TÜBİTAK

Turkish Journal of Agriculture and Forestry

http://journals.tubitak.gov.tr/agriculture/

Research Article

Turk J Agric For
(2019) 43: 334-350

doi:10.3906/tar-1807-83

Identification of chromosomal regions in the genetic control of quality traits in durum wheat (*Triticum turgidum* L.) from the Fertile Crescent

Ahmad ALSALEH[1,2,3,*], Faheem Shehzad BALOCH[4], Mohamad AZRAK[2], Aladdin HAMWIEH[2], Gönül CÖMERTPAY[5], Rüştü HATİPOĞLU[6], Miloudi NACHIT[2], Hakan ÖZKAN[6]

[1]Department of Biotechnology, Institute of Natural and Applied Sciences, Çukurova University, Adana, Turkey
[2]International Center for Agricultural Research in the Dry Areas, Aleppo, Syria
[3]Science and Technology Application and Research Center (BİLTEM), Yozgat Bozok University, Yozgat, Turkey
[4]Department of Field Crops, Faculty of Agricultural and Natural Sciences, Bolu Abant İzzet Baysal University, Bolu, Turkey
[5]Eastern Mediterranean Agricultural Research Institute, Doğankent, Yüreğir, Adana, Turkey
[6]Department of Field Crops, Faculty of Agriculture, Çukurova University, Adana, Turkey

Received: 13.07.2018 • **Accepted/Published Online:** 16.01.2019 • **Final Version:** 11.06.2019

Abstract: Durum wheat genetic resources from Turkey and Syria are expected to harbor novel alleles for most traits that are of interest to breeders and consumers. However, there have not been sufficient efforts to investigate the genetic structure of this gene pool. In this study, cultivar Kunduru-1149 (selected from one of the unique landraces, Kunduru) from Anatolia was crossed with a Syrian cultivar, Cham1, to produce recombinant inbred lines (RILs) for quantitative trait locus (QTL) analysis. The RIL population was genotyped with simple sequence repeats, amplified fragment length polymorphism, and seed storage protein markers and analyzed for 9 different important quality traits of durum wheat in 8 different environments in Turkey, Syria, and Lebanon. We identified 59 QTLs of various quality and rheology traits using single-marker analysis. Some of the QTLs were also reported in earlier studies; however, new major QTLs were also identified in our QTL mapping population. In future studies, after validation, the markers linked with these QTLs can be used in marker-assisted durum wheat breeding.

Key words: End-use quality, Fertile Crescent, genetic dissection, molecular markers, QTL analysis, *Triticum turgidum* L.

1. Introduction

Durum wheat grown in Mediterranean countries contributes more than 75% of the durum wheat grown worldwide and it plays a significant role in the diet of the local people and traditional farming practices of the region (Baloch et al., 2017). Although durum wheat is used in various forms, such as pasta, bread, couscous, bulgur, and freekeh (Alsaleh et al., 2015, 2016), it is mostly used for pasta production throughout the world because durum seed possesses the most suitable characteristics for this purpose. Pasta production mainly depends upon gluten strength (GS), which is determined by a sedimentation volume (SV) test, yellow pigments (YPs), grain protein content (GPC), and many other quality traits (Porceddu, 1995).

Quality characters are complex quantitative traits composed of numerous individual characteristics, determined by various techniques and specialized technological equipment. The majority of quality traits are inherited in a polygenic fashion, and the degree of their manifestation depends on environmental and growth conditions (Li et al., 2009). Many of the analytical techniques used to measure wheat quality traits are based on the use of chemicals. In order to choose the most appropriate methodology, a high-level of precision and speed is required. Marker-assisted selection (MAS) seems to be more efficient and reliable for the early screening of genotypes to be used in breeding programs (Cömertpay et al., 2019).

Breeding efforts in Turkey and Syria have produced many durum wheat cultivars, which support the local durum wheat industry. Southeastern Turkey and northern Syria constitute the central part of the Fertile Crescent, which is considered to be a key area in the domestication of wheat. Genetic resources obtained from the Fertile Crescent have greatly contributed to worldwide durum wheat breeding by producing elite durum wheat varieties using input from the International Center for Agricultural Research in the Dry Areas (ICARDA). These varieties are now grown in many countries around the world.

* Correspondence: ahmad.alsaleh@bozok.edu.tr

One of the major targets of durum wheat breeding programs is to improve the end-use quality. Identification of the genes controlling the expression of quality traits in durum grain would assist breeding efforts in selecting genotypes with elevated quality through direct selection of desirable alleles at critical loci (Singh et al., 2009). Furthermore, the data currently available on quantitative trait loci (QTLs), genes, and markers related to durum grain quality are expected to increase in the near future with the development of genotyping by sequencing techniques. There is still a need for a better genetic understanding of quality traits to obtain a complete picture of different genetic factors that affect the quality traits of this important food crop. In durum wheat, QTLs have an effect on most quality traits, including GS, GPC, YPs, and milling quality (Ma et al., 2005; Huang et al., 2006; Mann et al., 2009). However, most QTL studies have certain limitations, such as low coverage due to a low number of markers, instability of the identified QTLs due to phenotyping being undertaken in one or few environments, and a low number of individuals in the mapping population. In addition, some of the earlier QTLs were identified in interspecific crosses and therefore have limited contributions for modern durum germplasm. Most of the wheat genetic maps created have been used to identify QTLs for various agronomic traits with only a few being utilized for the determination of quality traits, but they were all constrained by the limitations described above (Zhang and Dubcovsky, 2008). Durum wheat genetic resources from Turkey and Syria are expected to harbor novel alleles for most traits that are of interest to breeders and consumers; however, the genetic structure of this gene pool has not been fully investigated. Furthermore, examination of QTLs that affect most quality traits has been even more neglected, resulting in a lack of essential data concerning the genetic structure of cultivars from Turkey, especially from the Anatolian peninsula. In a previous study, we developed a molecular linkage map using simple sequence repeats (SSRs), amplified fragment length polymorphism (AFLP), and seed storage protein (SSP) markers (Alsaleh et al., 2015). In the current study, we aimed to use this map for QTL analysis for certain quality traits in durum wheat varieties representing the central Fertile Crescent. We particularly aimed to provide an understanding of the genetic structure of specific grain components, detect QTLs associated with quality traits, and discover additional QTLs expressed under different environmental conditions within the Fertile Crescent using a recombinant inbred line (RIL) mapping population.

2. Materials and methods

2.1. Plant material

The mapping population was developed at ICARDA using the single-seed descent method from the cross of Kunduru-1149 × Cham1 and consisted of 141 RILs (Nachit et al., 1995). Kunduru-1149 was selected from a Turkish durum landrace called Kunduru, originating from the Anatolian Plateau, and released as a cultivar in 1967. Kunduru-1149 is a winter cultivar that has adapted to high-altitude areas; it is drought- and cold-tolerant, tall, and late-flowering. Cham1 is an ICARDA cultivar with a spring habit that was released for commercial production in several countries in the Mediterranean basin. Its pedigree is Pelicano/Ruff//Gaviota/Rolette. Cham1 is early-flowering and resistant to yellow rust and Russian wheat aphid, but it is susceptible to leaf rust, septoria leaf blotch, and powdery mildew, and it combines wide adaptation with high yield potential and yield stability. The parents are a combination of major quality and flour rheological traits, which are given in Table 1. More information about their pedigrees can be obtained from wheatpedigree.net. The genetic linkage map for this mapping population was described by Alsaleh et al. (2015).

Table 1. Contrasting qualitative characteristics of the parents of Kunduru-1149 and Cham1 mapping population.

Trait	Abbreviation/unit	Kunduru-1149 (P1)	Cham1 (P2)
Gluten strength	GS (mL)	Medium strength	Fairly weak
Grain protein content	GPC (%)	High protein content	Medium protein content
Yellow pigment	YP (ppm)	Low	High
Vitreousness	Vit (%)	Fairly vitreous	Vitreous
Thousand kernel weight	TKW (g)	Large size	Medium size
Farinograph development time	FDT (min)	Medium strength	Weak
Farinograph stability time	FST (min)	Strong	Weak
Farinograph mixing tolerance	FMT (BU)	Strong	Weak
Test weight	TW (kg/hL)	Light hectoliter weight	Medium hectoliter weight

2.2. Field experiments

The phenotypic assessment for the quality traits was achieved through field experiments conducted over 2 years at 8 different locations in 3 countries of the Fertile Crescent: Syria (in the first year, irrigated and rainfed field experiments; in the second year, 1 rainfed and 2 irrigated field experiments in Tel Hadya), Turkey (both years were rainfed field experiments in Adana), and Lebanon (only the second year was an irrigated field experiment during the 2009–2010 growing season). More information about the experimental locations is given in Table 2.

A total of 141 RILs (F_{14}), along with their parents, were grown in 6 rows, each 2.5 m in length, with 30 cm of distance between the rows during November 2009 and 2010. The RILs, their parents, and 5 controls (Omrabi5, Haurani27, Korifla, Waha, and Gidara2) were sown according to the augmented experimental design at all of the locations (Federer, 1956). All of the experimental plots were kept weed- and disease-free through the application of herbicides and fungicides, respectively. Agronomic and plant protection measures were taken according to the local standard agronomic practices throughout the experimental period.

2.3. Quality evaluation in RILs

In each field experiment, the RILs and parents were mechanically and separately harvested and threshed. Thousand-kernel weights (TKWs) were determined by counting and weighing 200 kernels, taken randomly from the grains harvested from each plot using a seed counter (NUMIGRAL). The vitreousness (Vit) was visually evaluated using 200 durum wheat kernels. A cyclone sample mill (UDY Corporation, Fort Collins, CO, USA) was used to mill grain samples to obtain whole grain flour for the measurement of the following quality traits: GPCs by near-infrared reflectance (NIR System, scanning monochromatic model 5000) according to the procedure described by AACC International (1995) Method 39-11, sedimentation value according to the method described by Pena et al. (1990), YP estimation according to Method 14-50 of AACC International (1999), and test weight according to Method 55-10 of AACC International (2000).

2.4. Rheological analyses

Farinograph stability time (FST), farinograph mixing tolerance (FMT), and farinograph development time (FDT) were determined using a Brabender farinograph according to Method 115 of the ICC (1992). Since a sufficient number of seeds was not obtained from all of the environments, only 4 environments (A26-09, Tur-09, B8-10, and Tur-10) were included for rheological analyses.

2.5. Seed storage protein

The gliadin assay was applied to the seeds of each RIL with the parents according to the protocol of A-PAGE with the modifications described by Tkachuk and Metlish (1980). The modified sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) procedure of Alvarez et al. (1999) was applied to the high- and low-molecular-weight (HMW and LMW) glutenin subunits.

2.6. Molecular marker analysis and genetic mapping

The total genomic DNA was isolated according to the SDS procedure (ITMI, 1994) and the genetic linkage map was constructed using 141 RILs derived from a cross between Kunduru-1149 and Cham1. More information about the genetic linkage map construction and mapping distance can be obtained from Alsaleh et al. (2015).

2.7. Statistical analysis

All of the quality characteristics obtained from all of the locations were analyzed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA) The frequency distribution of each quality trait was performed with the mean values of 8 locations/years using the Kolmogorov–Smirnov (K-S) test.

The quality and rheological traits were measured and adjusted for the block effect, and the Genstat program (VSN International, Hemel Hempstead, UK) was used for general statistics parameters. QTLs effecting the quality traits were detected according to single-marker

Table 2. Information for the experiment locations in different countries.

Year	Environment	Country	Environment abbreviation	Field/location	Condition	Precipitation (mm)	10-year average	Altitude mas
2008/09	I	Syria	C8-09	C8-Tel Hadya	Rainfed	282	336	300
	II	Turkey	Tur-09	Adana	Rainfed	578	720	200
	III	Syria	A26-09	A26-Tel Hadya	Irrigated	282	336	300
2009/10	IV	Syria	C7-10	C7-Tel Hadya	Rainfed	275	336	300
	V	Syria	B8-10	B8-Tel Hadya	Irrigated	275	336	300
	VI	Turkey	Tur-10	Adana	Rainfed	606	720	200
	VII	Lebanon	Leb-10	Terbul	Rainfed	596	535	890
	VIII	Syria	A26-10	A26-Tel Hadya	Irrigated	275	336	300

analysis (SMA) implemented in JMP Genomics 9.0 (SAS Institute, 2018), and the MapQTL6 package (Van Ooijen, 2009) and Qgene (Nelson, 1997) were also used based on simple interval mapping (SIM), while log of odds (LOD) thresholds ($P < 0.01$) were empirically determined for the trait using a permutation test with 10,000 iterations. Only loci with LOD of ≥3 were taken into consideration, except for some segment fragments that joined at LOD ≥2.5 if detected in more than one environment.

3. Results

3.1. Linkage map

The linkage analysis constructed 395 polymorphic marker loci (213 SSRs, 146 AFLPs, and 36 SSPs) and resulted in a final linkage map of 4853.8 cM. The detected loci were distributed over 15 linkage groups on 14 whole chromosomes of durum wheat. Most of the markers (70.7%) used in this genetic map were segregated according to Mendelian fashion (Alsaleh et al., 2015).

3.2. Phenotypic variation

Nine important quality and rheological traits were phenotyped across all of the environments during 2009 and 2010. The traits showed a wide variation in both parents and the RILs in the tested environments. The frequency distributions of the mean values for the all of the traits are presented in Figure 1 and Table 3. The frequency distribution of the RIL population for the quality traits showed the presence of extreme outlier groups from the parental lines. The RILs showed transgressive biparental segregation for all of the quality traits examined. Some RILs produced higher values for almost all of the quality traits than both parents and varied greatly for all of the quality characteristics, indicating that the parents used to develop this population differed in terms of these traits. The phenotypic results (mean, standard deviation, variance, skewness, and kurtosis) for all of the quality traits for all of the environments of the parents and RILs are shown in Table 3.

A correlation analysis was conducted to determine the pattern of association between different quality traits, and it showed significant positive and negative correlations between most of the quality traits, making it possible to select the desired traits and QTLs that have a simultaneous effect on the other traits/QTLs. Significant positive correlations were found between FST and FDT and between GS and FST ($r = 0.84$ and 0.64, respectively).

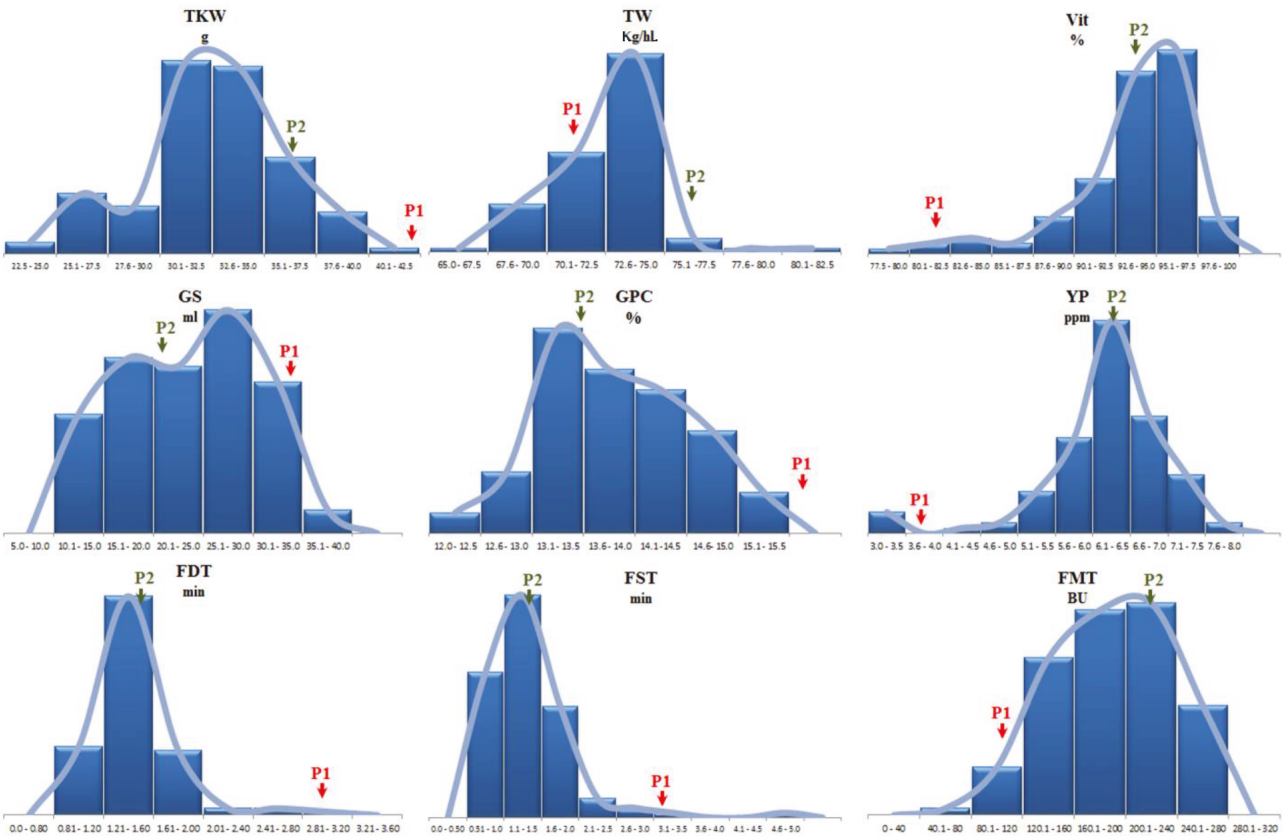

Figure 1. Frequency distribution of the mean values for the quality and rheology traits of Kunduru-1149 × Cham1 recombinant inbred lines. The parental genotypes Kunduru-1149 and Cham1 are indicated by arrows.

Table 3. Phenotypic performance of durum wheat genotypes Kunduru-1149, Cham1, and recombinant inbred lines (RILs) in 8 environments for gluten strength (GS), grain protein content (GPC), yellow pigment (YP), vitreousness (Vit), thousand-kernel weight (TKW), farinograph development time (FDT), farinograph stability time (FST), farinograph mixing tolerance (FMT), and test weight (TW).

		Parents					RILs			
Trait	Environment	Kunduru-1149	Cham1	Min	Max	Mean	Std	Variance	Skewness	Kurtosis
GS, mL	I	40	29	12	50	28.54	9.27	85.16	0.43	–0.40
	II	34	21	9	43	23.41	8.54	72.26	0.23	–0.75
	III	32	22	10	38	22.99	6.62	43.40	–0.06	-0.79
	IV	33	18	0	34	21.83	6.00	35.68	–0.27	0.74
	V	27	17	10	37	17.86	6.41	40.75	0.83	0.45
	VI	38	23	8	60	23.72	9.83	95.75	0.77	0.78
	VII	33	23	10	40	23.00	7.87	61.37	–0.15	–1.01
	VIII	37	20	8	48	27.61	9.30	85.66	–0.02	–0.62
Mean		34.25	21.56	8.4	43.8	23.62	7.98	65.00	0.22	–0.20
GPC, %	I	18.8	17.3	15.7	19.1	17.68	0.81	0.64	–0.41	–0.40
	II	13.3	11.5	10.3	14.4	11.90	0.91	0.81	0.52	0.06
	III	16.1	13.8	12.8	17.2	14.61	1.01	1.01	0.48	–0.39
	IV	17.2	16.3	13.8	17.7	15.91	0.84	0.70	–0.40	–0.31
	V	13.0	9.8	7.0	16.2	9.95	1.64	2.65	1.14	1.64
	VI	15.6	13.3	10.5	16.9	13.42	1.59	2.49	0.14	–0.87
	VII	14.1	12.8	11.1	15.8	12.57	0.82	0.66	0.87	1.36
	VIII	17.0	13.2	12.8	18.7	15.05	1.30	1.67	0.58	0.11
Mean		15.64	13.51	11.8	17.0	13.89	1.11	1.33	0.36	0.15
YP, ppm	I	3.9	6.5	2.9	7.6	5.80	0.97	0.93	–0.56	0.70
	II	3.4	5.5	2.9	8.6	6.51	0.95	0.90	–1.18	3.49
	III	3.8	6.8	1.8	7.7	5.62	0.89	0.78	–1.29	4.64
	IV	3.8	6.5	3.1	7.7	6.13	0.81	0.66	–1.47	3.92
	V	3.8	6.0	2.7	8.5	6.69	0.97	0.93	–1.66	4.90
	VI	3.3	5.8	2.9	9.3	7.25	1.21	1.45	–1.08	2.08
	VII	4.1	5.8	3.4	8.8	6.76	0.92	0.83	–1.43	3.83
	VIII	3.7	7.1	2.6	8.1	6.07	0.90	0.81	–1.40	4.14
Mean		3.71	6.25	2.8	8.3	6.35	0.95	0.91	–1.26	3.46
Vit, %	I	87	98	89	100	97.90	2.46	6.00	–1.22	0.87
	II	70	91	24	100	94.21	10.28	104.69	–4.68	26.27
	III	92	97	90	100	98.86	1.63	2.62	–2.97	12.28
	IV	83	97	39	100	87.54	13.29	174.88	–1.48	1.70
	V	74	77	15	100	81.71	15.59	240.70	–1.93	4.85
	VI	66	95	51	100	94.90	7.14	50.52	–3.45	15.17
	VII	88	96	82	100	97.39	4.16	17.15	–2.10	4.14
	VIII	95	99	94	100	99.13	1.16	1.34	–1.94	4.54
Mean		81.88	93.75	61	100	93.95	6.96	74.74	–2.47	8.73
TKW, g	I	33.5	29.3	17.8	40.9	26.15	3.94	15.39	0.43	0.99
	II	54.3	50.1	32.3	55.1	44.12	4.44	19.50	–0.26	0.14

Table 3. (Continued).

	III	50.1	35.8	27.2	52.1	41.15	5.07	25.48	–0.10	–0.25
	IV	36.8	30.4	19.6	38.3	29.55	3.16	9.92	0.01	0.88
	V	39.5	36.0	23.3	42.8	33.35	3.90	15.10	–0.03	–0.28
	VI	40.2	37.0	19.0	47.1	31.92	6.74	45.05	0.25	–0.67
	VII	45.3	40.6	28.0	46.7	37.36	3.91	15.13	–0.13	–0.31
	VIII	47.1	31.7	25.3	50.0	37.65	5.56	30.68	–0.18	–0.47
Mean		43.34	36.35	24.1	46.6	35.16	4.59	22.03	0.00	0.00
FDT, min	II	2.1	1.4	0.9	2.2	1.41	0.28	0.08	0.56	0.08
	III	3.1	1.1	0.8	3.7	1.35	0.36	0.12	3.11	18.87
	V	3.1	1.8	0.6	4.1	1.56	0.50	0.25	2.38	9.04
	VI	3.1	1.7	0.8	4.1	1.51	0.43	0.18	2.83	14.57
Mean		2.86	1.50	0.8	3.5	1.46	0.39	0.16	2.22	10.64
FST, min	II	2.4	1.4	0.4	4.2	1.42	0.70	0.48	1.56	2.99
	III	5.3	1.4	0.4	7.5	1.32	0.81	0.66	4.49	31.92
	V	2.7	1.3	0.4	3.7	1.18	0.56	0.31	1.40	2.98
	VI	2.2	1.2	0.3	5.8	1.36	0.73	0.53	2.61	12.44
Mean		3.14	1.31	0.4	5.3	1.32	0.70	0.49	2.52	12.58
FMT, BU	II	98	163	31	267	152.26	56.90	3206.37	0.04	–0.80
	III	105	298	32	323	193.64	64.99	4182.83	–0.32	–0.79
	V	132	234	74	324	231.82	54.91	2987.55	–0.53	–0.19
	VI	106	189	56	282	167.68	50.16	2492.33	0.00	–0.69
Mean		110.20	221.13	48.3	299.0	186.35	56.74	3217.27	–0.20	–0.61
TW, kg/hL	II	71.4	75.7	66.7	79.9	76.12	2.30	5.24	–1.36	3.56
	III	70.0	74.0	69.7	75.8	73.72	1.42	2.00	–0.82	0.08
	V	73.4	76.4	71.3	80.8	77.35	1.83	3.31	–0.63	0.58
	VI	73.1	74.3	57.3	85.4	72.63	5.40	28.89	–0.52	0.20
	VIII	70.7	77.6	65.2	80.2	74.80	3.55	12.44	–0.75	–0.03
Mean		71.71	75.60	66.0	80.4	74.93	2.90	10.38	–0.82	0.88

On the other hand, significant negative correlations were found between GS and FMT, FST and FMT, and FMT and FDT (r = –0.78, –0.77, and –0.67, respectively) (Table 4).

3.3. Quantitative trait loci

SMA and SIM were used in the present study to determine the associations between 9 of the quality and rheology traits under the field conditions and genotypes for the RIL populations. Using SMA, 59 QTLs were detected, compiled, taken into account, and sufficiently discussed, but the QTLs identified by SIM were only included if detected in more than one environment in Table 5, without being discussed, in order to confirm their detection using both methods.

3.3.1. Gluten strength

Parental lines Kunduru-1149 and Cham1 showed a wide variation in GS for all 8 environments, with the former giving a higher value than the latter. The RIL population showed extreme GS values for all of the environments compared to the parents. However, environmental effects could not be eliminated for this trait. It was found that the GS value was lower in 2 of the 8 environments (i.e. irrigated fields in Tel Hadya/Syria and Adana/Turkey receiving high precipitation). This result was expected since the GS is usually low in environments with high precipitation.

Using SMA, 11 linked QTLs were identified for GS. Chromosomes 1A and 1B were found to harbor 3 and 4 QTLs, respectively. Furthermore, one minor QTL was determined on each of the following chromosomes: 2A, 4B, 6A, and 7A. Chromosome 1A was found to contain a major locus (*Glu-A1-HMW-1*) confirmed in all 8 environments, with an LOD score of 4.10–12.87, accounting for 14% to 41% of the variation in the GS values (Table 5; Figures 2, 3a, and 3b).

Table 4. Phenotypic correlation coefficients among the studied traits in Kunduru-1149, Cham1, and RIL populations based on average trait values across the environments

	GS	GPC	YP	Vit	TKW	FDT	FST	FMT	TW
GS	1								
GPC	0.19*	1							
YP	0.01	–0.16	1						
Vit	0.06	0.10	0.08	1					
TKW	0.01	–0.33**	0.15	0.39**	1				
FDT	0.56**	0.24*	–0.17	–0.11	–0.04	1			
FST	0.64**	0.17	–0.01	–0.13	–0.01	0.84**	1		
FMT	–0.78**	–0.002	0.05	–0.07	–0.19*	–0.67**	–0.77**	1	
TW	–0.003	–0.39**	0.17	0.07	0.56**	0.09	0.08	–0.16	1

*Correlation was significant at P ≤ 0.05, **Correlation was significant at P ≤ 0.01.

Roncallo and Echenique (2014) reported a QTL (*barc147-gwm493*) that affected the GPC, but in the current study, it was found that the QTL flanked between markers *Xgwm493* and *Xbarc218 bp190* was associated with GS and test weight (TW). Zhang and Dubcovsky (2008) reported a QTL for the GPC, wet gluten content, and cooked firmness associated with *gwm493*. Elouafi et al. (2001) also reported a QTL for GPC close to *gwm493*. Beecher et al. (2012) reported a QTL located on chromosome 4A for the SDS-SV levels and FMT that was significantly associated with the marker *barc170*, although in our study, this marker was linked to GPC. A result from both the literature and the present study showed that at least one marker, *gwm493*, was associated with GS.

3.3.2. Grain protein content

The GPC was high in Kunduru-1149 and medium in Cham1. Using SMA, 6 QTLs were identified for variation in GPC: chromosomes 4A and 5B had 1 on each, (Table 5) and chromosomes 2A and 4B had 2 on each. A vital locus (*Xwmc177)* was confirmed on chromosome 2A in 6 of the 8 environments (except C7-10 and Leb-10), with an LOD score of 3.88–10.22, accounting for 14% to 35% of the variation in GPC values (Table 5; Figures 3a and 3b).

3.3.3. Yellow pigments

The YP content was higher in Cham1 than in Kunduru-1149. Seven different QTLs linked with YP contents were identified: chromosomes 1B, 2A, 3B, 5A, and 7B had 1 on each, while 2 were detected on chromosome 7A (Table 5).

The first QTL showed a significant peak on the *Xbarc80* loci on chromosome 1B in all of the environments, except for 3 (C8-09, Tur-09, and C7-10). This QTL was consistently associated with YP in the 5 environments with an LOD score of 3.09–3.99 and was responsible for 10% to 14% of the variation in the YP contents (Table 5; Figures 3a and 3b). Li et al. (2011) reported a QTL linked with *Xbarc80* for flour whiteness, FST, and FMT. However, the QTL found in this study for YP on chromosome 6A (*Xwmc201-Xbarc353*) was more compatible with the findings of Roncallo et al. (2012), although they reported a QTL affecting the flour redness (Fa*), yellow color (Fb*), and YP near *barc353*. Zhang and Dubcovsky (2008) also reported a QTL for YP, but it was located in a position 100 cM from the marker *barc80* locus. However, they reported several QTLs located near *wmc201* or *barc353* for YP, semolina and pasta color, mixograph peak height, mixograph peak width, and ash contents. Blanco et al. (2011) also identified a YP-QTL on chromosome 2A. Similarly, Jing et al. (2007) reported one QTL for YP on chromosome 2A, detected by markers *Xbarc80-Xgwm818*, and also demonstrated the associations between *barc309* and grain moisture, storage protein, and hardness in *T. monococcum*.

3.3.4. Vitreousness

For Vit, 4 QTLs were detected: chromosomes 2A and 3A had 1 on each, while 2 were found on 7A, where chromosome 7A contained a locus (*XE38-M41bp538*) confirmed in 3 environments only (Table 5; Figures 3a and 3b).

3.3.5. Thousand-kernel weight

For the TKW, 7 QTLs were detected: chromosomes 2A, 2B, 3B, 4B, 5A, 6B, and 7A had 1 on each, while a major QTL was observed on chromosome 2A (*Xwmc177*) in 6 environments (Table 5; Figures 3a and 3b).

3.3.6. Farinograph development time

Only 4 environments (Tur-09, A26-09, B8-10, and Tur-10) were included in the rheology analysis for the reasons given in the Section 2. There were 3 QTLs linked with FDT,

Table 5. Quantitative trait loci (QTL) identified in the Kunduru-1149 × Cham1 RIL population of tetraploid wheat, detected by single-marker analysis (SMA), simple interval mapping (SIM), log of the odds (LOD), percentage of explained variance (R^2), and region overlapping across traits (ROAT).

Chr.	Trait	Environment*	Linked marker (SMA)	Linked marker position (SMA)	Linked markers (SIM)	Linked markers position (SIM)	LOD	R^2	Probability
1A	GS	I - II - III - IV - VII	*XE38-M41bp217*	7.8	*XE38-M41bp217*	7.8	2.60–4.88	0.09–0.17	<0.0001–0.0025
	TW	III	*XE38-M41bp289*	10.7	*XE36-M41bp742 - XE36-M41bp394*	51.8–52.8	3.85	0.14	0.0001
	GS	III - IV	*Xbarc83*	42.7			2.94–4.21	0.10–0.14	<0.0001–0.0011
	GS	I - II - III - IV - V - VI - VII - VIII	*Glu-A1-HMW-1*	75.7	*Glu-A1-HMW-1*	75.7	4.112.87	0.14–0.41	<0.0001
	FST	II - V	*Glu-A1-HMW-1*	75.7	*Glu-A1-HMW-1*	75.5	3.78–4.24	0.13–0.15	<0.0001–0.0002
	FMT	II - III - V	*Glu-A1-HMW-1*	75.7	*Glu-A1-HMW-1*	75.5	3.24–4.97	0.11–0.18	<0.0001–0.0006
			ROAT	75.5					
1B	GS	IV - VII - VIII	*Gli-B1-w30*	3			3.1–3.6	0.11–0.13	0.0003–0.0008
	GS	I - II - III - VI - VII - VIII	*Gli-A1-ω33, 35, & 38*	49.5	*Gli-A1-ω33, 35, &38*	49.5	3.03–4.43	0.10–0.15	<0.0001–0.0002
	FST	II - VI	*Gli-A1-ω33, 35, & 38*	49.5			2.773.68	0.09–0.12	0.0002
	FMT	II - VI	*Gli-A1-w38*	49.5			2.703.16	0.09–0.11	0.0007–0.002
			ROAT	49.5					
	GS	I - II - III - VI - VII - VIII	*Glu-B3-LMW-g*	246.7	*Gli-B1-γ45-Glu-B3-LMW-b*	246.7248.7	3.02–4.37	0.10–0.15	<0.0001–0.0004
	FDT	VI	*Glu-B3-LMW-g*	246.7			3.40	0.12	0.0004
	FST	II - VI	*Glu-B3-LMW-g*	246.7	*Glu-B3-LMW-g-Glu-B3-LMW-b*	246.7–247.7	3.62–4.09	0.13–0.14	<0.0001–0.0002
	FMT	II - VI	*Glu-B3-LMW-g*	246.7	*Glu-B3-LMW-g*	246.7	3.604.12	0.13–0.14	<0.0001–0.0003
			ROAT	246.7					
	FST	V	*Xbarc187*	301.1			3.1	0.1	0.0009
	FST	V	*XE35-M36bp769*	331.1			3.1	0.1	0.0007
	GS	I - II - III - V - VI - VII - VIII	*XE36-M50bp520*	377.1	*XE36-M50bp522 - XE36-M50bp69*	375.1–382	2.88–9.85	0.10–0.34	<0.0001–0.0013
	FST	II - V - VI	*Xbarc61*	378.9	*XE35-M36bp652 - XE36-M50bp520*	361.8–377.1	2.82–6.38	0.10–0.22	<0.0001–0.0003
	FDT	II - III - V - VI	*Glu-B1-HMW-20*	380	*XE36-M50bp520 - Glu-B1-HMW-20*	377.1–379.9	3.49–5.74	0.12–0.21	<0.0001–0.0003
	FMT	II - III - V - VI	*Glu-B1-HMW-20*	380	*XE35-M36bp652 - XE36-M50bp69*	371.8–381	3.03–11.46	0.10–0.39	<0.0001–0.0009
			ROAT	377.1–380					
	YP	III - V- VI - VII - VIII	*Xbarc80*	469.7	*Xbarc80 - Xgwm818*	472.7482.7	3.09–3.99	0.10–0.14	0.0008–0.0001

Table 5. (Continued).

2A	GPC	I - II - III - V - VI - VIII	*Xwmc177*	0	*Xwmc177 - XE36-M50bp116*	0 - 9	3.88–10.22	0.14–0.35	<0.0001
	Vit	IV	*Xwmc177*	0	*Xwmc177 - XE36-M50bp116*	4	7.54	0.26	<0.0001
	YP	I - VI	*Xwmc177*	0	*Xwmc177 - XE36-M50bp116*	2–5	2.85–5.59	0.10–0.20	<0.0001–0.0014
	TKW	I - II - V - VI - VII - VIII	*Xwmc177*	0	*Xwmc177 - XE36-M50bp116*	2–9	2.50–7.22	0.08–0.25	<0.0001–0.0005
	TW	VI	*Xwmc177*	0	*Xwmc177 - XE36-M50bp116*	5	5.2939	0.19	<0.0001
			ROAT	0					
	GS	II - V - VII	*XE33-M44bp398*	335.8			2.57–3.67	0.09–0.12	0.0002–0.0027
	GPC	II	*XE33-M49bp370*	344.2			3.34	0.33	0.0005
2B	TW	II	*Xgwm210*	127.2			3.06	0.10	0.0009
	TKW	III	*XE36-M41bp260*	318.7	*XE36-M41bp260*	318.7	3.51	0.13	0.0003
	TW	V	*XE36-M41bp260*	318.7			3.01	0.11	0.001
			ROAT	318.7					
3A	Vit	V	*Xgwm674*	70.8			3.17	0.11	0.0007
3B	YP	I	*Xbarc133*	12.3			3.01	0.10	0.001
	TKW	VII	*Xbarc133*	12.3			3.11	0.10	0.0008
			ROAT	12.3					
	TW	V	*Xbarc164*	141.1			3.21	0.11	0.0006
4A	FMT	II - VI	*Xbarc106*	22.5	*Xgwm1093 - Xgwm610*	19–28.5	2.97–3.89	0.10–0.13	0.0001–0.0011
	GPC	II	*XE37-M60bp121*	63.5	*XE37-M60bp121 - Xbarc170*	64.5	3.86	0.15	0.0001
4B	GPC	II	*XE36-M50bp586*	74.6			3.05	0.13	0.0009
	TKW	III - VIII	*Xgwm368*	213	*Xgwm368 - Xbarc199*	216–219.5	2.77–4.45	0.09–0.15	<0.0001–0.0017
	TW	II - III - V - VIII	*XGWM368*	213	*Xbarc193 - Xgwm368*	206.5–213	3.30–4.80	0.11–0.18	<0.0001–0.0005
			ROAT	213					
	GPC	IV	*XE37-M60bp90*	261.9	*XE37-M60bp90 - Xbarc163*	263.9	4.63	0.19	<0.0001
	GS	II - V - VI	*XE37-M33bp196*	398.7			2.78–3.39	0.11–0.13	0.001–0.0017

Table 5. (Continued).

	FDT	III	*XE37-M33bp196*	398.7	*XE37-M33bp196 - Xbarc337bp225*	399.7	3.59	0.14	0.0003
	FMT	II - III - VI	*XE37-M33bp196*	398.7			3.00–3.22	0.12–0.13	0.0006–0.001
			ROAT	398.7					
5A	TKW	I - III - VIII	*Xbarc180*	42.7	*Xbarc180-Xbarc360*	47.7–39.2	2.53–4.73	0.08–0.16	<0.0001–0.0029
	YP	VII	*Xgwm156*	65.5			2.604	0.09	0.0025
5B	GPC	II	*XE36-M50bp190*	317.4			3.11	0.14	0.0008
6A	GS	I - II - III - VI - VII - VIII	*Glu-A3-LMW-f*	0	*Glu-A3-LMW-f*	0	2.56–4.00	0.08–0.14	<0.0001–0.0027
	FST	II - VI	*Glu-A3-LMW-f*	0	*Glu-A3-LMW-f*	0	3.04–3.71	0.11–0.13	0.0002–0.0009
	FMT	II - VI	*Glu-A3-LMW-f*	0			2.61–3.11	0.09–0.11	0.0008–00.25
			ROAT	**0**					
6B	FMT	III	*XE36-M50bp363*	0			3.54	0.14	0.0003
	TKW	II - III	*Xbarc354*	186.3			2.68–3.18	0.09–0.11	0.0007–0.0021
7A	Vit	II - VI - VII	*XE38-M41bp538*	102.8	*XE36-M50bp560 - XE38-M41bp538*	100.7–102.7	3.14–6.07	0.11–0.21	<0.0001–0.0007
	YP	II - VIII	*Xgwm282*	395.8			2.57–2.68	0.08–0.09	0.0021–0.0027
	GS	II - IV - VIII	*Xcfa2028*	512.2			2.87–4.20	0.11–0.16	<0.0001–0.0013
	YP	VI - VII	*Xwmc17*	581.1	*Xwmc17- XE45-M39bp262*	581.1–583.1	3.52–4.13	0.12–0.14	<0.0001–0.0003
	TKW	I - III	*Xbarc281bp225*	632.7	*Xbarc281bp225 - Xbarc281bp220*	638.7	2.60–3.40	0.08–0.11	0.0004–0.0025
	Vit	II - VII	*XE45-M39bp341*	678.2			2.57–3.28	0.10–0.12	0.0005–0.0027
7B	YP	IV	*Xgwm111*	121.9	*Xwmc396 - Xgwm111*	110.1–111.1	3.2803	0.1509265	0.0005

Sedimentation volume (GS), grain protein content (GPC), yellow pigment (YP), vitreousness (Vit), thousand-kernel weight (TKW), farinograph stability time (FST), farinograph development time (FDT), farinograph mixing tolerance (FMT), test weight (TW). *See environment abbreviations in Table 2.

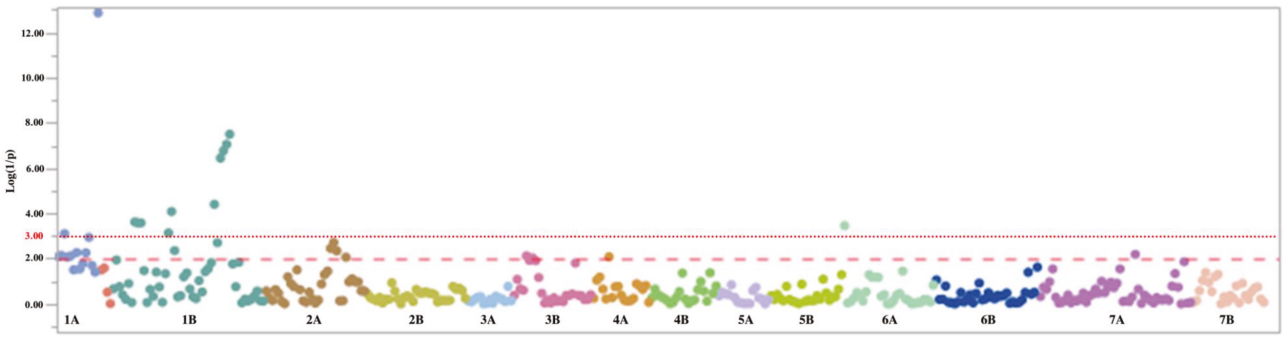

Figure 2. Manhattan plot of the single-marker association analysis for the gluten strength (GS) trait in the A26-09 environment.

which were identified on chromosomes 1B and 4B (Table 5; Figures 3a and 3b). The major QTL on chromosome 1B showed a significant peak at *Glu-B1-HMW-20* in all of the environments. This QTL had an LOD score of 3.49–5.74, accounting for 12% to 21% of the phenotypic variance in FDT. The highest LOD was detected in the Tur-09 environment, while the lowest was in Tur-10.

3.3.7. Farinograph stability time

A total of 7 QTLs were identified as responsible for the variation in FST (Table 5; Figures 3a and 3b). Of these, the one located on chromosome 1B showed a significant peak at *Xbarc61* and was consistently observed in 3 of the 4 environments (except A26-09). These QTLs had an LOD score varying between 2.82 and 6.38, accounting for 10% to 22% of the phenotypic variance for the FST.

3.3.8. Farinograph mixing tolerance index

Over the different environments, 8 QTLs associated with FMT were detected; chromosomes 1A, 4A, 4B, 6A, and 6B had 1 on each, while 3 were found on chromosome 1B (Table 5; Figures 3a and 3b). One major QTL was located on chromosome 1B, in close vicinity to the glutenin-coding loci *Glu-B1*, and was consistently observed across all environments. These QTLs had a significant peak at the *Glu-B1-HMW-20* loci and an LOD of 3.03–11.46, accounting for a high percentage (10% to 39%) of phenotypic variations in the different environments. The highest LOD was detected in Tur-09, while the lowest was in B8-10 (Figure 4). For FMT, another favorable allele was contributed by Kunduru-1149. The second peak of the QTL was observed on chromosome 1B in 2 different environments, located 133.3 cM apart from *Glu-B3-LMW-g*, with an LOD of 3.60–4.12, accounting for 13% to 14% of the phenotypic variance for this trait (Table 5; Figures 3a and 3b). In 3 environments (Tur-09, A26-09, and B8-10), another QTL for FMT was detected on chromosome 1A, linked by *Glu-A1-HMW-1*, with an LOD of 3.24–4.97, accounting for 11%–18% of the phenotypic variance. Zhang and Dubcovsky (2008) reported a QTL for pasta color located close to *barc78* and another QTL flanked between *Xbarc78* and *Xwmc219* associated with FMT. In addition, Roncallo et al. (2012) identified a QTL strongly linked with the marker *wmc219* for flour YP.

3.3.9. Test weight

Six different QTLs were detected and located: chromosomes 1A, 2A, 3B, and 4B had 1 on each, and in addition, 2 QTLs on 2B influenced TW. The major QTL, which was consistently detected in different environments on chromosome 4B, showed a significant peak at *Xgwm368* and had an LOD of 3.30 to 4.80, accounting for 11% to 18% of the variation for this trait. The highest LOD for the TW was found in A26-10, while the lowest was in A26-09 (Table 5; Figures 3a and 3b).

4. Discussion

To determine the best strategy for the selection of desirable traits, it is crucial to understand the genetic structure of these traits (Nadeem et al., 2018a). With successful applications of MAS in crop plant breeding, it is possible to identify suitable markers linked with the trait of interest (Baloch et al., 2016; Nadeem et al., 2018b). The improvement of durum wheat quality is a complex breeding objective involving many phenotypic characteristics controlled by a range of metabolic pathways and a number of genes/QTLs controlling the grain architecture. In addition to this, the GPC, GS, TKW, and Vit are some of the most important quality parameters in durum wheat. In the parents, it was found that the TKW, GPC, GS, FST, and FDT values of Kunduru-1149 were higher when compared to Cham1, while TW, Vit, and YP were higher in Cham1.

The Kunduru-1149 cultivar was selected from famous and unique durum wheat landraces adapted to a marginal area with low precipitation located in the Southeast Anatolian region of Turkey. Therefore, this cultivar donated positive alleles for GPC, GS, TKW, FST, and FDT, whereas Cham1 contributed positively to TW, Vit, YP, and FMT.

Application of the statistical methods for QTL detection is the most critical task and is an essential bridge between the trait phenotype and the genotype. To detect associations between molecular markers and

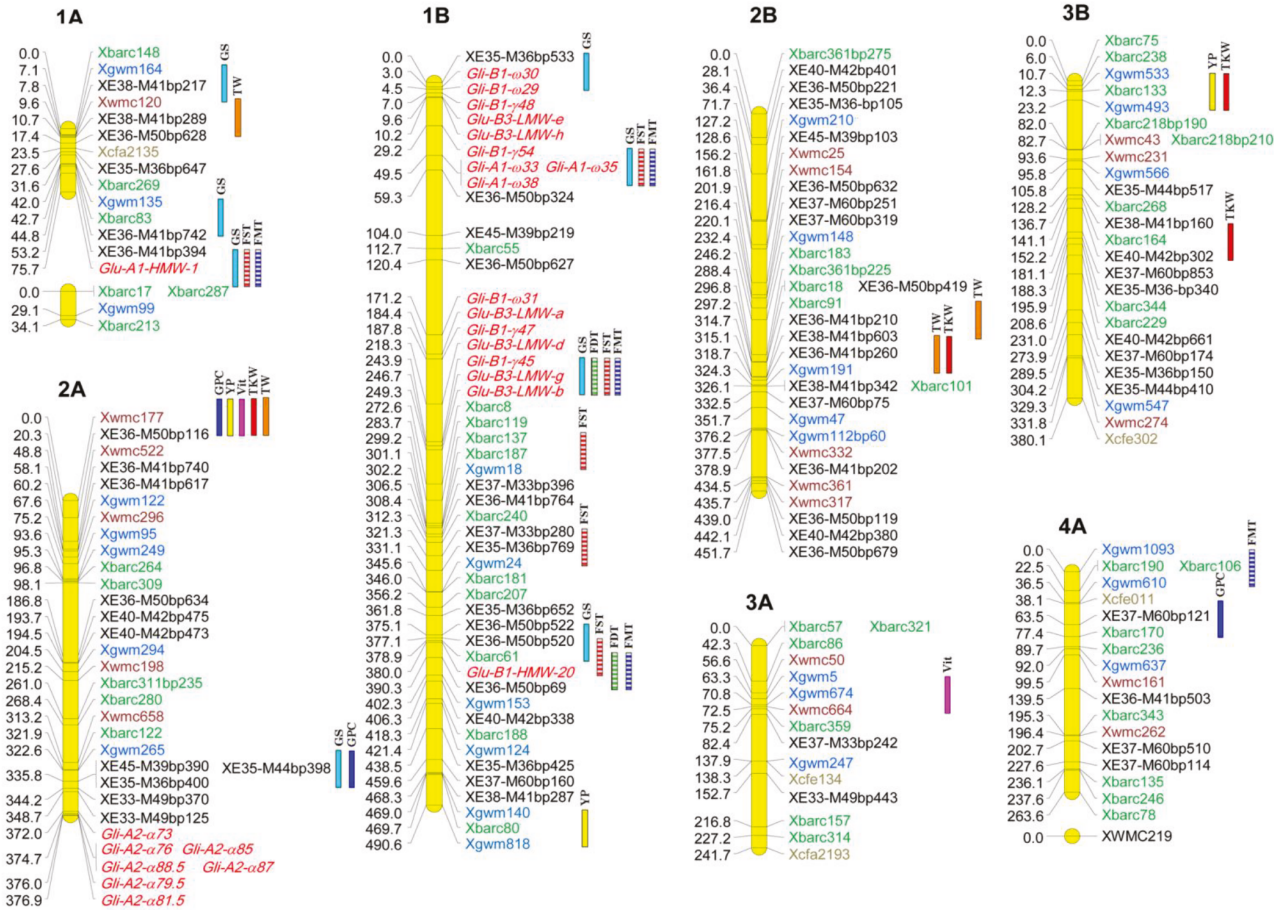

Figure 3. Linkage maps (a, b) of the Kunduru-1149 × Cham1 population supported by the estimated locations of significant QTLs for durum quality and rheology with an LOD of ≥2.5.

traits of interest, data analysis approaches include SMA, SIM, multiple interval mapping, and composite interval mapping, each having advantages and disadvantages. Therefore, the choice of an appropriate statistical approach is one of the most important tasks during QTL analysis. SMA and SIM were used in the present study to determine associations between the phenotype for quality traits in durum wheat under field conditions and the genotype for the RIL populations. SMA is one of the simplest and easiest methods for QTL detection. In the present study, QTL analysis was done by two different statistical approaches, and QTLs detected by SMA were only taken into consideration. Major QTLs with the highest phenotypic variations were identified through both statistical methods; however, some additional QTLs with an LOD score lower than 2.5 and/or expressed in some environments were identified through SMA.

The detected QTLs were spread across all of the chromosomes, and 1A, 1B, 2A, 4B, and 7A harbored the largest number of QTLs identified. For example, 1B possessed 15 QTLs, while 2A and 4B harbored 7 QTLs each, and chromosomes 1A and 7A also harbored 6 QTLs each. The major QTLs were intensively detected on chromosomes 1A, 1B, and 2A, which may be because these chromosomes significantly contribute to quality and rheology traits and thus possess many genomic loci controlling quality traits in durum wheat.

The GS of the durum wheat cultivar is commonly measured by SV, reflecting the quality of gluten in endosperm proteins. Pasta with good firmness after cooking is usually produced with durum wheat cultivars with strong GS quality (Pogna et al., 1990). Thus, GS is one of the most important indicators of durum wheat quality. In this study, the GS trait was affected by many genes located on chromosomes 1A, 1B, 2A, 4B, 6A, and 7A; however, the first 2 chromosomes possessed major QTLs controlling the GS of durum wheat. One major QTL, predominantly associated with GS, was identified on chromosome 1A on the locus *Glu-A1-HMW-1*, accounting for the highest phenotypic variation ranging from 14% to 41%, which was contributed by Kunduru-1149. Li et al. (2009) reported that variations in SV were affected by 4

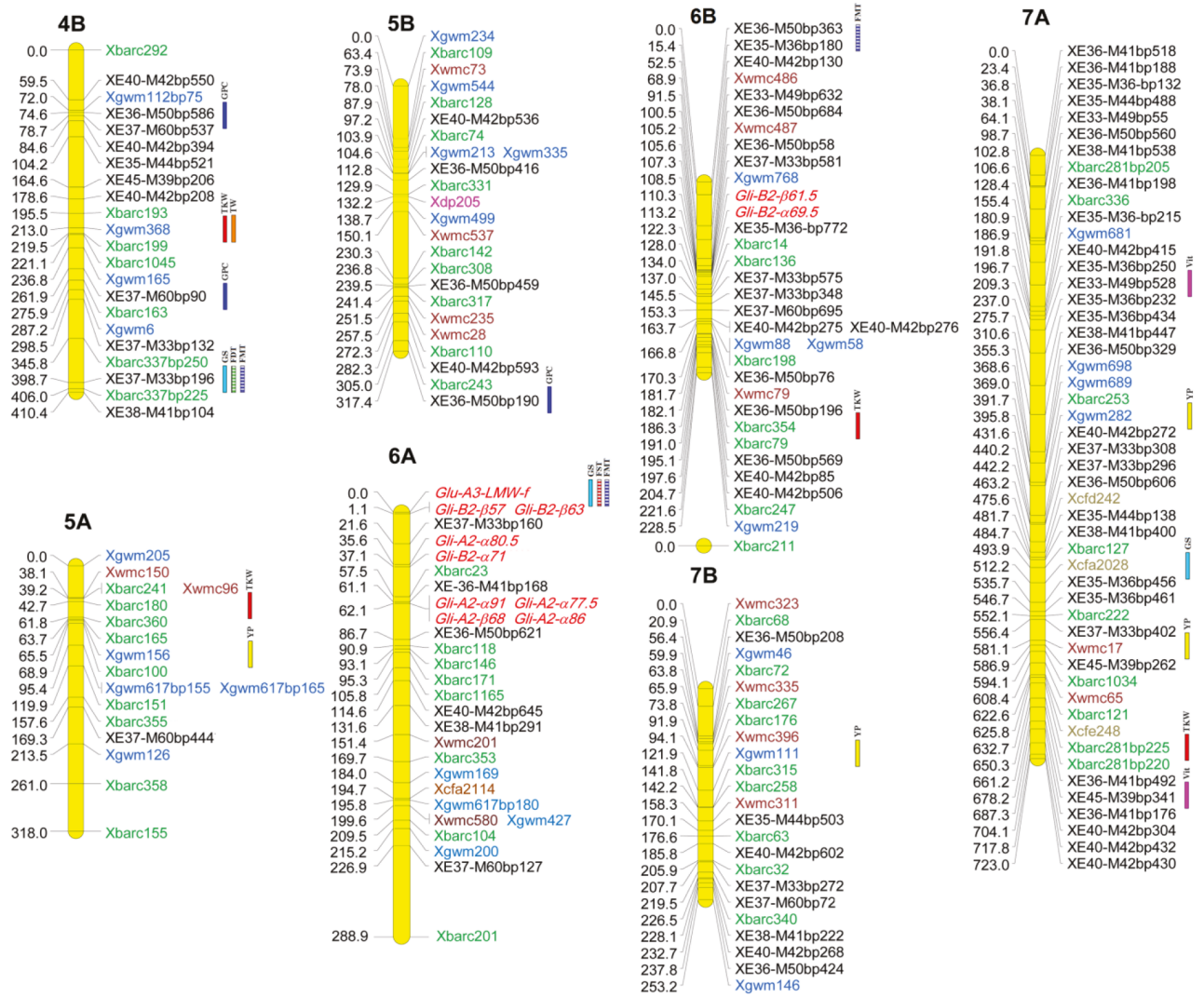

Figure 3. (Continued).

types of genes; one was *HMW-GS*, located on chromosome 1A, which was attributed to the *Glu-A1* locus. Conti et al. (2011) identified 3 QTLs on chromosome 1A. Deng et al. (2013) indicated that the *Glu-A1* locus has greater impacts on mixograph properties associated with dough mixing. Jin et al. (2016) reported many QTLs linked with *Glu-A1-HMW* for the mixograph midline peak value, midline peak width, and mixograph development time, and the most important QTLs causing significant variations in the studied traits were located on chromosomes 1BL, 6AL, 6BL, and 7AS. The second major QTL detected by our current study for GS was identified in 7 environments located on chromosome 1B, linked with *XE36-M50bp520*, in close proximity to *Glu-B1*, accounting for 10% to 34% of the phenotypic variation for this trait. This QTL was also associated with FMT, FDT, and FST, and the phenotypic correlation coefficient also showed a positive significant correlation between FST and FDT and between GS and FST (Table 4). Elouafi et al. (2001) also reported QTLs linked with markers (*Xgwm131b*, and *Glu-B1*) for FDT traits. Kumar et al. (2013) identified a consistent QTL contributing up to 90% of the phenotypic variation located on chromosome 1B. The *Glu-B1* locus was previously reported to be a poor indicator of GS in durum wheat (Du Cros, 1987; Vázquez-Laslop et al., 1996; Patil et al., 2009). This can be explained by the lower magnitude of the effect of *Glu-B1* compared to that of *Glu-B3*. In addition to this major QTL for GS on 1B, 3 main QTLs affecting GS were identified and linked with *Glu-A1* and *Glu-B1*. All of these major and minor QTLs were associated with other quality and rheology traits, and the majority of those associated with GS and other rheology traits were also linked with *Gli-A1*, *Gli-B1*, or *Gli-B3* on chromosomes 1A and 1B.

The GPC value ranged from 13.0% to 18.8% for Kunduru-1149 and 9.8% to 17.3% for Cham1. Environmental factors had a major impact, not only on

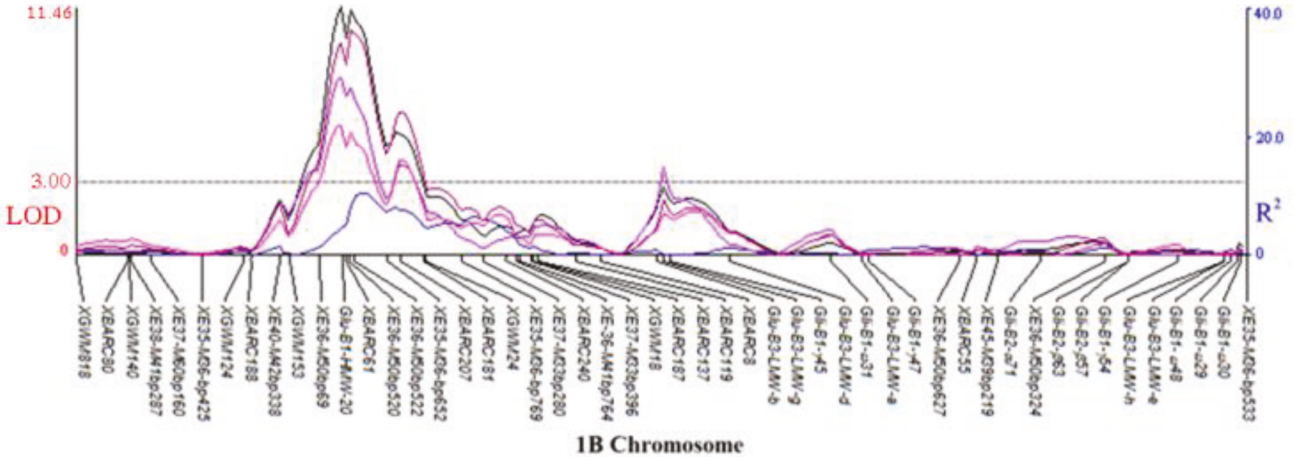

Figure 4. The FMT-QTL positions, LOD scores, and percentage of explained variance R^2; each color of the chart corresponds to a specific environment in addition to a line representing the average of the environments' data.

the total protein content but also on the relative expression of protein (Dupont and Altenbach, 2003). Across the environments, 6 QTLs were identified for GPC. One major QTL, responsible for 14% to 35% of the GPC variance, was observed on chromosome 2A, linked by *Xwmc177*, with an LOD of 3.88 to 10.22. This QTL explained a large proportion of the variation in GPC in all 6 locations. This result was compatible with those reported by Zlatska et al. (2004), which demonstrated a link with a particular locus (*wmc177*) on the short arm of the 2A chromosome of wheat. In addition, Zanke et al. (2014) also detected marker trait associations for chromosome 2A (markers *wmc177* and *wmc522*), most likely corresponding to the series of photoperiod genes *Ppd* on the short arms of the homoeologous group 2 chromosomes. Interestingly, the association between increased GPC and the locus on the short arm of chromosome 2A has also been reported by other researchers (Groos et al., 2003; Prasad et al., 2003). Li et al. (2009) identified one QTL for GPC on chromosome 1B, located between *barc81* and *barc188*. Additionally, Zhang and Dubcovsky (2008) observed QTLs for GS, mixograph time to peak, and ash traits linked with *Glu-B1-cfa2129-psr162*, located approximately 45.8 cM from the *barc81* locus. Li et al. (2009) found that only major QTLs significantly influenced GPC on chromosome 7B. However, other studies, like that of Olmos et al. (2003), have suggested that chromosome 6B of *Triticum turgidum* could provide a promising source of alleles to increase the GPC. In this study, major QTLs were identified on chromosome 2A in most of the studied environments. Nevertheless, most of the other QTLs were identified only in one environment, indicating that GPC was significantly influenced by environmental conditions. This major QTL at 2A was also associated with TW, TKW, Vit, and YP (Table 5). We have to mention here that this marker has been reported for gluten trait (Li et al. 2009) and was linked with heading date by Maccaferri et al. (2008). Additionally, Séne et al. (2001) reported that the Vit or semolina yield of maize was linked to a location less than 16 cM from a protein-content QTL on chromosome 2.

On chromosome 1B, one major QTL for YP was identified with a phenotypic variation of 11.5–16.1 in 5 of the 8 environments. Zhang and Dubcovsky (2008) also identified one QTL for YP on the 1B chromosome, accounting for 14% of the phenotypic variation. However, the QTL identified in our study may be different from that reported by Zhang and Dubcovsky (2008). Other QTLs have been identified on chromosomes 2A, 3B, 5A, 7A, and 7B; however, these were only identified in 1 or 2 of the environments. Elouafi et al. (2001) found QTLs on chromosomes 7A and 7B, while Patil et al. (2008) detected 5 different QTLs linked to YP content on chromosomes 1A, 3B, 5B, 7A, and 7B across 5 different environments. The strongest of these QTLs was located on the distal part of the long arm of chromosome 7A. In addition, Roncallo et al. (2012) identified 3 major QTLs on the long arm of chromosome 6A.

The genetic structure of durum wheat processing characteristics, such as dough rheology, is not well understood, and there are limited data concerning the genetic control of dough rheological parameters. In this study, a total of 59 major and minor QTLs were identified by SMA: 41 QTLs for grain quality were identified on all of the chromosomes, and 18 QTLs for rheology traits were observed on chromosomes 1A, 1B, 4A, 4B, 6A, and 6B. The major QTLs of the dough rheology traits were consistently detected on chromosome 1B, where the FDT, FST, and FMT traits were evaluated in 4 environments, and 3 genomic regions affected these traits. Only 1 major QTL was detected on chromosome 1B, which was found to be stable and was expressed in all 4 environments (Table 5). In the case of FST, 5 genomic regions of chromosome 1B were found to be involved, one of which was expressed in

3 of the 4 environments and the other in 2 environments. Based on these results, it can be concluded that in addition to other chromosomes, 1B may play a vital role in the genetic control of rheology traits. QTLs for various traits were identified in various environments, such as the QTL for GS in 8 environments; in 7 for GPC, TKW, and YP; in 5 for Vit and TW; in 4 for FDT and FMT; and in 3 for FST. In wheat end-use quality, GS, FST, FMT, TKW, and YP are important factors. In the case of Vit, 4 QTLs were equally identified in the Tel Hadya-Syria, Turkey, and Lebanon environments but none were stable. Only one QTL for Vit was detected in 3 of the 8 environments. This QTL was present on chromosome 7A, identified only in the Adana-Turkey and Terbul-Lebanon locations. QTLs expressed consistently across different environments are considered to be stable and thus have high potential to be used for marker-assisted breeding and further research to develop functional markers for these QTLs.

This study provides evidence for the argument that wheat quality is a consequence of a network of interacting genes. Ten genomic regions showed a consistent effect on a wide range of parameters. For example, significant pleiotropic effects were found in some of the quality and rheology QTLs. This study identified several major overlapping QTLs; chromosome 1B contained 3 most highly variable regions overlapping across traits (ROATs), for 3, 4, and 4 different traits, respectively. One ROAT located on chromosome 1A was detected near *Glu-A1-HMW-1*. Chromosomes 2A, 2B, 3B, 4B, and 6A also harbored ROAT regions containing QTLs for different traits; for example, on chromosome 6A, there was one ROAT linked by *Glu-A3-LMW-f*. In general, the results confirmed that the loci for SSPs, especially the HMW and some LMW subunits of glutenin, as well as ω-gliadin markers played a key role in many quality traits, especially in the formation and structure of gluten. Therefore, these genomic regions are likely related to the inheritance control of GS and other traits such as FST, FMT, and FDT.

For TKW and TW, 3 regions on chromosomes 2A, 2B, and 4B harbored genetic loci controlling both test and grain weight traits. The most important QTL for TKW with a phenotypic variation of more than 40% in 6 of the 8 environments was located on chromosome 2A, and the QTL with the highest phenotypic variation in TW was found on chromosome 4B. Both these regions were associated with significant increases in both grain weight and TW (Table 5). Similarly, Houshmand et al. (2008) identified QTLs for TW on chromosome 4B with a phenotypic variation of more than 45% and detected a QTL for grain weight on chromosome 2A.

The GS trait had the highest number of detected QTLs, followed by FMT, TKW, YP, FST, FMT-GPC, TW, Vit, and FDT. Chromosomes 1A, 1B, 2A, and 4B harbored major QTLs. Many QTLs for quality and rheology traits showed a high distribution on various chromosomes. For example, the QTLs of TKW were distributed across 7 different chromosomes, while GS, YP, and FMT were distributed across 6 different chromosomes. To date, a high number of DNA markers (e.g., SSRs, SNPs) have been developed and mapped in several durum wheat mapping populations. Our results show that the significant QTLs of GS, YP, FDT, FST, and FMT were located on chromosomes 1A and 1B; significant QTLs of GPC and TKW were located on chromosome 2A; and significant QTLs of TW were located on chromosome 4B. QTLs identified in the present study will be useful in improving the quality and rheology of durum wheat. Fine mapping of these regions could be useful for the identification of genes for quality and breeding applications in durum wheat. Although some of these DNA markers have already been used in previous studies, this study has shown that those markers were linked with quality or rheology traits and would be useful in MAS programs to improve the quality of durum wheat.

Acknowledgment
We wish to thank Dr Susan Duraa, University of Jordan, Amman, Jordan, for her assistance and recommendations concerning the statistical analysis.

References

AACC International (1995). Approved Methods of Analysis Method 39-11. Grain Protein Contents by Near-infrared Reflectance (NIR System Model 5000 Scanning Monochromatic) Method. St. Paul, MN, USA: AACC International.

AACC International (1999). Approved Methods of Analysis Method 14-50. Yellow Pigment Estimation Method. St. Paul, MN, USA: AACC International.

AACC International (2000). Approved Methods of Analysis Method 55-10. Test Weight Method. St. Paul, MN, USA: AACC International.

Alsaleh A, Baloch FS, Derya M, Azrak M, Kilian B, Nachit MM, Ozkan H (2015). Genetic linkage map of Anatolian durum wheat derived from a cross of Kunduru- 1149 × Cham1. Plant Mol Biol Rep 33: 209-220.

Alsaleh A, Baloch FS, Nachit M, Özkan H (2016). Phenotypic and genotypic intra-diversity among Anatolian durum wheat "Kunduru" landraces. Biochem Syst Ecol 65: 9-16.

Alvarez JB, Martin A, Martin LM (1999). Allelic variation of the D-prolamin subunits encoded at the Hch genome in a collection of primary hexaploid tritordeums. Theor Appl Genet 99: 296-299.

Baloch FS, Alsaleh A, Andeden EE, Derya M, Hatipoğlu R, Nachit M, Özkan H (2016). High levels of segregation distortion in the molecular linkage map of bread wheat representing the West Asia and North Africa region. Turk J Agric For 40: 352-364.

Baloch FS, Alsaleh A, Shahid MQ, Çiftçi V, de Miera LES, Aasim M, Nadeem A, Aktaş H, Özkan H, Hatipoğlu R (2017). A whole genome DArTseq and SNP analysis for genetic diversity assessment in durum wheat from central Fertile Crescent. PLoS One 12: e0167821.

Beecher BS, Carter AH, See DR (2012). Genetic mapping of new seed-expressed polyphenol oxidase genes in wheat (*Triticum aestivum* L). Theor Appl Genet 124: 1463-1473.

Blanco A, Colasuonno P, Gadaleta A, Mangini G, Schiavulli A, Simeone R, Digesù AM, Vita PD, Mastrangelo AM, Cattivelli L (2011). Quantitative trait loci for yellow pigment concentration and individual carotenoid compounds in durum wheat. J Cereal Sci 54: 255-264.

Cömertpay G, Habyarimana E, Baloch FS, Güngör H, Dokuyucu T, Akkaya A, Dumlupinar Z (2019). Geographical description and molecular characterization of genetic structure and diversity using 6K SNP Array in Turkish oat germplasm. Can J Plant Sci 99: 12-21.

Conti V, Roncallo PF, Beaufort V, Cervigni GL, Miranda R, Jensen CA, Echenique VC (2011). Mapping of main and epistatic effect QTLs associated to grain protein and gluten strength using a RIL population of durum wheat. Theor Appl Genet 52: 287-98.

Deng Z, Hu S, Zheng F, Chen J, Zhang X, Chen J, Sun C, Zhang Y, Wang S, Tian J (2013). Genetic dissection reveals effects of interaction between high-molecular-weight glutenin subunits and waxy alleles on dough-mixing properties in common wheat. J Genet 92: 69-79.

Du Cros DL (1987). Glutenin proteins and gluten strength in durum wheat. J Cereal Sci 5: 3-12.

Dupont FM, Altenbach SB (2003). Molecular and biochemical impacts of environmental factors on wheat grain development and protein synthesis. J Cereal Sci 38: 133-146.

Elouafi I, Nachit MM, Martin LM (2001). Identification of a microsatellite on chromosome 7b showing a strong linkage with yellow pigment in durum wheat *Triticum turgidum* L var durum. Hereditas 135: 255-261.

Federer WT (1956). Augmented designs. Hawaiian Plant Rec 55: 191-208.

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.

Houshmand S, Knox RE, Clarke FR, Clarke JM, Pozniak CP (2008). Quantitative Trait Loci Associated with Kernel Weight and Test Weight in Durum Wheat. Sydney, Australia: Sydney University Press.

Huang XQ, Cloutier S, Lycar L (2006). Molecular detection of QTLs for agronomic and quality traits in a doubled haploid population derived from two Canadian wheats *Triticum aestivum* L. Theor Appl Genet 113: 753-766.

ICC (1992). Brabender, Method No. 115. Vienna, Austria: International Association for Cereal Science and Technology

ITMI (1994). Wheat mapping workshop. In: McGuire PE, Qualset CO, editors. Proceedings of 4th Public Workshop, San Diego, CA, USA.

Jin H, Wen W, Liu J, Zhai S, Zhang Y, Yan J, He Z (2016). Genome-wide QTL mapping for wheat processing quality parameters in a Gaocheng 8901/Zhoumai 16 recombinant inbred line population. Front Plant Sci 7: 1032.

Jing HC, Kornyukhin D, Kanyuka K, Orford S, Zlatska A, Mitrofanova OP, Koebner R, Hammond-Kosack K (2007). Identification of variation in adaptively important traits and genome-wide analysis of trait–marker associations in *Triticum monococcum*. J Exp Bot 58: 3749-764.

Kumar A, Elias EM, Ghavami F, Xu X, Jain S, Manthey FA, Mergoum M, Alamri MS, Kianian PMA, Kianian SF (2013). A major QTL for gluten strength in durum wheat (*Triticum turgidum* L var. *durum*). J. Cereal Sci 57: 21-29.

Li F, Hasegawa Y, Saito M, Shirasawa S, Fukushima A, Ito T, Fujii H, Kishitani S, Kitashiba H, Nishio T (2011). Extensive chromosome homoeology among Brassiceae species were revealed by comparative genetic mapping with high-density EST-based SNP markers in radish (*Raphanus sativus* L). DNA Res 18: 401-411.

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.

Ma W, Appels R, Bekes F, Larroque O, Morell MK, Gale KR (2005). Genetic characterisation of dough rheological properties in a wheat doubled haploid population: additive genetic effects and epistatic interactions. Theor Appl Genet 111: 410-422.

Maccaferri M, Sanguineti MC, Corneti S, Araus O, Ben JA, Salem M, Deambrogio JBE, Garcia Del Moral LF, Demontis A, El-Ahmed A et al. (2008). Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* Desf.) across a wide range of water availability. Genetics Society of America 178: 489-511.

Mann G, Diffey S, Cullis B, Azanza F, Martin D, Kelly A, McIntyre L, Schmidt A, Ma W, Nath Z (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.

Nachit M, Baum M, Impiglia A, Ketata H (1995). Studies on some grain quality traits in durum wheat grown in Mediterranean environments. In: Proceedings of the Seminar on Durum Wheat Quality in the Mediterranean Regions, Zaragoza, Spain, pp. 181-188.

Nadeem MA, Habyarimana E, Çiftçi V, Nawaz MA, Karaköy T, Comertpay G, Shahid MQ, Hatipoğlu R, Yeken MZ, Ali F et al. (2018a). Characterization of genetic diversity in Turkish common bean gene pool using phenotypic and whole-genome DArTseq-generated silicoDArT marker information. PLoS One 13: e0205363.

Nadeem MA, Nawaz MA, Shahid MQ, Doğan Y, Comertpay G, Yıldız M, Hatipoğlu R, Ahmad F, Alsaleh A, Labhane N et al. (2018b). DNA molecular markers in plant breeding: current status and recent advancements in genomic selection and genome editing. Biotechnol Biotechnol Equip 32: 261-285.

Nelson JC (1997). QGENE: Software for marker based genomic analysis and breeding. Mol Breed 3: 239-245.

Olmos S, Diestelfeld A, Chicaiza O, Schatter 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.

Patil RM, Oak MD, Tamhankar SA, Sourdille P, Rao S (2008). Mapping and validation of a major QTL for yellow pigment content on 7AL in durum wheat *Triticum turgidum* L ssp *durum*. Mol Breeding 21: 485-496.

Pena RJ, Amaya A, Rajaram S, Mujeeb-Kazi A (1990). Variation in quality characteristics associated with some spring 1B/1R translocation wheats. J Cereal Sci 12: 105-112.

Pogna N, Autran E, Mellini JC, Lafiandra FD, 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.

Porceddu E (1995). Durum wheat quality in the Mediterranean countries. In: Di Fonzo N, Kaan F, Nachit M, editors. Durum Wheat Quality in the Mediterranean Region. Zaragoza, Spain: CIHEAM, pp. 11-21.

Prasad M, Kumar N, Kulwal PL, Röder M, 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.

Roncallo P, Cervigni G, Jensen C, Miranda R, Carrera A, Helguera M, Echenique V (2012). QTL analysis of main and epistatic effects for flour color traits in durum wheat. Euphytica 185: 77-92.

Roncallo P, Echenique V (2014). Identification of molecular markers associated with yield and quality traits for Argentinean durum wheat breeding programs. In: Porceddu E, Damania AB, Qualset CO, editors. Proceedings of the International Symposium on Genetics and Breeding of Durum Wheat. Rome, Italy: CIHEAM, pp. 577-582.

SAS Institute (2018). JMP Genomics, Version 9. Cary, NC, USA: SAS Institute.

Séne M, Gallet T, Doré T (2001). Phenolic compounds in a Sahelian sorghum (*Sorghum bicolor*) genotype (CE145-66). J Chem Ecol 27: 81-92.

Singh A, Reimer S, Pozniak CJ, Clarke FR, Clarke JM, Knox RE, Singh AK (2009). Allelic variation at Psy1-A1 and association with yellow pigment in durum wheat grain. Theor Appl Genet 118: 1539-1548.

Tkachuk R, Metlish VG (1980). Wheat cultivar identification by high voltage gel electrophoresis. Ann Technol Agric 292: 207-212.

Van Ooijen JW (2009). MapQTL 6, Software for the Mapping of Quantitative Trait Loci in Experimental Populations of Diploid Species. Wageningen, the Netherlands: Kyazma BV.

Vázquez-Laslop TNK, Tenney K, Bowman BJ (1996). Characterization of a vacuolar protease in *Neurospora crassa* and the use of gene RIPing to generate protease-deficient strains. J Biol Chem 271: 21944-21949.

Zanke CD, Ling J, Plieske J, Kollers S, Ebmeyer E, Korzun V, Argillier O, Stiewe G, Hinze M, Neumann K et al. (2014). Whole genome association mapping of plant height in winter wheat (*Triticum aestivum* L.) PLoS One 9: e113287.

Zhang W, Dubcovsky J (2008). Association between allelic variation at the Phytoene synthase 1 gene and yellow pigment content in the wheat grain. Theor Appl Genet 116: 635-645.

Zlatska AV, Shytikova YV, Kanyuka K, Hammond-Kosack K (2004). Transfer of Genes Controlling of Agronomic Important Traits from Artificial Hexaploid Wheat into Common Wheat Gene Pool: Kyiv, Ukraine: Ukrainian Institute for Plant Varieties Examination.