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Mapping QTL with additive effects and additive×additive epistatic interactions for plant architecture in wheat (*Triticum aestivum* L.)

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Abstract

In bread wheat (*Triticum aestivum* L.), crop height is an important determinant of agronomic performance. To map QTLs with additive effects and additive×additive epistatic interactions, 148 recombinant inbred lines and their parents, ('YecoraRojo' and Iranian landrace (No. #49)) were evaluated under normal and water deficit conditions. The experiments were carried out on research farms of Mahabad University and Miyandoab Agricultural Research Center in 2014-2015. The experimental design was an alpha lattice design with two replications. Quantitative trait loci (QTL) for the studied traits were carried out for additive effects and additive×additive epistatic interactions using the QTL Network 2.0 software based on the mixed-linear model. A number of 177 microsatellite and 51 retrotransposon markers were used to construct the linkage map. In the present study stem length, plant weight, peduncle length, and peduncle weight were measured. Results showed that under both normal and water deficit conditions, both positive and negative transgressive segregations were significant, also the highest and lowest broad and narrow sense heritability were estimated for stem length (73.69 and 36.74 percent) and peduncle length (40.51 and 20.25 percent), respectably. The results showed that under the normal condition, seven QTLs (R^2_A=5 to 11%), and eight additive×additive epistatic interactions (R^2_{AA}=1.66 to 10.92%) were significant. Under the water deficit condition seven QTLs (R^2_A=4.27 to 9%), and five additive×additive epistatic interactions (R^2_{AA}=3.8 to 14.58%) were significant. Five QTLs from the 14 QTLs identified in this study were located in chromosome 5A, indicating the importance of this chromosome in controlling the plant architecture characteristics and possibly using it for marker-assisted selection and genetic engineering.

Key words: Microsatellite marker, QTL mapping, Retrotransposon, Stem length.

INTRODUCTION

Optimum plant height is required for better yield in wheat, as tall plants are susceptible to lodging and excessively short plants are often associated with a yield penalty in resource-limited areas (e.g., moisture stress environment) (Griffiths *et al.,* 2012).

Polygenes with quantitative effects on plant height have been mapped on all 21 bread wheat chromosomes (Schnurbusch *et al.,* 2003; Mccartney *et al.,* 2005; Liu *et al.,* 2006). Dwarfing genes *Rht-D1b* and *Rht-B1b*, have increased grain yield in most resource rich

environments from reducing lodging susceptibility and increased grain number (Rebetzke *et al.,* 2012). Since the *Rht-D1b* and *Rht-B1b* alleles are also related to reduced coleoptile length and poor seedling vigor, there is an interest in introducing alternative gibberellic acid responsive dwarfing alleles with a potential for reducing plant height without changing in coleoptile length. The *Rht8* gene on chromosome 2DS is a potential candidate in the development of semi-dwarf bread wheat varieties with long-coleoptiles (Rebetzke *et al.,* 2012; Griffiths *et al.,* 2012). Also, dwarfing genes, photoperiod-insensitive alleles at *Ppd*-D1 on chromosome 2DS and *Ppd-B1* on 2BS have pleiotropic effects on plant height (Griffiths *et al.,* 2012). Besides these major genes, several studies indicated the presence of QTL for plant height. Huang *et al*. (2006) mapped four QTL for plant height on chromosomes 4B, 4D, 5D, and 7B using 185 doubled haploid (DH) lines, and the QTL on chromosome 4D (closest marker *Xwmc52*) explained 29.2% of the phenotypic variation. In the study of Zhang *et al.* (2008) several QTLs were found on chromosomes 3A, 4B, 4D, 5A, 6A, 7B, and 7D. They also reported five pairs of epistatic effects for plant height. In the study of El-Feki, (2010) ten plant height related QTLs were detected in Colorado environments, and a QTL detected on chromosome 6A was stable across the environments. Wang *et al*. (2010) detected six additive QTLs and four pairs of epistatic QTLs for plant height, among them, three additive QTLs (QPh. cgb-1B.3, QPh.cgb-4D.1, QPh.cgb-5B.2) and three pairs of epistatic QTLs (QPh.cgb-1B.1–QPh.cgb-1B.3, QPh.cgb-2A.1–QPh.cgb-2D.1, QPh.cgb-2D.1–QPh.cgb-5B.2) were stable QTLs. In the Neumann *et al*. (2011) several QTLs detected on chromosomes 1A, 2B, 4A, and 7B for plant height and peduncle length. Griffiths *et al.* (2012) evaluated four doubled haploid populations (DH) with population size ranging from 93 to 202, and reported 16 QTLs for plant height on chromosome 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 4D, 5A, 5B, 6A, 6B, and 6D. Because in previous studies QTL interactions with QTL over different years and different environmental conditions were less studied, the present research and its results can be different from other similar studies. The purpose of this research was mapping QTL with additive effects and additive×additive epistatic interactions for plant architecture in bread wheat under normal and water deficit conditions. The results will be helpful for bread wheat breeders to improve the plant architecture.

MATERIALS AND METHODS

The mapping population comprised of 148 F8 recombinant inbred lines (RILs) bred by single seed descent from crossing between a genotype Iran #49 and Yecora Rojo. Iran #49 (hereafter referred to as #49) is a tall late spring landrace collected in Bluchestan, Southeast of Iran. Yecora Rojo is a spring modern Mexican derived, two gene dwarf cultivar with small root system growing in Southern California for more than 40 years.

The plant materials were produced at Riverside University (California America) and was placed at the disposal of this research by the Center of Molecular Breeding, University of Tabriz.

The studied lines with the parents were planted on research farms of Mahabad University and Miyandoab Agricultural Research Center in 2014-2015. The above-mentioned regions are grouped into semi-arid areas of Iran. In both experimental locations, the experimental design was alpha lattice design with two replications. Each plot had two rows with 2.5 m long and 20 cm distance between the rows. The seeds were planted with five cm interval space.

Irrigation under the stress and the non-stress conditions were carried out after 90 mm evaporation from class A pan. Under the water-deficit stress conditions, the irrigation was stopped at the heading stage, but under the normal irrigation conditions, it was continued until the maturity stage. At the physiological maturity stage , 20 plants were selected from each line and stem length, plant weight, peduncle length, and peduncle weight were measured.

Genetic parameters were estimated according to the following formulas (Equations 1 and 2):

(1) Positive transgressive segregation=Best RIL–Best parent

(2) Negative transgressive segregation=Worst RIL–Worst parent

Heritability estimates were obtained using variance components as below (Equation 3):

(3)
$$h^2 = \frac{\delta_g^2}{\left(\delta_g^2 + \frac{\delta_{gylt}^2}{r} + \frac{\delta_{gyl}^2}{rt} + \frac{\delta_{gyt}^2}{rl} + \frac{\delta_{glt}^2}{ry} + \frac{\delta_{gt}^2}{ryl} + \frac{\delta_{gl}^2}{ryt} + \frac{\delta_{gy}^2}{rlt} + \frac{\delta_e^2}{rylt}\right)}$$

Where, σ^2_g=genetic variance; σ^2_e=environmental variance; σ^2_y=years variance; σ^2_l=locations variance; σ^2_t=conditions variance; r=number of replications; y=number of years; l=number of locations; t=number of conditions (Carter *et al.,* 2005).

Because the genetic variance among the recombinant

inbred lines is an estimation of twice the additive genetic variance of the primary population (Carter *et al.,* 2005), therefore, all of the genetic variances among the studied lines are additive and the estimated heritability is the narrow sense heritability.

For QTL analysis the existing linkage map including 177 microsatellites and 51 retrotransposons markers were used. In this map, 202 markers belonged to 36 linkage groups with a length of 691.36 centi Morgan (cM) and 26 markers were not associated with any linkage groups. According to the linkage maps provided for bread wheat (Marone *et al.,* 2012; Cui *et al.,* 2014; Kumar *et al.,* 2016), 34 linkage groups correspond with 19 chromosomes out of 21. The average distance between adjacent markers on the map was 3.42 centi Morgan (cM). QTL analysis was performed using QTL network 2.0 software by mixed-linear and Composite Interval Mapping (CIM) methods. Given that the population of recombinant inbred lines is a permanent population QTL×QTL interactions were examined. In this study, the F index calculated by QTL network software was used to detect significant QTLs, this index under normal condition was set at 5.82 for additive QTLs and was set at 6.10 for additive×additive QTLs. Under water deficit conditions, F values above 5.97 for additive QTLs and 5.96 for incremental QTLs were considered as significant QTLs.

RESULTS

Phenotypic performance of RIL lines and parents

The results showed (Table 1) that there was a significant difference between the two parents in all the studied traits. Under both normal irrigation and water deficit conditions, both positive and negative transgressive segregations on the studied traits were significant (LSD, Table 1). Due to the substantial transgressive segregation, some of the RILs had higher values for the studied traits compared with the parents under both conditions. Also, the mean values of the RILs were in the middle range of parental values. The results revealed that stem length showed the highest broad sense heritability and narrow sense heritability by 73.69% and 36.74%, respectively. While the lowest broad sense heritability and narrow sense belonged to peduncle length by 40.51% and 20.25% respectively. In the present study, there was a significant and continuous phenotypic variation among the genotypes indicating the quantitative nature of these traits. Under both environmental conditions, the values of skewness and kurtosis were less than one for the studied traits. According to these results, it can be stated that the studied traits had a normal distribution, polygenic inheritance, and were suitable for QTL analysis.

QTL mapping

QTL analysis revealed that under the normal condition, seven QTLs (R^2_A=5 to 11%) and eight

Table 1. Phenotypic summary of plant architecture for Yecora Rojo (P1), #49 (P2), and the wheat RILs at two years and two locations in normal and water deficit conditions.

Parameters	Stem length (cm)		Stem weight (g)		Peduncle length (cm)		Peduncle weight (g)	
	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit
Yecora Rojo	47.16	39.31	0.67	0.37	25.90	20.10	0.29	0.24
#49	66.83	55.35	0.73	0.39	28.89	25.72	0.33	0.26
RILs Mean	59.34	47.84	0.65	0.42	28.79	24.33	0.31	0.24
Minimum	38.37	34.20	0.400	0.29	22.11	17.06	0.25	0.19
Maximum	80.60	62.28	0.890	0.57	33.97	29.60	0.37	0.33
Positive transgressive segregations	13.78	6.96	0.16	0.18	5.09	21.5	0.05	0.08
Negative transgressive segregations	-8.79	5.71	-0.27	-0.08	-3.79	-3.04	-0.04	-0.06
Broad sense heritability	73.69	72.75	54.74	48.78	47.83	40.51	58.92	57.47
Narrow sense heritability	36.74	36.37	27.37	24.39	23.92	20.25	29.12	28.73
Std. Deviation	6.91	5.65	0.085	0.05	2.08	2.34	0.03	0.02
Skewness	0.144	0.24	0.216	0.12	-0.134	-0.22	0.117	0.37
Kurtosis	0.426	-0.51	0.235	-0.003	0.326	-0.188	-0.800	0.41
LSD (5%)	2.05	3.57	0.09	0.05	2.05	4.96	0.03	0.02

additive×additive epistasis effects (R^2_{AA}=1.66 to 10.92%) were significant. However, under the water deficit conditions, seven QTLs (R^2_A=4.27 to 9%) and five additive×additive epistasis (R^2_{AA}=3.8 to 14.58%) were significant (Table 2).

Additive QTL

Stem length: Under the normal condition, two QTL on chromosome 5A were significant for stem length (Table 2 and Figure 1). These QTLs were linked with markers *Barc197-LTR6149/Nikita.740* and explained 16% of the total phenotypic variation. The QTL *QSL5A1-N*, *QSL5A2-N* with additive value of -2.33 and 1.95, inherited favorable alleles from Yecora Rojo and #49 parents, respectively.

Under the water deficit condition, a major QTL was found on chromosome 3A *QSL3A-S* between markers *Barc164- Sukkula/ISSR4.590*, with additive value of -2.83 shared by Yecora Rojo, and explained 4.27% of the phenotypic variation.

Stem weight: The results revealed that under the normal condition stem weight was significantly affected by two additive QTLs located on chromosomes 6B and 7B. *QSTW6B-N* and *QSTW7B-N* QTL were flanked by '*Sukkula/ISSR10.400-'5LTR.2/Nikita.770* and *'Wms297- Sukkula/Nikita.520* markers. The QTL *QSTW6B-N*, with R^2_A and additive value of 8% was inherited by #49 parent, while QTL *QSTW7B-N* with R^2_A and additive value of 7% inherited by Yecora Rojo parent.

Three regions on chromosomes 3A, 5A, and 2B, related to the stem weight, were identified under the water deficit condition. These loci explained 17% of the total phenotypic variation. Favorable alleles *QSTW3A-S* and *QSTW5A-S* were inherited by Yecora Rojo parent, with an additive value of 0.012 and 0.014, respectively, while the other (*QSTW5A-S*), originating from #49, increased stem weight.

Peduncle length: Under the normal condition, two

Table 2. Detected QTL for the studied traits in the RIL population of wheat obtained from Yecora Rojo×#49 at two years and two locations under the normal condition.

Trait	Chromosome	QTL	Marker interval	Position (cM)	A	F Value	R^2_A (%)
			Normal				
	5A	*QSTL5A-N*	*Barc197-LTR6149/Nikita.740*	14	-2.33	5.98	11
Steam length	5A	*QSTL5A-N*	*Barc197- LTR6149/Nikita.740*	19	1.95	6.01	6
							16
			Water deficit				
	3A	*QSTL3A-S*	*Barc164- Sukkula/ISSR4.590*	188.3	-2.83	7.46	4.27
			Normal				
	6B	*QSTW6B-N*	*Sukkula/ISSR10.400-5LTR.2/Nikita.770*	38.5	0.03	6.01	8
	7B	*QSTW7B-N*	*Wms297- Sukkula/Nikita.520*	22.4	-0.02	6.12	7
Steam weight							15
			Water deficit				
	3A	*QSTW3A-S*	*Gwm66.2-5LTR.2/ISSR9.210*	85.2	-0.014	7.12	6
	5A	*QSTW5A-S*	*Barc48-Gwm194*	2	-0.012	5.98	5
	2B	*QSTW5A-S*	*Gwm66.1-Cfa2043*	11.1	0.012	7.18	6
							17
			Normal				
Peduncle length	5A	*QPL5A-N*	*Gwm443-Wms154*	7	0.52	6.89	5
	5A	*QPL5A-N*	*Barc330-Gwm617*	50.5	0.48	8.11	6
							11
			Normal				
	5B	*QPL5B-N*	*Barc59-Wmc28*	4	-0.007	10.14	5.5
Peduncle weight			Water deficit				
	6A	*QPW6A-S*	*Wmc786-5LTR.2/ISSR9.170*	9.4	0.008	10.59	9
	2B	*QPW2B-S*	*Gwm66.1-Cfa2043*	10.7	0.006	6.18	5
	1B	*QPW1B-S*	*Gwm413-Wmc216.2*	23.2	0.006	6.01	5
							19

QTL on chromosomes 5A for peduncle length were mapped (Table 2). One of these QTL (*QPL5A-N*) was linked with marker *'Gwm443-'Wms154*, positioned within a seven cM and the other (*QPL5A-N*) was linked with *'Barc330-'Gwm617*, positioned within a 50.5 cM. R^2 value for the first QTL was 5% and the second QTL was 6%. The additive value of these QTLs were 0.52 and 0.48, respectively. The desirable alleles for both QTLs were inherited by #49 parent.

Peduncle Weight: QTL, *QPW5A-N*, with its allele shared through Yecora Rojo, was mapped to the *Barc59-Wmc28* interval on chromosome 5A and justified 5.5% of the phenotypic variation and had negative effects on the peduncle weight.

Peduncle weight was controlled by three QTL located on chromosomes 6A, 2B, and 1B with R^2_A=5 to 9% under the water deficit condition (Table 2). QTLs *QPW6A*-S, *QPW2B*-S, and *QPW1B*-S flanked by markers *Wmc786-'5LTR.2/ISSR9.170, 'Gwm66.1-'Cfa2043,* and *'Gwm413-'Wmc216.2* showed additive effects of 0.008, 0.006, and 0.006, respectively. The alleles of all these three QTL originating from #49 parent had positive effects on the peduncle weight.

Additive×additive epistatic QTL

Stem Length: Under the normal condition, two pairs of additives×additive epistatic interactions were detected for the stem length located between chromosomes 3A/3A and 1D/31, respectively (Table 3). These effects explained 13.9% of the phenotypic variation. The QTL pair *QSL3A-N*/*QSL3A-N* with additives×additive value of -2.41 acted in favor of the recombinant types, accounting for 8.84% of the phenotypic variation. The other QTL pair in favor of the parent type *QSL1D*-N/ Q*SL31*-N -N, had additives×additive value of 2.27 and explained 5.06% of the phenotypic variation.

Two pairs of additive×additive epistatic interactions were significant under the water deficit condition for stem length. Both interactions (*QSL3A-S*/*QSL1B-S*

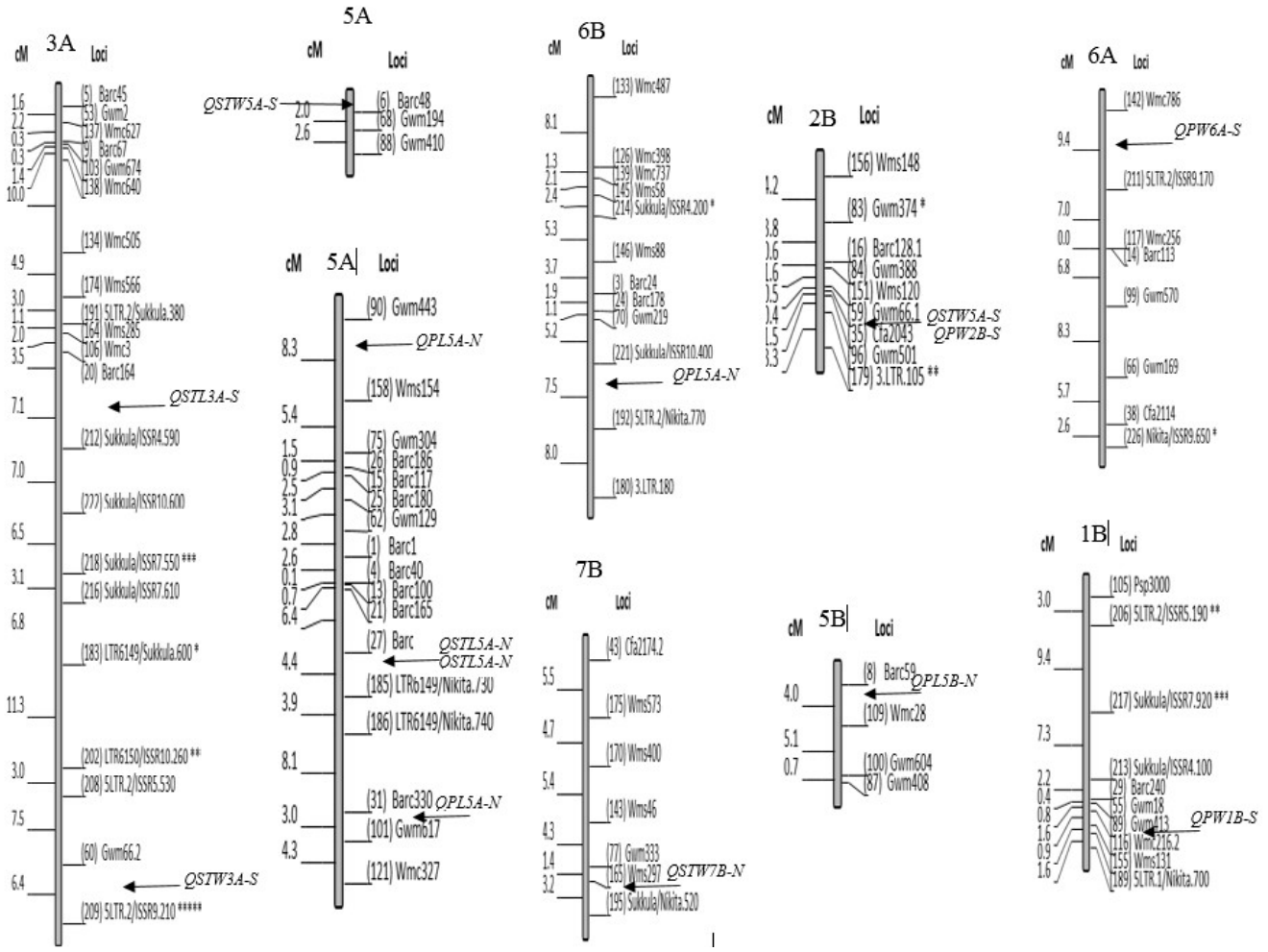

Figure 1. Positions of additive QTL for the plant architecture traits for wheat recombinant inbred lines (RILs) at two years and two locations under normal and water deficit conditions.

Table 3. Additive×additive epistatic QTL interactions for the studied traits in two years and two locations under the normal condition.

Trait	Chromosome I	Marker interval	Position	Chromosome J	Marker interval	Position	AA	F Value	R^2 (%)
		Normal							
	3A	*Gwm674-Wmc640*	15	3A	*Sukkula/ISSR7.550-Sukkula/ISSR7.610*	293.7	-2.41	8.73	8.84
Stem length	1D	*Wmc216.1- Wmc590*	5.7	31	*Psp299-Wmc336*	14.3	2.27	6.70	5.06
		water deficit							13.9
	3A	*Wms285 -Wmc3*	32.1	1B	*Wmc44-Sukkula/ISSR7.230*	0.0	3.210	10.38	14.58
	4B	*Sukkula.1220-Gwm192*	24.6	2A	*Cfa2263-Wms372*	38.9	2.843	9.75	11.58
									26.16
		Normal							
	5A	*Gwm617-Wmc327*	418.2	2A	*Wmc198-Wms122*	2.5	0.024	7.26	5.72
	1D	*Wmc590-Gwm337*	6.1	7B	*Wms400-Wms46*	17.7	0.018	6.20	2.08
Stem weight		water deficit							7.8
	5B	*Sukkula/Nikita.130-Wmc410*	131.8	7D	*Wmc317-Wmc361*	3.0	0.022	7.39	3.8
	4A	*Wms610-Cfa2256*	39	2D	*Wms515-Gwm349*	30.5	-0.022	12.12	10.72
									14.52
		Normal							
Peduncle length	4A	*Barc78-Gwm494*	7.1	4A	*Wms610-Cfa2256*	26	-1.064	11.89	10.92
	4B	*Wms121-Sukkula.1300*	56.6	2A	*Wms47-Wmc198*	0.0	-0.418	10.84	1.66
									12.78
		Normal							
	3A	*Wmc627-Barc67*	9.4	1D	*Wms106-Wmc432*	30.1	0.012	7.26	10.08
Peduncle weight	7D	*Barc352-Wms111*	6	1B	*Wmc44-Sukkula/ISSR7.230*	0.0	0.013	6.20	9.76
									19.84
		water deficit							
	6B	*5LTR.2/Nikita.77-3.LTR.180*	217.5	3A	*Gdm63-Gwm480*	8.0	-0.015	9.37	11.18

and *QSL4B-S*/*QSL2A-S*) with additives×additive value of 3.210 and 2.843 acted to increase the values of the parental types. They could explain 26.16% of the total phenotypic variation (Table 3).

Stem weight: Two pairs of additives×additive epistatic interactions between chromosomes 5A/2A and 1D/7B were identified for stem weight under the normal condition. Both additive×additive epistatic interactions between 5A/2A and 1D/7B acted in favor of the parental types, which explained 2.08 to 5.72% of the phenotypic variation.

For stem weight, two pairs of additives×additive epistatic interactions were detected under water deficit condition. One interaction (*QSW5B-S*/*QSW7D-S*) with R^2_{AA} and additives×additive value of 3.8% and 0.022 acted to increase the values of the parental types, while the other (*QSW4A-S*/*QSW2D-S*) with R^2_{AA} and additives×additive of 10.72% and -0.022 acted to increased, recombinant effects.

Peduncle length: The results showed that under the normal condition peduncle length was significantly affected by the two additive×additive QTL interactions.

Both interactions between *QPL4A-N*/*QPL4A-N* and *QPL2A-N*/*QPL4B-N* with the additives×additive value of -1.064 and -0.418 acted to increase the values of the recombinant types and were accounted for 1.66 and 10.92% of the phenotypic variance, respectively.

Peduncle weight: Two pairs of additive×additive epistatic interactions between chromosomes 3A/1D and 7D/1B under the normal condition were detected for peduncle weight (Table 3). The QTL pair *QPW3A-N/QPW1D-N* had the largest effect, contributing a stem length of 0.012 and accounting for 10.08% of the phenotypic variance, the other QTL pair *QPW7D-N/QPW1B-N* had an effect of 0.013 and explained 9.76% of the phenotypic variation. It should be noted that both the QTL pairs acted in favor of the parental types.

Under the water deficit condition, there was one pair additive×additive epistatic interaction between chromosome 6B/3A for peduncle weight. The QTL pair *QPW6B*-S/QPW*3A*-S acted in favor of the recombinant types and contributing a peduncle weight of 0.015 and accounted for 11.18% of the phenotypic variance.

DISCUSSION

In the recent years the general correlation of crop height and yield (Law *et al.,* 1978) has been dissected into single QTL effects (e.g. Zhang *et al.,* 2004; Maccaferri *et al.,* 2008) and it has been shown that some crop-height-increasing effects also increase grain yield while others have a neutral effect.

In the present research study few QTL were found for plant architecture, The reason probably could be due to the effect of a large number of QTLs with low effects on the studied traits (Tanksley, 1993) or the effect of environmental effect on the expression of QTLs (George *et al.,* 2003), However, in the present research five QTLs for peduncle length and stem length were detected on chromosomes 5A (Four QTLs) and 3A (One QTL) under all both environmental conditions.

Therefore, the QTL on 5A should be considered to increase plant height in wheat molecular breeding. Also, for stem length four pairs of epistatic interactions (3A/3A and 1D×31 under the normal and 1B/3A and 2A/4B under the water deficit condition) and for peduncle length two pairs of epistatic interactions (4A/4A and 2A/4B under the normal condition) were detected.

The results showed that under the normal condition additive QTLs and under the water deficit condition additive×additive epistatic effects had a significant role in the control of stem length. However, to control the stem weight under both conditions, the effects of additive QTLs were more important than the additive×additive epistatic effects. In controlling the peduncle length, the role of additive QTLs and additive×additive epistatic effects were almost equal under the normal conditions. For peduncle weight, under the normal conditions, the role of additive×additive epistatic effects and under the water deficit condition the role of additive QTLs was more important.

Zhang *et al.* (2008) found four additive QTLs and five pairs of epistatic effects for plant height, which were located on chromosomes 3A, 4B, 4D, 5A, 6A, 7B, and 7D. They also reported that the detected QTLs had 46.07% additive effects and 19.89% epistatic effects. Griffiths *et al*. (2012) reported 16 QTL for plant height on chromosome 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 4D, 5A, 5B, 6A, 6B, and 6D. Zhang, *et al.* (2008) detected four additive QTLs and five pairs of epistatic effects for plant height which were distributed on chromosomes 3A, 4B, 4D, 5A, 6A, 7B, and 7D.

In our research, nine QTL on chromosomes 6B, 7B, 5B, 3A, 5A, 2B, 6A, 2B, and 1B were observed for stem and peduncle weight in both studied environments. Furthermore, four pairs of epistatic interactions (2A/5A

and 7B/1D under the normal and 7D/5B and 2D/4A in water deficit condition) for stem weight and three pairs of epistatic interactions for peduncle weight (1D/3A and 1D/7B under normal and 3A/6B in water deficit condition) were detected.

CONCLUSIONS

In the present study, five QTLs from the 14 QTLs identified in this study were located on chromosome 5A, indicating the importance of this chromosome in controlling the plant architecture characteristics and possibly using it for marker-assisted selection and genetic engineering.

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