits

Trait[a]	QTL_i[b]	Marker $interval_i$	Peak QTL_i	QTL confidence $interval_i$	QTL_j	Marker $interval_j$	Peak QTL_j	QTL confidence $interval_j$	QiQj effect[c]	QiQj E1	P-value	QiQj E2	P-value	QiQj E3	P-value	QiQj E6	P-value
Tgw	*QTgw.cerz-1AS.1*	*Bla-wmc95*	0.0	0.0-5.5	*QTgw.cerz-1BS*	*gwm273-wmc626*	34.4	31.7-38.1	-0.82								
Tgw	*QTgw.cerz-5BL.2*	*barc232-wmc28*	136.4	131.9-140.9	*QTgw.cerz-7BL.1*	*wmc396-barc278*	85.3	83.8-92.8	-0.78								
Ph	*QPh.cerz-1BL.2*	*wg241-ksm176*	144.4	133.1-145.4	*QPh.cerz-3AS.2*	*gwm369-wmc50*	22.3	17.8-28.2	-1.52								
Ph	*QPh.cerz-6BL*	*wmc62-barc134*	138.7	136.2-138.7	*QPh.cerz-7BS*	*gwm46-barc23*	53.1	51.2-53.6	0.79								
PdL	***QPdL.cerz-5AL.3***	*gwm179-wmc727*	193.5	191.8-197.7	*QPdL.cerz-7BL.3*	*Psy-B1-cfa2257*	191.0	190.5-196.0	0.24								
PdL	*QPdL.cerz-5BL*	*gwm371-barc331*	51.1	41.2-54.5	*QPdL.cerz-6BS.1*	*ksm45-gwm613*	0.0	0.0-0.6	0.28								
HI	*QHi.cerz-1AL.1*	*gwm135-BM140362_603*	86.4	76.4-89.3	***QHi.cerz-7AS.1***	*gwm635-barc70*	10.0	0.0-15.0	-0.01								
Sne	*QSne.cerz-1BS*	*wmc626-wmc85*	35.1	35.1-40.1	*QSne.cerz-4BS*	*BE446304_110-ksm62*	22.2	22.2-27.2	0.06	0.15	0.004						
Sne	***QSne.cerz-1BL.1***	*BE443797_436-barc302*	52.1	46.4-57.1	*QSne.cerz-6AS*	*CD491758_81-barc146*	12.3	9.0-22.3	0.17								
Sne	*QSne.cerz-1BL.2*	*psr162-wg241*	143.6	123.6-143.6	*QSne.cerz-4BS*	*BE446304_110-ksm62*	22.2	22.2-27.2	0.06								
Sne	*QSne.cerz-4AL.3*	*wmc258-wmc718*	57.8	49.8-67.8	*QSne.cerz-5BL*	*barc142-wmc160*	121.0	115.3-126.0	-0.19								
Fse	*QFse.cerz-1AL*	*cfa2129-dupw38*	106.6	102.1-112.6	*QFse.cerz-7BS*	*wmc323-barc279*	10.7	7.5-12.4	-0.41								
Gwe	*QGwe.cerz-2AL*	*gwm275-gwm515*	67.1	65.8-70.0	*QGwe.cerz-4BL.1*	*gwm495-wmc657*	48.9	47.4-51.9	0.03	-0.03	0.037			0.03	0.018		
Gnfs	*QGnfs.cerz-1BL*	*barc181-Glu-B1*	74.3	69.3-79.8	*QGnfs.cerz-5AL.3*	*wmc577-gwm179*	193.3	191.8-195.5	0.05								
Gnfs	*QGnfs.cerz-6BS.1*	*gwm613-barc14*	0.6	0.0-12.1	*QGnfs.cerz-7AS.3*	*barc282-BQ170462_176*	72.6	69.9-72.6	0.04								
Gnts	*QGnts.cerz-2AS*	*gwm275-gwm515*	69.1	66.3-71.0	***QGnts.cerz-3BS.1***	*gwm493-cfd79*	13.0	11.8-15.5	-0.03								
Gnts	*QGnts.cerz-2AS*	*gwm249-gwm71*	77.3	72.8-79.0	*QGnts.cerz-3BS.2*	*cfd79-ksm45*	30.5	24.5-34.5	-0.02							0.04	0.025
Yld	*QYld.cerz-1AS*	*wmc329-wmc24*	24.4	23.8-31.9	*QYld.cerz-6AL*	*barc118-barc107*	43.7	42.0-46.7	76.96								
Ssm	*QSsm.cerz-1AS*	*wmc95-wmc329*	23.8	16.5-24.3	*QSsm.cerz-4BL*	*cfd39-wmc47*	97.8	91.3-97.8	-5.37	-14.2	0.000						
Snp	*QSnp.cerz-3AS.2*	*gwm369-wmc50*	22.8	17.3-30.0	*QSnp.cerz-3BS.3*	*gwm285-ksm151*	107.5	97.4-109.5	-0.07	-0.08	0.008	-0.07	0.022	0.08	0.006		
Snp	*QSnp.cerz-3AS.2*	*gwm369-wmc50*	22.8	17.3-30.0	*QSnp.cerz-3BS.2*	*cfd79-ksm45*	29	22.0-41.8	0.05	0.07	0.021						
Gnp	*QGnp.cerz-3AS.2*	*gwm369-wmc50*	25.8	20.3-29.5	*QGnp.cerz-3BS.3*	*gwm285-ksm151*	107.5	98.9-109.0	-2.79			-3.32	0.001	2.25	0.031		
Gnp	*QGnp.cerz-3AS.2*	*gwm369-wmc50*	25.8	20.3-29.5	*QGnp.cerz-3BS.2*	*cfd79-ksm45*	30	24.5-41.3	2.53								
Gwp	*QGwp.cerz-3AS.2*	*gwm369-wmc50*	26.3	19.3-35.5	*QGwp.cerz-3BS.3*	*gwm285-ksm151*	107.5	96.9-109.0	-0.13			-0.15	0.010				
Gwp	*QGwp.cerz-3AS.2*	*gwm369-wmc50*	26.3	19.3-35.5	*QGwp.cerz-3BS.2*	*ksm45-wmc43*	38.3	28.5-42.8	0.20								
Bpp	*QBpp.cerz-3AS.2*	*wmc50-cfa2163*	28.2	18.3-35.0	*QBpp.cerz-3BS.2*	*ksm45-wmc43*	40.8	35.3-48.9	0.32								
Bpp	*QBpp.cerz-3AS.2*	*wmc505-barc359*	29.5	16.3-33.0	*QBpp.cerz-3BS.3*	*gwm285-ksm151*	107.5	96.9-109.0	-0.27			-0.57	0.000				
Hd	*QHd.cerz-3AL.1*	*ksm28-wmc428*	51.4	48.3-53.4	*QHd.cerz-7AS.1*	*gwm635-barc70*	0	0.0-3.0	-0.44								
Hd	*QHd.cerz-3AL.2*	*BF293500_113-cfa2193*	130.7	117.7-130.7	*QHd.cerz-3BS.3*	*gwm285-ksm151*	109	86.4-112.5	-0.49								
Hd	*QHd.cerz-3BL.2*	*BQ159467_233-barc164*	123.3	118.8-128.8	*QHd.cerz-4BS*	*ksm62-gwm113*	29.9	26.7-33.9	-0.48								
Flt	*QFlt.cerz-1AS.1*	*Bla-wmc95*	0.0	0.0-6.0	*QFlt.cerz-4AL.1*	*wmc617a-dupw4*	28.1	25.8-33.1	-0.48								
Flt	*QFlt.cerz-1AS.1*	*Bla-wmc95*	0.0	0.0-6.0	*QFlt.cerz-1BL.2*	*psr162-wg241*	113.6	99.1-122.1	0.70								
Flt	***QFlt.cerz-2BS.2***	*gwm410-wmc167*	44.1	43.2-56.6	*QFlt.cerz-4BS/4BL.1*	*barc337-gwm540*	39.2	36.4-45.9	-0.47								

[a] *Hd* heading date, *Flt* flowering time, *Ph* plant height, *PdL* peduncle length, *Yld* grain yield, *Bpp* biomass per plant, *Ssm* spike number per square meter, *Snp* spike number per plant, *Gne* grain number per ear, *Gnp* grain number per plant, *Sne* spikelet number per ear, *Fse* number of fertile spikelet per ear, *Gwe* grain weight per ear, *Gwp* grain weight per plant, *Gnfs* grain number per fertile spikelet, *Gnts* grain number per spikelet, *Hi* harvest index, *Sf* spike fertility, *Tgw* thousand grain weight

[b] Bold indicates a QTL with significant main effect and shaded cells correspond to QTL with main effect on another traits

[c] QiQj effect, epistatic additive effect between QTLi and QTLj; QiQjE, QTLi × QTLj × environment interaction, where E1 is CA 2006, E2 is BW 2006, E3 is BC 2006, and E6 is BC 2007. A negative number indicates decreased trait value; a positive number indicates increased trait value due to interaction

detected for the traits involved in each cluster (Tables S3a–g).

Twenty clusters with significant MCIM (LOD values higher than 3.0) involving different traits and/or the joint-trait (Table S6; Figures S2–S8) suggested putative pleiotropic effects for QTL mapping in the same region. For several clusters, the use of MCIM increased the power of QTL detection power on the joint-trait compared to each trait separately. Four clusters showed a MCIM with LOD > 3 involving quality traits. In three of them, the highest LOD value was obtained when these quality traits were included.

Discussion

Genomic analysis of complex traits requires the discovery of genes/QTL and their validation in different genetic backgrounds and environments for further use in MAS. The stability of QTL across years and locations determines their suitability for MAS in a breeding program. It is also necessary to consider the interactions among genomic regions during selection using multiple markers. The RIL mapping population used in this study proved to be highly useful for QTL mapping of traits like the ones analyzed here.

Four major clusters for yield-related traits

Linked clusters 13 and 14 (3BS.1 and 3BS.2)

The main genomic region associated with yield and related traits was represented by cluster 13 (3BS.1 region) involving 11 traits. This finding is in agreement with previous reports of an important QTL on 3BS (Marza et al. 2006; Maccaferri et al. 2008; Blanco

et al. 2012; Graziani et al. 2014). This region also showed the highest number of QTL × environment interactions. However, only 1 trait (Gnts) showed epistatic effects (QTL × QTL). No epistatic effects involving Yld, Ph, or Hd/Flt in cluster 13 were observed as was previously detected by Maccaferri et al. (2008). However, cluster 14, linked to cluster 13, showed epistatic interactions for five traits (Gnts, Snp, Gnp, Gwp, and Bpp). Cluster 14 was the second most important QTL affecting Hd and Flt. Our results give support to the presence of two linked genomic regions (clusters 13 and 14) based on the simultaneous detection of these two regions affecting Gnp (3BS.1 and 3BS.2) in the same environment, with alleles of opposite effect and without overlapping LOD intervals (15 cM apart). In agreement with this, Griffiths et al. (2009) reported two QTL for heading date in 3BS linked to *wmc500* and *wmc540*, near the position of cluster 14.

Markers *gwm493* and *barc147* flanking cluster 13 were associated with *Fusarium* head blight response in bread and durum wheat populations (Buerstmayr et al. 2009) and grain yield/plant height/heading date (Maccaferri et al. 2008). In our analyses, the QTL for peduncle length and plant height were the main QTL mapped in cluster 13 (explaining 40.7 and 45.0% of phenotypic variation, respectively). Previous studies reported the presence of semi-dwarfing gene *Rht5* with a large effect on plant height in the telomeric region of 3BS linked to *barc102* (Ellis et al. 2005; Rebetzke et al. 2012). Although this marker was not included in the UC1113 × Kofa linkage map and taking into account two different linkage maps (Maccaferri et al. 2008; Sourdille et al. 2004), SSRs linked to cluster 13 were located close to *barc102*. As to *Rht5*, it has not yet been cloned. However, the possibility of natural variation at the *Rht5* locus in our mapping population as a basis for the Ph QTL should not be discarded. Further work is needed to determine if this locus is involved.

Cluster 7 (2BS.1)

Heading date and flowering time are important traits related to the adaptability of crops. Phenotypic variation for these traits is controlled by the allelic combination of genes affecting vernalization requirements (*Vrn*), photoperiod response (*Ppd*), and earliness per se (*Eps*). These traits are responsible for variation in grain yield potential, particularly in stress environments. The *Vrn*-1 and *Ppd* genes are located in homoeologous groups 5 and 2, respectively (Kamran et al. 2013). *Eps* genes were reported on all wheat chromosomes (Kamran et al. 2013, 2014). In line with this, the second most important QTL cluster (cluster 7) was detected on chromosome 2BS (2BS.1), and affected eight traits. Previous research reported that SSR *gwm148* is linked to *Ppd-B1* (Hanocq et al. 2004; Mohler et al. 2004). Based on the bread wheat SSR consensus map, this marker was located in the same region as that of cluster 7 (Somers et al. 2004). We found a QTL in cluster 7 that also affected Sne and PdL and was strongly associated with Hd and Flt, explaining up to 32% of the phenotypic variation. This finding agrees with the presence of *Ppd-B1* in this region. Moreover, Maccaferri et al. (2008) found a QTL in the *gwm429-gwm148* region in chromosome 2BS with effects on Hd. Using a durum wheat RIL population, Patil et al. (2013) found microsatellite *gwm429* linked to Tgw and Gwe QTL. In addition, SSR *gwm148* in durum wheat was found to be associated with Hi (Golabadi et al. 2011).

In our study it could also be observed that among the traits involved in cluster 7, Kofa provided alleles responsible for increasing Sne and Hd/Flt whereas UC1113 provided alleles for high Yld and PdL. The association of positive alleles for Sne and Hd/Flt agreed with the correlation coefficients in each environment.

Cluster 3 (1BL.1)

Another important region identified was cluster 3 (1BL.1), which affected eight traits. This cluster was associated with Yld and seven yield components and showed a strong effect on Fse. Blanco et al. (2012) reported a QTL in a similar region associated with grain yield, thousand kernel weight, and kernel number per spike using the durum population Svevo × Ciccio. Graziani et al. (2014) and Maccaferri et al. (2008) mapped QTL in this region for Tgw (TKW), leaf greenness (SPAD units), and Yld. It is important to note that the population used in the present work and in the studies carried out by Maccaferri et al. (2008) and Graziani et al. (2014) shared Kofa variety as a parent. In bread wheat, a QTL associated with six yield-related traits (Gwp, Fse, and Sne in common) was identified in the same region (Wu

et al. 2012) based on the positions of SSR markers *gwm131* and *wmc156* in the consensus map (Somers et al. 2004). Another study also found that this region (*barc181-wmc156*) was associated with mean and maximum grain filling rate (GFR), Gwe, and Tgw, explaining about 20.2% of variation in the mean value of GFR (Wang et al. 2009). In addition, two linked QTL were mapped for earliness per se in a similar region in bread wheat (Kamran et al. 2013).

Cluster 11 (3AL.1)

This cluster, which was the main stable region affecting Yld, included 4 additional traits (Gne, Sf, Gnts, and Hi). Marker *wmc428*, located at the peak of the Yld QTL, was found to be near the centromere on chromosome 3A. The simultaneous detection of QTL for Yld and Sf/Gne/Hi/Gnts suggested that the increased yield associated with this region could be due to the high number of florets in the spike. Gne, Gnts, and Hi were found to be highly correlated traits and had a common positive allele from UC1113. Blanco et al. (2012) mapped a QTL for Tgw linked to *wmc428* in durum wheat. Several QTL for grain yield and yield components were detected in this region using the same mapping population of bread wheat (Campbell et al. 2003; Ali et al. 2011; Rustgi et al. 2013). Chromosome 3AL was also found to be associated with Flt (Ali et al. 2011; Mengistu et al. 2012), and it could be assumed that there is an *Eps* gene in this region (Mengistu et al. 2012). In support of this, we found that region 3AL.1 was involved in one of the three epistatic interactions for Hd (*QHd.cerz-3AL.1* × *QHd.cerz-7AS.1*). Previous research detected marker *cfa2193* in the peak of the adjacent cluster 12 (3AL.2) though not as a separate region (Mengistu et al. 2012). We found cluster 11 to be far from cluster 12. Based on our results and on previous evidence, we speculate that cluster 12 may correspond to region four reported by Ali et al. (2011).

Minor clusters

Cluster 1 (1AS.1)

The most important and stable QTL for Sne was located in cluster 1 within the interval *wmc95–barc148*, with a peak position at *wmc24*. In addition, cluster 1 was observed to have effects on Flt, Fse, Gne, and Gwe. Wang et al. (2011) mapped two linked QTL in the *wmc24* region, with effects on floret number per spikelet, spike number per plant, spikelet number per spike, and grain number per spike. In our study, two peak positions were mapped, but the presence of two different QTL was not evident due to a wide overlapping confidence interval. The flanking markers of this cluster were also involved in epistatic interactions affecting Yld (*QYld.cerz-1AS* × *QYld.cerz-6AL*) and Ssm (*QSsm.cerz-1AS* × *QSsm.cerz-4BL*). Dura et al. (2013) reported a Ph QTL linked to *wmc24*, whereas Börner et al. (2002) detected QTL for Ph, Gwe, and Gne at 38 cM on 1AS. Using an association mapping strategy, Maccaferri et al. (2011) found SSR *wmc24* associated with Yld and test weight. In addition, a QTL affecting Fse was mapped on 1AS in a telomeric position (Ma et al. 2007).

The positive relationship between the favorable alleles for Flt and Sne observed in this cluster was in agreement with the relationship previously discussed for Cluster 7. We therefore hypothesize that the increased number of spikelets could be a consequence of prolonged pre-heading time, thus allowing complete development of the terminal spikelets present in the culms. Likewise, Gonzalez et al. (2003) postulated that an increase in the pre-heading stage during stem elongation causes an increase in the number of fertile florets and grains.

Genomic regions previously associated with *Rht* genes

Several clusters with major or minor effects on Ph and/or PdL identified in the present work were located in genomic regions previously associated with *Rht* genes (*Rht1*, *Rht4*, *Rht5*, *Rht9*, *Rht12*) (Ellis et al. 2005). Our results showed that clusters 9 (2BL), 16 (4AS), 19 (4AL.3), 24 (5AL.2), and 25 (5AL.3) were associated with Ph and/or PdL, as stated above in relation to cluster 13 (3BS.1). Each of these clusters was coincident with known *Rht* positions (Maccaferri et al. 2008; Rebetzke et al. 2012; Ellis et al. 2002) (for further details see the Supplementary Discussion).

Although cluster 21 (4BS/4BL.1) showed no association with Ph and/or PdL, it was located near the reported position of *Rht-B1* (Ellis et al. 2002). Quarrie et al. (2005) detected a QTL for yield and yield components in the centromeric region of chromosome 4B, between markers *Rht-B1* and *gwm165.1*.

For further discussion about the remaining clusters, see the Supplementary Material section. The positions of QTL on the remaining chromosomes are shown in Fig. S1.

Multiple trait mapping for yield and yield-related traits

The location of multiple QTL in the same region affecting different traits could be indicative of the presence of a single locus with pleiotropic effects on several traits. The genetic effects on different traits are not independent if genes/QTL for different traits are either linked or pleiotropic. The MCIM method was used to determine if some of the QTL mapped in the same cluster represent a single gene/QTL.

The MCIM performed using mean data for traits mapped in cluster 13 showed a significant joint-trait QTL (LOD = 11.6) that was also significant for four individual traits (Yld, Ph, PdL, and Gwe; LOD > 3 to 9) (Figure S4 [4]). In addition, the analysis of cluster 7 (2BS.1) yielded a significant result for joint-trait QTL (LOD = 7.4). In this case, a LOD score > 3.5 was found for the individual traits Hd, Flt, and Sne (Fig. S3 [1]). For cluster 11 (3AL.1), Yld, Hi, and the joint-trait confirmed QTL results (LOD > 3) using 2 different trait combinations (Figure S4 [1, 2]).

The MCIM for different trait combinations was tested in 15 clusters and showed higher LOD values for joint-traits than for single traits in all cases. In some cases, results showed only the joint-trait to be significant. However, this test failed to detect QTL for individual traits, as in the case of clusters 26 (Figure S7 [1]), 28 (Figure S7 [4, 5]), 30 (Figure S8 [2]), and 35 (Figure S8 [8]). MCIM showed that clusters 7, 11, 13, and 35, among others, could be explained by a single gene/QTL.

Genomic regions co-localized for quality QTL and pleiotropy

Several regions analyzed in the present work co-localized with QTL affecting quality traits previously identified using the same mapping population (UC1113 × Kofa) (Conti et al. 2011; Roncallo et al. 2012). Cluster 35 was mapped for four traits (Gnfs, Sne, Hd, and Flt) and was involved in QQ (*QPdL.cerz-5AL.3* × *QPdL.cerz-7BL.4*) and QE (*QHd.cerz-7BL.4*) interactions. This region was the second-most important QTL for grain protein content (Gpc), Ypc, and flour yellow color (Fb) (Conti et al. 2011; Roncallo et al. 2012). The results derived from MCIM including quality traits (Fb, Ypc, and Gpc) for cluster 35 detected a significant joint-trait QTL with a LOD score higher than that for each individual trait (Figure S8 [9,10,11]), suggesting the presence of a single gene acting on these traits.

Cluster 13 was associated with Gpc (Conti et al. 2011). In the present work, MCIM was used to analyze the pleiotropic effect of yield and protein in this cluster. Both traits were significant (LOD > 3) and found at the same position.

Conclusions

Yield and related traits are under complex genetic control. Our analyses allowed us to construct a model for the genetic network involved in yield-related traits, as well as to catalog the number and importance of QTL by trait and epistatic QTL and/or environmental effect. It was possible to dissect four main genomic regions (clusters 13, 7, 3, and 11) located on 3BS.1, 2BS.1, 1BL.1, and 3AL.1. The first three regions were previously reported in durum wheat whereas the fourth was observed in bread wheat. In our study, 3AL.1 was found to affect 6 yield-related traits. Other important regions were also found to be located on 3BS.2, 1AS, 4AL.3, 5AL.2, and 5AL.3. The most stable traits mapped in the present study were plant height, peduncle length, spikelet number/ear, grain yield, heading date, and flowering time. Among these traits, spikelet number/ear, heading date, and flowering time were affected by the highest numbers of epistatic interactions.

The use of MTM allowed us to confirm that the most important pleiotropic regions (3BS.1, 2BS.1) could be explained by single genes/QTL.

As to the usefulness of these regions for MAS in breeding programs, it is interesting to note that the 3AL.1 region increased yield through its effect on Hi and Gne without altering grain protein content, gluten strength, flour yellow color, and crop phenology. 1AS, another important region, was associated with Sne and was consistently mapped in all environments tested as well as in the mean of all environments. No candidate gene(s) produced the effect described. In view of this the 1AS region is a good candidate for future studies.

An additional finding worthy of note was the presence of several QTL coincident with the positions reported for *Rht* genes, thus suggesting that it could be fruitful for breeders to explore and exploit the effects of these genes in obtaining higher yields.

Acknowledgements We gratefully acknowledge Dr. Jorge Dubcovsky for providing the molecular map and mapping population to carry out the present analysis. We thank the *Asociación de Cooperativas Argentinas*, INTA EEA Barrow, EEA Balcarce, and EEA Marcos Juárez represented by Ing. Rubén Miranda, Ing. Carlos Jensen, Ing. Horacio Bariffi, and Ing. Beatriz Formica, respectively, for providing the experimental fields and sowing the field trials. We also thank Ing. Patricia Gómez for her technical support. We gratefully acknowledge Dr Robert McIntosh by their carefully review of the manuscript. This project was financed by the *Consejo Nacional de Investigaciones Científicas y Técnicas* (CONICET), *Universidad Nacional del Sur* (UNS, PGI TIR 24/A185, and 24/TA11), and *Agencia Nacional de Promoción Científica y Tecnológica* (ANPCyT: PICT 1011, PAE 37108, and PICT 0660).

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