Genetic analysis for quantitative traits in bread wheat exposed to irrigated and drought stress conditions

Análisis genético de rasgos cuantitativos en trigo panificable bajo condiciones de riego y de sequía

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Abstract. Understanding the genetic control of traits associated with yield helps breeders to utilize their germplasm in a more efficient and consistent manner and to make good choices in breeding programs. The current study was carried out to study the genetic control of some quantitative traits in bread wheat (*Triticum aestivum* L.) and to examine plant responses under full irrigation and drought stress conditions. For this purpose, six generations derived from a cross between two lines (Bezostaya as tolerant parent and 518 as a susceptible parent) were evaluated for grain yield (GY), plant height (PH), peduncle (PL) and spike (SL) lengths, thousand grain weight (TGW) and harvest index (HI) using a randomized complete-block design with four replicates. Generation mean analysis indicated that non-allelic interactions were important factors in controlling the expression of these characters. The results indicated that GY under drought conditions, PL under full irrigation and drought stress conditions, and PH, SL and HI under full irrigation conditions were determined for additive gene effects. The PL and TGW were influenced by additive and over dominance gene effects under both irrigation conditions, respectively, and no plant response changes occurred. In general, selection in early segregating generations may be useful for those traits that are affected by additive gene effects.

Keywords: Drought stress; Genetic effect; Generation mean analysis; Wheat.

Resumen. El estudio de la resistencia genética a la sequía siempre ha sido un desafío para los fitomejoradores. Entender el control genético de los rasgos asociados con el rendimiento ayuda a los criadores a utilizar su germoplasma de una manera más eficiente y consistente y a tomar buenas decisiones en los programas de mejoramiento genético. El presente estudio tuvo como objetivo investigar el control genético de rasgos cuantitativos en trigo de pan (*Triticum aestivum* L.) y examinar los cambios relacionados bajo condiciones de riego completo y sequía. Para este propósito, se evaluaron seis generaciones derivadas de un cruce entre dos líneas (Bezostaya como padre tolerante y 518 como un padre susceptible) para rendimiento de grano (GY), altura de la planta (PH), longitudes del pedúnculo (PL) y de la espiga (SL), peso de mil granos (TGW), e índice de cosecha (HI) utilizando un diseño de bloques completamente al azar con cuatro repeticiones. El análisis de la media de generación indicó que las interacciones no alélicas fueron factores importantes en controlar la expresión de estos caracteres. Los resultados indicaron que GY bajo condiciones de sequía, PL bajo condiciones de riego completo y sequía, y PH, SL y HI bajo condiciones de riego completo fueron determinados por efectos de genes aditivos. El PL y TGW fueron influenciados por efectos aditivos y sobre dominancia de los genes en ambas condiciones de riego, respectivamente, y no se produjeron cambios en la respuesta de las plantas. En general, la selección en las primeras generaciones de segregación puede ser útil para aquellos rasgos que son afectados por los efectos génicos aditivos.

Palabras clave: Estrés por sequía; Efecto génico; Análisis de la media de generación; Trigo.

INTRODUCTION

Wheat is the most important cereal crop in the world. According to the FAO statistics (2014), 729 million tons of wheat were produced in 2014, and more than 220 million ha of the world farmlands were under wheat cultivation. Due to the persistent increasing of the world population, wheat plays a key role in the national economy of developing countries.

Drought stress is a major limiting factor that strongly affects crop yield and production worldwide (Dhanda & Sethi, 1998). Most of wheat planted areas are located in arid or semi-arid regions where abiotic stresses, especially drought stress, are a major constraint for crop production (Tahmasebi et al., 2014). Improved and suitable cultivars for drylands could increase crop yield and provide food security for the foreseeable future; however, developing new cultivars for drought-prone areas (generally for all abiotic stresses) is too complicated and difficult. Grain yield has been suggested as a selection criterion to improve drought tolerance in breeding programs. Nonetheless, recent studies reveal that grain yield is not a suitable index anymore and direct selection for high yield cannot be effective, because grain yield is a complex trait, controlled by different metabolic, biochemical and physiological processes (Ehdaie et al., 1994). On the other hand, non-additive gene effects could defeat selection for high yield cultivars. To improve several traits at the same time, it is important to estimate the relative magnitude of the genetic variance and type of gene action involved in the expression of traits (Khaled, 2013). Understanding the inheritance of quantitative traits and information about gene action are necessary for developing an efficient breeding strategy. Mean generation analysis is a simple and useful method to estimate main gene effects (additive and dominance) and digenic interactions (additive × additive, additive × dominance and dominance × dominance). This method would help to choose the best breeding strategies (Dvojković et al., 2010). For instance, when the additive effects are high, selection is the best way to improve the traits. By contrast, when the dominant effects are high, developing the hybrid varieties can improve the traits.

In their study, Ijaz and co-workers (2013) developed a cross between V-04189 and V-03138 wheat lines and reported that generation mean analysis revealed a two-parameter model for relative water content and excised leaf water loss. Furthermore, generation mean analysis indicated that the presence of additive genetic effects could be fixed in early segregating generations (Ijaz et al., 2013). Generation mean analyses were used to study the genetic background of drought stress tolerance in wheat. The results showed that several important characters were governed with dominance and non-allelic gene interactions so that breeders should delay selection to later generations and increase homozygosity (Said, 2014).

Understanding and knowing about gene action in breeding programs could improve the accuracy of selection and de-crease the breeding cost and time. Therefore, the aims of this study were to investigate the genetic parameters, gene action and heritability of some quantitative traits (grain yield, plant height, peduncle length, spike length, thousand grain weight and harvest index) in bread wheat, and to examine the related changes across irrigated and drought stress conditions.

MATERIALS AND METHODS

Genetic materials and experimental site. The experiment was conducted on a sandy loam soil during the 2014-2015 growing seasons at the research farm of Tehran University, Tehran, Iran (35° 48′ N, 51° 00′ E, 1323 m.a.s.l.). The region is characterized as semi-arid, with a mean annual precipitation of 250 mm, which mostly falls during the autumn and winter months (Saymohammadi et al., 2017). Two wheat genotypes, Bezostaya (P_1) as tolerant and 518 (P_2) as susceptible parents, were obtained from germplasm collection at the University of Tehran, Karaj, Iran (Najafabadi et al., 2004; Jalilvandy et al., 2013).

Experimental design and crop husbandry. The genotypes were crossed (Bezostaya as female and 518 as male parents) in 2009 to produce the F_1 generation. The F_2 generation was also produced by self-pollinating of F_1 hybrids in the following year. In addition, F_1 plants were back-crossed with Bezostaya (BC_1) and 518 (BC_2). In 2014/2015, the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the two crosses were grown in two separate experiments (normal and drought stress conditions) in a randomized complete-block design with four replicates for each one. Each replicate consisted of 20 plants in one row for each of the parents and F_1, 40 plants in two rows each of back cross, and 80 plants in four rows for the F_2 population. The number of rows in each plot was different depending on generation type. The F_2 had the maximum diversity, so the maximum number of rows (4 rows) was assigned to the F_2 generation. Rows were 2.0 m long and 30 cm apart, and distance between any two plants was 10 cm. The first experiment was under full irrigation (irrigated conditions), the second experiment was under limited irrigation (drought stress). There were 2.5 m gaps between the blocks, and a 1.5 m alley was established between each plot to prevent lateral water movement and other interferences.

The wheat was sown by hand at depths of 3-4 cm on 6 October 2014 to achieve the recommended plant density of 250 plants/m². Immediately after sowing, the soil was irrigated. Polyethylene pipelines were installed to control irrigation. The irrigation cycle of each plot was closed to avoid runoff. Irrigation was applied based on the furrow method and irrigation scheduling was determined according to daily changes of soil water content (ΔSW) at the depth of root development. A deficit approach was used to estimate irrigation requirements, and the soil water content at field capacity (FC) was defined as no

water deficit. Available water was determined by the difference between the water content at field capacity and the permanent wilting point (PWP). Under full irrigation conditions, irrigation was initiated after 40% of the available water was used; and under limited irrigation conditions (drought stress), irrigation was initiated after 80% of the available water was used. Nitrogen fertilizer (from urea source) was applied via top dressing at the three- to four-leaf stage (1/2 of N treatment) and the stem elongation stage (1/2 of the remaining N). Potassium and P were not applied because the soil had adequate amounts of these minerals. All weeds were removed throughout the growing season by hand hoeing. Time-domain reflectometry (TDR) probes with tube access (TRIME-FM, England) were used to measure soil water content (Θv) in the experimental plots at a soil depth of 0-60 cm (at 20 cm intervals).

Data recording and measurements. The crop was harvested at the maturity stage, and the generations were evaluated for six agronomic traits. Grain yield (g/m^2) was determined by weighting grains collected from all harvested plants grown in the central rows of each plot. Harvest index (HI) was calculated by dividing grain yield by the biomass. Seed weight as 1000-grain weight (g) was measured by weighing of a random grain sample using a digital laboratory balance. Plants from the center of each plot were selected randomly, and spike length (cm), peduncle length (distance between the last node and the bottom of a spike) (cm), and plant height (cm) were recorded. Data were recorded on 5 individual plants for non-segregate populations (P_1, P_2 and F_1), 10 plants for BC_1 and BC_2, and 60 plants for the F_2 population for each replicate.

Statistical analysis. Weighted variance analysis for collected data was carried out in both conditions (irrigation and drought stress). According to Mather and Jinks (1982) generation mean analysis was used (Mather & Jinks, 1982). In order to estimate the genetic parameters, a weighted least squares method was applied. The weights were obtained dividing the number of individuals by the generations variance. The adequacy of the model was tested by joint scaling test (Cavalli, 1952). Eliminating non-significant gene effects from six parameter model and six generations would allow us to test the goodness of fit of the model by chi-square with degree of freedom (Mather & Jinks, 1982). As joint scaling test uses all information of generations, it is a reliable test for determination and estimation of genetic parameters.

Total means of each trait were calculated by:
$$Y = m + \alpha d + \beta h + \alpha^2 i + 2\alpha\beta j + \beta^2 l$$

Where Y is mean of a generation, m is mean of all generations, d is sum of the additive effects, h is sum of the dominance effects, i is sum of the additive × additive effects, j is sum of the additive × dominance effects, l is sum of the dominance × dominance effects, and α and β are genetic parameters.

Broad-sense heritability (h^2_{bs}) and narrow-sense heritability (h^2_{ns}) were estimated according to Kearsy and Pooni (1998) and Warner (1952) equations.

$$h^2_{bs} = V_{F2} - (V_{P1} \times V_{P2}) / V_{F2}$$

$$h^2_{ns} = 2V_{F2} - (V_{BC1} + V_{BC2}) / V_{F2}$$

Also, variance components were estimated by Mather and Jinks equations (Mather & Jinks, 1982).

$$E = \frac{\sigma^2_{P1}}{4} + \frac{\sigma^2_{P2}}{4} + \frac{\sigma^2_{F1}}{2}$$

$$D = 4\sigma^2_{P1} - 2(\sigma^2_{BC1} + \sigma^2_{BC2})$$

$$H = 4(\sigma^2_{BC1} + \sigma^2_{BC2} - \sigma^2_{F2} - E)$$

$$F = \sigma^2_{BC2} - \sigma^2_{BC1}$$

Where E is environmental variance, D is additive variance; H is dominance variance and F results from the correlation between h and d in all loci. Dominance ratio ($\sqrt{H/D}$) and dominance deviation ($F/\sqrt{HD}$) were estimated for all traits. If dominance be in one direction then F would be equal with $\sqrt{HD}$ and dominance deviation would be one. But if dominance varies in the different directions, F would be smaller than $\sqrt{HD}$.

RESULTS

Analysis of variance showed that there were significant differences between generations for all traits obtained under irrigated and drought conditions. The only exception was spike length under drought stress conditions (Table 1). These results confirm considerable genetic variation for all the generations and all the measured traits (except in case of spike length under drought stress conditions).

On the other hand, all traits showed lower values under water stress than irrigated conditions. There was 13-40% reduction on traits under drought in comparison with full irrigation conditions. The minimum reduction (13%) belonged to 1000-grain weight, whereas the maximum reduction (40%) belonged to grain yield. Phenotypic simple correlations between all studied traits under irrigated and water stress conditions are presented in Table 2. Under full irrigation, grain yield significantly correlated with plant height, harvest index and 1000-grain weight; however, under drought stress conditions, grain yield significantly correlated with all measured traits. Under drought stress conditions, grain yield showed the highest correlation with peduncle length and harvest index (Table 2).

Table 1. Analysis of variance for recorded traits.
Tabla 1. Análisis de la varianza para las características registradas.

SOV		d.f	MS					
			GY	PH	PL	SL	TGW	HI
Replication	N	3	31.43	61.85	75.09	1.81	1.57	0.002
	S	3	0.44	68.71	36.4	0.69	1.56	0.022
Generation	N	5	251.73**	729.9**	154.75**	5.14*	2.01**	0.007**
	S	5	0.5**	767.05**	52.38**	3.38 ns	1.92**	0.017*
Error	N	15	22.52	91.15	32.68	2.31	0.22	0.002
	S	15	0.079	112.68	23.86	3.8	0.21	0.007

N: normal irrigated environment, S: drought stress environment,
 GY: grain yield, PH: plant height, PL: peduncle length, SL: spike length, TGW: thousand grain weight, HI: harvest index.
* and ** significant at the 5% and 1% probability levels, respectively. ns: non-significance.

Table 2. Phenotypic simple correlations between the studied traits in the irrigated (above diagonal) and water stress (below diagonal) environments.
Tabla 2. Correlaciones simples fenotípicas entre las características estudiadas en los ambientes regados (por encima de la diagonal) y expuestos a estrés hídrico (por debajo de la diagonal).

	GY	PH	PL	SL	TGW	HI
GY	1	0.618**	0.248 ns	0.115 ns	-0.211*	0.592**
PH	0.702**	1	-0.127 ns	0.081 ns	-0.465**	-0.243*
PL	0.801**	0.437*	1	0.066 ns	0.020 ns	0.104 ns
SL	0.51**	0.003 ns	0.073 ns	1	-0.261*	0.171 ns
TGW	-0.172*	-0.478**	0.530**	-0.213*	1	-0.009 ns
HI	0.761**	-0.301**	0.254 ns	0.194*	0.007 ns	1

GY: grain yield, PH: plant height, PL: peduncle length, SL: spike length, TGW: thousand grain weight, HI: harvest index.
* and ** significant at the 5% and 1% probability levels, respectively. ns: non-significance.

The results indicated that 1000-grain weight negatively correlated with grain yield under both conditions of water availability. Furthermore, harvest index positively correlated with grain yield, and negatively correlated with plant height, under both water availability conditions. Interestingly, there was no significant correlation between peduncle length and any of traits under irrigated conditions (Table 2). For those traits that were significantly different among generations, generation mean analysis and parameter estimation was conducted. The joint scaling test was employed to identify significant additive (d), dominance (h) and non-allelic interactions including additive × additive (i), additive × dominance (j) and dominance × dominance (l) effects for the recorded traits (Table 3). Non-significant parameters didn't enter into the model (Mather & Jinks, 1982).

The model for most of the traits indicated that non-allelic interactions were important factors in controlling the expression of those characters. However, the simple additive-dominance model was the best-fit model for spike length and harvest index under irrigated conditions. The degree of dominance (h/d) showed that the additive effect was more important than the dominance effect for the measured traits (except for peduncle length and spike length) under irrigated conditions (Table 3). Harvest index and peduncle length in the drought stress condition and spike length under irrigated conditions showed positive and greater than one degree of dominance. Plant height and peduncle length under drought stress and irrigated conditions showed negative and greater than one degree of dominance, respectively.

The variance components and heritability are given in Table 4. Negative estimates were assumed to be zero (Robinson et al., 1955). Additive variance was higher than dominance variance for plant height, peduncle length, and spike length as well as harvest index under irrigated conditions. In addition, grain yield and peduncle length showed greater additive variance under drought stress conditions. By contrast, dominance variance was greater than additive dominance for grain yield under irrigated conditions, for plant height and harvest index under drought stress conditions and for 1000-grain weight under both conditions of water availability. The environmental variance was lower than the genetic variance for all traits. Broad sense heritability ranged from 0.48 to 0.83 under irrigated conditions, and from 0.45 to 0.82 under drought stress conditions. Narrow sense heritability ranged from 0.19 to 0.71 under irrigated conditions, and from 0.09 to 0.67 in the drought stress treatment (Table 4).

Table 3. Genetic parameter estimation, degree of dominance and their standard errors for the studied traits under irrigated and water stress environments.

Tabla 3. Estimación de parámetros genéticos, grado de dominancia y sus errores estándar para las características estudiadas bajo condiciones de riego y de estrés hídrico.

		m	[d]	[h]	[i]	[j]	[l]	χ²	[h/d]
GY	N	11.39 ± 0.5**	1.38 ± 0.96*		-0.21±0.15*			0.61	-
	S	7.55 ± 0.98**	2.47 ± 1.16*			-3.66 ± 2.2*		0.303	-
PH	N	86.2 ± 0.4**	31.46 ± 8.79**	-12.46 ± 1.76**			-20.99 ± 9.32**	1.45	-0.39
	S	75.52 ± 3.88**	-9.47 ± 4.31**	19.39 ± 7.8*		14.87 ± 13/4*		0.808	-2
PL	N	31.11 ± 1.32**	-3.67 ± 1.5*	7.54 ± 2.55**		3.04 ± 4.7*		1.56	-2
	S	24.18 ± 1.34**		19.58 ± 5.42**			-16.29 ± 5.34**	1.56	-
SL	N	9.67 ± 0.46**	-1.14 ± 0.32**					1.09	-
	S	-	-	-	-	-	-	-	-
TGW	N	2.97 ± 0.2**	0.74 ± 0.2**	0.66 ± 0.23**	0.28 ± 0.26*			0.63	0.9
	S	2.6 ± 0.05**	0.74 ± 0.1**		0.15 ± 0.12*			1.42	-
HI	N	0.39 ± 0.007**	-0.025 ± 0.01*					3.31	-
	S	0.28 ± 0.06**	0.05 ± 0.02**	0.19 ± 0.06*		-0.06 ± 0.04*	-0.17 ± 0.12*	0	3.8

N: normal irrigated environment, S: drought stress environment,
 GY: grain yield, PH: plant height, PL: peduncle length, SL: spike length, TGW: thousand grain weight, HI: harvest index.
* and ** significant at the 5% and 1% probability levels, respectively. ns: non-significance.

Table 4. Components of variance and heritability estimations for the studied traits under irrigated and water stress environments.

Tabla 4. Componentes de la varianza y estimaciones de heredabilidad para las características estudiadas en los ambientes de riego y estrés hídrico.

		D	H	E	F	√H/D	h²$_{bs}$	h²$_{ns}$
GY	N	24.87	92.8	7.00	24.04	1.93	0.79	0.19
	S	16.27	0.59	10.04	0.53	0.19	0.45	0.34
PH	N	304.5	28.72	31.83	3.86	0.31	0.83	0.71
	S	105.18	136.25	20.69	43.1	1.14	0.59	0.18
PL	N	48.69	10.2	16.01	-11.26	0.46	0.62	0.56
	S	110.66	17.84	12.12	-3.99	0.4	0.82	0.67
SL	N	5.4	-4.75	1.69	-0.33	-	0.48	0.34
	S	-	-	-	-	-	-	-
TGW	N	0.34	0.52	0.11	-0.15	1.23	0.66	0.42
	S	0.26	0.46	0.103	0.08	1.32	0.68	0.38
HI	N	0.038	0.014	0.009	-0.012	0.60	0.56	0.41
	S	0.06	0.59	0.08	-0.16	3.14	0.81	0.09

N: normal irrigated environment, S: drought stress environment,
 GY: grain yield, PH: plant height, PL: peduncle length, SL: spike length, TGW: thousand grain weight, HI: harvest index.

DISCUSSION

All traits were significant (Table 1) over all generations under both conditions of water availability (except for spike length in the drought stress treatment). These results suggest genetic variation for these traits. Genetic variation in wheat for grain yield and yield components, and also some other ag-ronomic traits, has been reported by many authors (Tammam, 2005; Mohammadi et al., 2012; Khaled, 2013; Said, 2014). Genetic diversity is a well-recognized value for plant breeders. Existence of genetic variability is the first step in a plant breeding program. In fact, the efficient selection (without waste of time and money) largely depends upon the magnitude of the genetic variability in the population (Farshadfar et

al., 2001; Farshadfar et al., 2008). Our results indicated that all traits were affected by drought stress. This may be due to undesirable effects of drought on gametes (pollen and ovule) fertility, causing significant spikelet fertility losses and adversely affecting yield (BeNCze & Veisz, 2011; Prasad et al., 2011; Pradhan et al., 2012; Tahmasebi et al., 2014). Global production of wheat is frequently affected by drought stress, particularly in the dry regions. Reduction of wheat production in drylands could make more than two billion inhabitants vulnerable to crop failure (Daryanto et al., 2016). The best solution to overcome this situation would be having improved cultivars.

Compared to irrigated conditions, the maximum reduction was observed in grain yield, but 1000-grain weight was less affected under drought stress conditions. This might be due to the fact that 1000-grain weight is determined in early post-anthesis whereas other yield components are determined mainly in pre-anthesis (Koocheki et al., 2014). Therefore, it would be expected that 1000-grain weight be affected less by the adverse effects of drought stress. Grain yield, as economic yield in wheat, positively and highly correlated with plant height, peduncle length and harvest index under drought stress conditions, indicating their importance as a selection criterion. Studies on wheat and barley genotypes commonly grown in the last century, showed that grain yield correlated with harvest index (Cattivelli et al., 1994; Slafer et al., 1994) directly and positively, whereas total biomass accumulation remained almost unchanged due to a decrease in plant height (Cattivelli et al., 2008). The current findings showed that there was no significant correlation between peduncle length and yield under irrigated conditions. These results differ from those which indicated the importance of this trait under drought stress conditions. Wheat peduncle is a transient source of water-soluble carbohydrates and it might play a crucial role in increasing final wheat yield by 10-12% under irrigated conditions and more than 40% under drought and heat stress conditions (Davidson et al., 1992). In addition, wheat peduncle, because of having a high photosynthetic intensity and proximity to the spike, plays an important role in transferring photosynthates during the grain filling stage.

In both conditions of water availability, grain yield was negatively correlated with 1000-grain weight. This result doesn't support other findings. Simmonds and co-workers (2014) identified and validated a major QTL on chromosome 6A that significantly improved yield (5.5%) and 1000-grain weight (5.1%) of bread wheat. Moreover, there are many reports on non-significant relations between yield and 1000-grain weight (Ali et al., 2008; Yani & Rashidi, 2012; Fellahi et al., 2013). Based on scaling test, the mean parameters [m] for all traits across the environments were significant indicating that these traits are controlled by minor genes and quantitatively inherited. Generation mean analysis revealed that epistatic effects are important in con-

trolling bread wheat traits. These results correspond with reports of other studies (Novoselovic et al., 2004; Khaled, 2013; Zaazaa et al., 2012). Additive gene effect [d] was significant for grain yield across both water availability conditions, and dominance effect [h] was negligible and inconsiderable. On the other hand, second rank parameters (variance and its components) showed that dominance variance (H) was larger than additive variance (D) under irrigated conditions. These inconsistent results are due to the opposite directions of dominance gene effects [h] under irrigated conditions. Thus, using hybrid vigor will be more effective than selection under irrigated conditions. Also, direct selection for high yield varieties should be made in early segregating generations, while using a pedigree selection program could be useful under drought stress conditions. Under full irrigation conditions, although additive and dominance effects play an important role in controlling plant height, the magnitude of the additive effect was larger than that of the dominance effect, and complementary epistasis was involved in determining that trait. In addition, the additive effect under irrigated conditions changed to over dominance effect ($\sqrt{H/D}=1.14$) when plants faced drought stress. This finding was confirmed by diallel cross in wheat (Arshad & Chowdhry, 2003). Dominance effects contributed more than additive effects in determining peduncle length, and gene action remained in the same situation under irrigated and drought stress conditions. Due to over dominance, selection for this trait in early generations is difficult in breeding programs. This situation is even more complicated under drought stress conditions due to the presence of duplicate epistasis. Spike length was governed by additive effects without non-allelic interactions. These results are in accordance with results of authors who reported that spike length is not expressed by epistatic effects (Akhtar & Chowdhry, 2006; Zaazaa et al., 2012; Kaukab et al., 2014). Walia and co-workers (1995) and Awaad (1996) reported that additive gene effects are more important than dominance effects in controlling spike length. However, Kaukab and-co-workers (2014) revealed that this trait is expressed by over dominance gene effects. For 1000-grain weight, additive and dominance gene effects were detected as significant, and also additive × additive gene effects were identified under irrigated conditions. Furthermore, only additive and additive × additive gene effects were identified in the drought stress treatment. Regarding to variance and its components, 1000-grain weight was controlled by over dominance genes ($\sqrt{H/D}>1$) under both conditions of water availability. These inconsistent results can arise due to opposite directions of dominance gen effects [h] or concentration of increasing alleles in one parent leading to an underestimation of dominance gene effects. Fatehi and co-workers (2008) and Said (2014) reported additive and partial dominance for 1000-grain weight in wheat, while Afiah and co-workers (2000) identified over dominance gene effect

for this trait. Chowdhry and co-workers (1999) showed that over dominance gene effects under irrigated conditions moved to partial dominance gene effects in the drought stress treatment. Additive gene effects without epistatic interactions were involved in the expression of harvest index under irrigated conditions. The current findings showed that the additive gene effects changed to over dominance gene effects under drought stress, and duplicate epistasis effects contributed to controlling this trait. Many authors have reported over dominance gene effects for harvest index under drought stress (Golparvar et al., 2006; Abbasi et al., 2013; Golparvar, 2014) and additive gene effects under irrigated conditions (Akhtar & Chowdhry, 2006; Hassan & Gul, 2006; Farooq et al., 2011). These results showed that selection in early segregating generations will be just effective under irrigated conditions, and breeders should take into account in considering non-additive gene effects under drought stress conditions.

As a result from heritability, the highest value of narrow sense heritability belonged to plant height. Although we know plant height as a quantitative trait, Rht-B1 and Rht-D1 genes have been used nowadays as a main source of semi-dwarfism in bread wheat, and identified QTLs often coincide with these genes. Therefore, it can be concluded that this trait is rather under genetic control (like a qualitative trait), and selection in early segregated generations is the best way to improve it.

CONCLUSION

Using a breeding strategy largely depend upon the magnitude of the genetic parameters. Thus, a better understanding of the complexities of genetic control and response changes across different conditions will be useful for cultivar improvement. The results of the present study indicated that non-allelic interactions, in addition to additive and dominant effects, are important factors in controlling the expression of the studied characters, and genetic responses may be different across different conditions (e.g., irrigated vs. drought stress conditions). Both additive and non-additive gene effects were involved in the expression of the different traits. Thereafter, it is recommended that breeding methods, which make the best use of additive effects such as direct selection, are applied for those traits where dominant effects are negligible. However, using hybrid vigor will be more effective than selection for those traits that show high levels of dominant effects.

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