



RESEARCH PAPER

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Generation mean analysis in wheat (*Triticum aestivum* L.) under water deficit stress condition, using mixed linear models

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Article published on February 28, 2019

Key words: Epistasis, Generation mean analysis, Heritability, Mixed linear model, Wheat.

Abstract

Drought stress is one of the most important factors reducing crop production in the world. Understanding the type and relative amount of genetic components is essential for determining the breeding methods for genetic improvement of drought tolerance related traits. In the present study, generation means and variances analyses were employed to estimate additive, dominance and epistatic effects as well as additive, dominance and environmental variances based on mixed linear model method. The results of generation mean analysis through six generations (P₁, P₂, F₁, F₂, BC₁, BC₂) revealed significant epistasis for flag leaf length, flag leaf width, spike weight, harvest index, weight of 100 grains and grain yield per plant under normal and water deficit conditions, and for plant height, peduncle length, effective tiller number, spike length and straw weight under water deficit condition. The nature and value of gene effects for majority of traits were different under normal and stress conditions. Broad-sense heritability values for flag leaf width, spike length, effective tiller number, harvest index and weight of 100 grains were higher in stress than in normal conditions, (>0.4), whereas the narrow-sense heritability values for most traits (except flag leaf width, spike length, effective tiller number and harvest index) were lower in stress than normal conditions.

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Introduction

Wheat (*Triticum aestivum* L.) is one of the three major cereal crops in the world that feeds about 35-40% of the world population. Production of wheat is noticeably affected by the various biotic and abiotic stresses (FAO, 2015; Kosova *et al.*, 2016). To feed the world population, wheat production should increase up to 70% by 2050 to meet future demands (FAO, 2009; Ray *et al.*, 2013), which needs a 2.4% of yield increase annually. This will be more challenging in regions with climate changes and water restriction such as north-west of Iran, one of the most important regions for wheat production. Nonetheless, the efficient way to increase wheat yield is the identification of genetic control of drought tolerance and development of well adapted cultivars to a wide range of drought stress conditions (Akhtar and Chowdhry, 2006).

Knowledge about inheritance and genetic control of traits is very important in choosing breeding methods for crop improvement (Verma and Singh, 2017). Generation mean analysis (GMA) is a simple but useful tool for estimating genetic components underlying quantitative traits. The analysis provides information on the relative importance of the effects of genes (additive effects, dominance deviations, effects due to non-allelic gene interactions) (Pooni and Treharne, 1994; Iqbal and Nadeem, 2003; Checa *et al.*, 2006; Sharmila *et al.*, 2007). In GMA, the Mather's scaling test or Cavalla's joint scaling test are mostly used for testing the adequacy of additive-dominance model and estimation of gene effects *via* the goodness-of-fit with a t-test or chi-square test (Mather and Jinks, 1982; Kearsey and Pooni, 1996;). In these methods, the error terms are usually computed based on within-plot variances (Mather and Jinks, 1982) and due to ignorance of between-plot variance and also existence of genetic variation within segregating generations, the results may not be very accurate (Piepho and Mohring, 2010). In mixed linear model proposed by Piepho and Mohering (2010) the problem was solved and genetic effects as well as variance components are estimated at a single step.

GMA has extensively been used for genetic analysis in different crops such as Okra (El-Gendy and El-Aziz, 2013), common bean (Akhshi *et al.*, 2014), eggplant (Sabolu *et al.*, 2014), cauliflower (Verma and Singh, 2017), cowpea (Gupta *et al.*, 2017) and Wheat (Moroni *et al.*, 2013).

The objectives of present investigation were to estimate genetic parameters and heritability of quantitative traits related to yield in a cross of Alvand×Navid using generation mean analysis based on P₁, P₂, F₁, F₂, BC₁ and BC₂ generations by mixed linear model analysis under normal irrigation and water deficit stress conditions.

Materials and methods

Plant materials consisted of F₁, F₂, BC₁ and BC₂ generations derived from the cross of Alvand (female parent and drought tolerant) with Navid (male parent and drought susceptible) spring wheat cultivars along with parental lines. The field experiments were carried out at the experimental station of Faculty of Agriculture, University of Tabriz, Iran (latitude of 46°, 17'N and longitude of 37°, 5'E with 1360 m elevation and the maximum and minimum temperatures of 38 °C and 25 °C during the growing season, respectively). The six generations were sown in two separate experiments (normal condition and water deficit stress at the pollination stage) using randomized complete blocks design with three replications during 2014 and 2015 growing seasons. Each plot consisted of 40 plants in two rows for each of the parents and F₁, 120 plants in 6 rows for each back cross generation and 140 plants in seven rows for the F₂ population. Each row was in 2 m length with the within-row spacing of 10 cm and between-row spacing of 30 cm. space between rows. Ammonium nitrate was applied to the soil as nitrogen fertilizer in amount of 50 kg/ha before planting and at tillering stage. Plant height (cm), peduncle length (cm), flag leaf length (cm), flag leaf width (cm), effective tiller number, spike weight (g), spike length (cm), straw weight (g), harvest index, weight of 100 grains (g), and grain yield per plant (g) were measured.

Generation mean analysis was performed based on the genetic model of Mather and Jinks (1982) using mixed linear model (MLM) proposed by Piepho and Mohering (2010) as follows; $Y = m + \alpha[d] + \beta[h] + \alpha_2[i] + 2\alpha\beta[j] + \beta_2[l]$, where Y, m, d, h, i, j and l are mean of all generations, sum of additive effects, sum of dominance effects, sum of additive × additive, sum of additive × dominant and sum of dominant × dominant interactions, respectively. The fitness of additive-dominance model was examined using Wald-type F-test (Piepho and Mohering, 2010).

Broad-sense and narrow-sense heritabilities (Wright, 1968) as well as degree of dominance (Halluer and Miranda, 1988) were estimated using following formula:

$$h_{bs}^2 = \frac{V_G}{V_G + V_E}, h_{ns}^2 = \frac{V_A}{V_G + V_E}, \bar{a} = \sqrt{\frac{2V_D}{V_A}}$$

Where V_G , V_A , V_D , and V_E are genotypic variance, additive variance, dominant variance and environmental variance, respectively.

Results

Analysis of variance revealed significant differences among generations for all the traits under normal and water deficit conditions indicating the presence of sufficient genetic variability for carrying out generation mean analysis and estimating heritability. For the most studied traits except peduncle length, effective tiller number under normal and water deficit stress conditions and flag leaf length, flag leaf width, spike length and straw weight under normal condition, the mean of F1 generation was between those of parental values. Water deficit reduced the values of studied traits in all the generations as compared with normal condition (Table 1).

Table 1. Generation means (±SE) for studied traits in bread wheat under normal (N) and water deficit (S) conditions.

Generations	Traits							
	PH (cm)		PL (cm)		FLL (cm)		FLW (cm)	
	N	S	N	S	N	S	N	S
P1	49.27±0.73	46.59±0.56	28.91±0.77	26.69±0.57	17.59±0.34	15.42±0.27	1.62±0.03	1.31±0.02
P2	47.55±0.73	38.65±0.56	27.43±0.77	21.40±0.57	17.08±0.33	10.92±0.26	1.52±0.03	1.13±0.02
F1	46.61±0.73	42.58±0.56	26.51±0.77	18.56±0.57	16.59±0.34	12.02±0.26	1.49±0.04	1.18±0.02
F2	45.64±0.54	41.92±0.25	25.64±0.63	21.92±0.26	16.70±0.26	12.80±0.15	1.48±0.03	1.24±0.01
BC1	47.41±0.56	41.73±0.28	27.29±0.65	21.75±0.29	16.56±0.26	11.40±0.16	1.65±0.04	0.97±0.02
BC2	45.16±0.55	43.14±0.27	25.14±0.66	23.16±0.28	15.21±0.26	12.05±0.15	1.64±0.03	1.03±0.01

Table 1. Continued

Generations	Traits							
	ETN		SW (g)		SL (cm)		STW (g)	
	N	S	N	S	N	S	N	S
P1	4.80±0.22	4.03±0.21	9.69±0.42	7.01±0.29	7.78±0.18	7.35±0.12	6.93±0.34	6.08±0.32
P2	4.69±0.22	3.22±0.21	8.46±0.41	4.45±0.29	7.55±0.18	6.15±0.12	7.31±0.34	4.71±0.32
F1	4.26±0.22	3.11±0.21	8.64±0.42	5.52±0.30	7.50±0.19	6.64±0.12	5.98±0.34	5.21±0.32
F2	4.62±0.12	3.69±0.15	9.32±0.21	7.09±0.19	7.17±0.15	6.36±0.06	6.45±0.24	4.32±0.25
BC1	4.19±0.13	3.54±0.15	6.38±0.15	4.70±0.17	7.68±0.15	6.62±0.07	6.98±0.23	5.88±0.25
BC2	4.30±0.12	3.57±0.15	6.38±0.16	5.21±0.18	7.15±0.14	6.79±0.07	6.62±0.23	5.43±0.25

Table 1. Continued

Generations	Traits					
	HI		100-SW (g)		GY (g)	
	N	S	N	S	N	S
P1	46.43±1.73	36.53±1.16	3.11±0.05	3.07±0.03	8.42±0.36	5.54±0.19
P2	33.11±1.72	18.74±1.16	3.07±0.05	2.48±0.03	5.19±0.36	1.79±0.19
F1	36.08±1.73	27.85±1.17	3.09±0.06	2.66±0.03	5.60±0.36	2.95±0.19
F2	38.48±1.15	29.83±0.46	3.88±0.04	3.43±0.01	4.23±0.21	1.85±0.07
BC1	22.11±1.10	16.33±0.36	2.77±0.04	2.48±0.01	3.05±0.17	1.74±0.05
BC2	22.28±1.07	17.47±0.34	2.75±0.03	2.49±0.01	2.92±0.17	1.87±0.05

PH: plant height, PL: peduncle length, FLL: flag leaf length, FLW: flag leaf width, ETN: effective tiller number, SW: spike weight, SL: spike length, STW: straw weight, HI: harvest index, 100-SW: weight of 100 grains, GY: grain yield per plant.

Table 2. Estimate of gene effects (\pm SE of mean) in normal (N) and water deficit (S) conditions for studied traits of bread wheat in the cross Alvand \times Navid using mixed linear model.

Traits	m	[d]	[h]	[i]	[j]	[l]	Wald-F	Epistasis
PH								
N	49.93 ^{**} \pm 3.12	0.92 ^{ns} \pm 0.61	-1.62 ^{ns} \pm 2.46	0.71 ^{ns} \pm 3.03	4.39 ^{ns} \pm 2.11	0.31 ^{ns} \pm 0.76	5.32 ^{**}	-
S	38.30 ^{**} \pm 2.26	3.46 ^{**} \pm 0.54	12.69 [*] \pm 5.44	2.21 ^{ns} \pm 2.18	-14.54 ^{**} \pm 1.62	-11.60 ^{**} \pm 3.56	28.38 ^{**}	Duplicate
PL								
N	27.21 ^{**} \pm 3.14	0.99 ^{ns} \pm 0.61	-2.35 ^{ns} \pm 2.50	0.43 ^{ns} \pm 1.04	4.17 ^{ns} \pm 2.12	0.50 ^{ns} \pm 0.77	4.38 [*]	-
S	18.38 ^{**} \pm 2.28	3.67 ^{**} \pm 0.54	15.17 [*] \pm 5.48	2.34 ^{ns} \pm 2.19	-14.92 ^{**} \pm 1.63	-16.81 ^{**} \pm 3.58	18.09 ^{**}	Duplicate
FLL								
N	24.43 ^{**} \pm 1.12	0.29 ^{ns} \pm 0.25	-20.30 ^{**} \pm 2.71	-6.73 ^{**} \pm 1.09	3.59 ^{**} \pm 0.79	13.06 ^{**} \pm 1.75	19.66 ^{**}	Duplicate
S	17.97 ^{**} \pm 1.51	1.56 ^{**} \pm 0.27	-13.27 ^{**} \pm 3.61	-5.56 ^{**} \pm 1.47	-5.86 ^{**} \pm 1.01	6.86 [*] \pm 2.28	29.67 ^{**}	Duplicate
FLW								
N	0.71 ^{**} \pm 0.14	-0.2 ^{ns} \pm 0.12	2.43 ^{**} \pm 0.35	0.83 ^{**} \pm 0.14	0.18 ^{ns} \pm 0.09	-1.64 ^{**} \pm 0.22	16.91 ^{**}	Duplicate
S	2.63 ^{**} \pm 0.14	0.08 ^{**} \pm 0.02	-4.11 ^{**} \pm 0.35	-1.49 ^{**} \pm 0.14	-0.28 ^{**} \pm 0.09	2.57 ^{**} \pm 0.22	46.18 ^{**}	Duplicate
ETN								
N	4.41 ^{**} \pm 0.23	0.13 ^{ns} \pm 0.20	-1.01 ^{ns} \pm 0.52	-	-	-	1.93 ^{ns}	No epistasis
S	-1.75 ^{ns} \pm 1.1	0.63 ^{**} \pm 0.19	12.94 ^{**} \pm 2.64	4.93 ^{**} \pm 1.08	-1.65 [*] \pm 0.73	-9.16 ^{**} \pm 1.66	8.26 ^{**}	Duplicate
SW								
N	18.94 ^{**} \pm 1.99	1.66 ^{**} \pm 0.37	-33.47 ^{**} \pm 4.77	-7.53 ^{**} \pm 1.94	-3.39 [*] \pm 1.33	23.78 ^{**} \pm 3.02	33.89 ^{**}	Duplicate
S	2.75 [*] \pm 0.98	2.99 ^{**} \pm 0.21	2.22 ^{ns} \pm 2.34	4.25 ^{**} \pm 0.94	-8.55 ^{**} \pm 0.68	0.92 ^{ns} \pm 1.52	72.31 ^{**}	-
SL								
N	6.64 ^{**} \pm 0.76	0.24 ^{ns} \pm 0.15	1.75 ^{ns} \pm 1.82	0.86 ^{ns} \pm 0.74	1.03 ^{ns} \pm 0.51	-1.24 ^{ns} \pm 1.16	4.63 ^{**}	-
S	4.51 ^{**} \pm 0.55	0.42 ^{**} \pm 0.11	5.78 ^{**} \pm 1.32	1.88 ^{**} \pm 0.54	-1.97 ^{**} \pm 0.38	-4.34 ^{**} \pm 0.85	14.90 ^{**}	Duplicate
STW								
N	6.11 ^{**} \pm 0.36	-0.03 ^{ns} \pm 0.29	1.77 ^{ns} \pm 0.88	-	-	-	1.47 ^{ns}	No epistasis
S	-0.57 ^{ns} \pm 1.53	0.67 [*] \pm 0.25	16.30 ^{**} \pm 3.65	4.88 ^{**} \pm 1.49	-0.59 ^{ns} \pm 1.00	-12.03 ^{**} \pm 2.29	8.65 ^{**}	Duplicate
HI								
N	74.72 ^{**} \pm 8.12	6.44 ^{**} \pm 1.42	-152.25 ^{**} \pm 19.41	-30.22 ^{**} \pm 7.92	-16.09 ^{**} \pm 5.35	122.44 ^{**} \pm 12.21	60.84 ^{**}	Duplicate
S	53.58 ^{**} \pm 5.43	12.19 ^{**} \pm 0.97	-110.29 ^{**} \pm 12.98	-21.24 ^{**} \pm 5.29	-28.69 ^{**} \pm 3.59	93.50 ^{**} \pm 8.19	76.82 ^{**}	Duplicate
100-SW								
N	4.19 ^{**} \pm 0.26	0.25 ^{**} \pm 0.05	-3.92 ^{**} \pm 0.64	-0.78 [*] \pm 0.26	-0.44 [*] \pm 0.18	2.99 ^{**} \pm 0.40	35.30 ^{**}	Duplicate
S	3.24 ^{**} \pm 0.10	0.34 ^{**} \pm 0.02	-2.28 ^{**} \pm 0.25	-0.38 ^{**} \pm 0.09	-0.80 ^{**} \pm 0.07	1.93 ^{**} \pm 0.16	76.75 ^{**}	Duplicate
GY								
N	15.73 ^{**} \pm 1.53	1.61 ^{**} \pm 0.29	-34.33 ^{**} \pm 3.67	-7.72 ^{**} \pm 1.49	-3.06 ^{**} \pm 1.03	24.84 ^{**} \pm 2.33	62.81 ^{**}	Duplicate
S	5.02 [*] \pm 0.51	2.50 ^{**} \pm 0.12	-10.60 ^{**} \pm 1.24	-0.82 ^{ns} \pm 0.49	-5.77 ^{**} \pm 0.37	9.33 ^{**} \pm 0.81	119.77 ^{**}	Duplicate

PH: plant height, PL: peduncle length, FLL: flag leaf length, FLW: flag leaf width, ETN: effective tiller number, SW: spike weight, SL: spike length, STW: straw weight, HI: harvest index, 100-SW: weight of 100 grains, GY: grain yield per plant.

Ns: Non-significant, *Significant at $P \leq 0.05$; **Significant at $P \leq 0.01$, m: mean effect, [d]: additive effect, [h]: dominance effect, [i]: additive \times additive effect, [j]: additive \times dominance effect, [l]: dominance \times dominance effect.

Wald-F test revealed significant digenic epistatic interactions of majority of the studied traits under both conditions. However, the additive-dominance model explained the genetic basis of effective number of tiller and straw weight under normal condition. For plant height and peduncle length the digenic epistatic model was satisfied under both conditions, but additive effects, additive \times dominance and dominance \times dominance epistasis were more important as compared with other genetic effects under water deficit condition. The results were same for spike length with differences that all the effects were significant in the six parameter model under stress condition. Significant and negative additive \times dominance gene effect, also significant and positive additive and additive \times additive gene effects were

observed for spike weight under stress conditions. For this trait significant and positive additive and dominance \times dominance gene effects, also significant and negative dominance, additive \times additive and additive \times dominance gene effects under normal condition were observed.

For flag leaf length and width, six-parameter model was adequate under both conditions and all effects except additive effect for flag length and width and additive \times dominance effect for flag width under normal condition were significant. For effective number of tiller, the three-parameter model was adequate under normal condition, while the model containing significant additive, dominance and all digenic epistatic effects was satisfied under stress condition.

The six- parameter model was satisfied for straw weight and all genetic effects were significant under both experimental conditions except additive × dominance effects under water deficit condition. For this trait significant positive additive, dominance and additive× additive interaction and negative dominance × dominance interaction were observed.

Duplicate epistatic effect was found for harvest index under normal and stress conditions. Significant negative dominance, additive× additive interaction and additive× dominance interaction were observed under normal and stress conditions, whereas, significant positive additive and dominance × dominance interaction under both conditions were obtained. For 100 grain weight, all digenic epistatic effects as well as additive and dominance effects in six-parameter model was significant under normal and water stress conditions demonstrating the importance of both additive and non-additive gene action for this trait. For this trait, significant negative dominance, additive× additive interaction and additive× dominance interaction were observed under normal and stress conditions, whereas, significant positive additive and dominance × dominance interaction under both conditions were obtained. The positive significant additive and dominance × dominance interaction were found for grain yield. In addition, duplicate type of gene action

was observed for the grain yield per plant, harvest index and 100 grain weight under both conditions.

The estimates of additive, dominance, and environmental components of variance, broad-sense and narrow-sense heritabilities and degree of dominance for different traits under normal and water deficit conditions are presented in Table 3. Additive variance was higher than dominance variance for plant height, flag leaf length, effective number of tiller, spike length and straw weight under both conditions. For peduncle length, additive variance was higher compared with dominance component only under normal irrigation condition. By contrast, dominance variance was higher than additive for spike weight, harvest index and grain yield under both conditions, peduncle length and 100 grain weight under water deficit stress and flag leaf width under normal condition. Broad sense heritability ranged from 0.12 (spike length) to 0.71 (grain yield) under normal, and 0.15 (flag leaf length) to 0.72 (flag leaf weight) under water deficit stress condition. Narrow sense heritability varied from 0.03 (flag leaf weight) to 0.36 (plant height) under normal irrigation, and 0.12 (flag leaf length) to 0.36 (flag leaf weight) under water deficit stress (Table 3). In this study, the average dominance ratio for all studied traits was greater than unity under both conditions except flag leaf length under both environments and effective number of tiller under stress condition.

Table 3. Estimates of variance components using restricted maximum likelihood for mixed linear model

Variance	PH (cm)		PL (cm)		FLL (cm)		FLW (cm)	
	N	S	N	S	N	S	N	S
δ^2_A	21.44±4.04	14.41±4.42	20.64±4.01	14.34±4.43	1.12±0.88	0.58±0.72	0.001±0.008	0.04±0.008
δ^2_D	12.82±3.98	13.24±3.88	17.02±3.71	15.23±3.81	0.17±0.79	0.16±0.63	0.01±0.006	0.04±0.007
δ_{AD}	1.87±1.47	0.51±1.46	1.62±1.45	0.56±1.46	0.68±0.26	0.52±0.21	0.01±0.002	0.005±0.002
δ^2_e	26.46±2.30	22.56±1.92	21.47±1.85	20.50±1.75	5.52±0.46	4.19±0.36	0.02±0.002	0.03±0.002
h^2_{bs}	0.56	0.55	0.64	0.59	0.19	0.15	0.35	0.72
h^2_{ns}	0.36	0.29	0.35	0.28	0.16	0.12	0.03	0.36
\bar{a}	1.09	1.35	1.28	1.45	0.55	0.74	4.47	1.41

Table 3. Continued

Variance	ETN		SW (g)		SL (cm)		STW (g)	
	N	S	N	S	N	S	N	S
δ^2_A	0.73±0.45	1.22±0.26	14.41±1.86	2.56±0.71	0.12±0.27	0.33±0.17	3.98±1.12	0.51±0.50
δ^2_D	0.42±0.43	0.36±0.27	16.64±1.55	4.15±0.66	0.08±0.23	0.28±0.15	2.96±0.84	0.43±0.42
δ_{AD}	0.09±0.13	0.03±0.09	0.34±0.22	0.17±0.15	0.19±0.07	0.03±0.05	0.16±0.23	0.03±0.14
δ^2_e	3.45±0.29	2.05±0.17	13.78±1.17	5.78±0.48	1.49±0.12	0.96±0.08	5.56±0.47	2.68±0.23
h^2_{bs}	0.25	0.44	0.69	0.54	0.12	0.39	0.55	0.26
h^2_{ns}	0.16	0.34	0.32	0.20	0.07	0.21	0.32	0.14
\bar{a}	1.07	0.76	1.52	1.80	1.15	1.30	1.22	1.30

Table 3. Continued

Variance	HI		100-SW (g)		GY (g)	
	N	S	N	S	N	S
δ^2_A	82.09±18.98	48.54±9.81	0.16±0.03	0.1±0.01	11.37±1.36	1.93±0.29
δ^2_D	119.00±17.14	70.25±8.97	0.15±0.02	0.12±0.01	13.12±1.13	3.34±0.31
δ_{AD}	11.63±3.70	2.21±1.77	0.06±0.005	0.003±0.002	0.58±0.14	0.004±0.04
δ^2_e	149.09±12.73	80.44±6.85	0.18±0.01	0.11±0.009	10.24±0.86	3.19±0.26
h^2_{bs}	0.57	0.60	0.63	0.67	0.71	0.62
h^2_{ns}	0.23	0.24	0.33	0.30	0.33	0.23
a	1.70	1.70	1.37	1.55	1.52	1.86

PH: plant height, PL: peduncle length, FLL: flag leaf length, FLW: flag leaf width, ETN: effective tiller number, SW: spike weight, SL: spike length, STW: straw weight, HI: harvest index, 100-SW: weight of 100 grains, GY: grain yield per plant.

Discussion

The present study was undertaken to estimate additive, dominance and epistasis genetic effects that govern the inheritance of different agronomic traits under normal and water deficit conditions. The generation means analysis for both normal and water deficit conditions showed significant Wald-F for the three-parameter model for all of the studied traits, except effective tiller number and straw weight in the normal condition, indicating the presence of non-allelic interactions in governing the inheritance of these traits. Therefore, the three-parameter model (additive-dominance model with no epistasis) were fitted for effective tiller number and straw weight in the normal condition. For rest of the traits, the six-parameter model was used to estimate the genetic effects. Additive effects were significant and positive for spike weight, harvest index, 100 grain weight and grain yield under both conditions and for rest of the traits only under water deficient condition. This implies that the choice of parents was appropriate for crossing. These findings were in agreement with the results of Grzesik (2000), Erkul *et al.* (2010) and Tonk *et al.* (2011). The negative or positive signs for additive effects depends on which parent is chosen as P1 and has no meaning attached to it (Edwards *et al.*, 1975; Cukadar-Olmedo and Miller, 1997). In contrast, non-significant additive effects for some of the studied traits may be ascribed to large error variance (Edwards *et al.*, 1975). Erkul *et al.* (2010) found that both additive and dominance gene action were significant in the inheritance of spikelets per spike but dominance effect was negative and higher than additive effect.

The dominance gene effect was higher than additive for majority of the studied traits under both conditions indicating predominant role of dominant component of gene action in inheritance of these traits. Therefore, the selection intensity should be low or moderate in the earlier generations and delayed to later generation when dominant effect decreased. Asadi *et al.* (2015), Said (2014) and Ataei *et al.* (2017) also reported the importance of dominance gene action in wheat as compared to additive effects.

Effective tiller number and straw weight were fitted to the three-parameter model, which showed that the additive and dominance gene effects are unbiased by linkage disequilibrium (Hallauer and Miranda, 1981). The significance of both additive and non-additive type of gene action suggests the use of reciprocal recurrent selection and/or bi-parental mating for the improvement of the traits (Almeida *et al.*, 2018). Dominance by dominance interaction was significant and opposite in sign to those of dominance effects for most traits indicating the presence of a duplicate type of epistasis (15:1). According to Almeida *et al.* (2018), when duplicate epistasis is present selection should be delayed until a high level of gene fixation is attained. Samineni *et al.* (2010) pointed out that sign of different epistatic effects such as additive by additive and additive by dominance indicates the direction in which gene effects influence the population mean. In this study, sign of both additive by additive and additive by dominance interaction were negative for harvest index, 100 grain weight and grain yield per plant under both conditions, flag leaf

length and width under water deficit condition and spike weight under normal condition which reduces the efficiency of early selection in segregating generations for such traits.

Knowledge about heritability of a trait helps plant breeders to predict behavior of subsequent generations and to predict the response to selection. Broad and narrow-sense heritability estimates revealed importance of both additive and non-additive effects in genetic control of the traits. Broad-sense heritability estimates the genetic proportion (additive + dominant + interaction) of the total phenotypic variation, while estimates of narrow-sense heritability indicates that some additive effects are responsible for the genetic variation. However, medium to relatively high broad-sense heritability and low to moderate narrow-sense heritability under both conditions in the present study suggests that dominance gene action is more important than the additive type in controlling the majority of traits under consideration. This argument has also supported by Mohamed (2014) and Asadi *et al.* (2015). Erkul *et al.* (2010) stated that narrow-sense heritability was higher for number of spikelets per spike, single spike yield and fertile tiller number, but were lower for number of kernels per spike, thousand kernel weight and grain yield

The degree of dominance was greater than unity for almost all studied traits under both environments, indicating the presence of the over-dominance type of gene effects at some loci that justifies the low to medium narrow-sense heritability for the traits. Selection for agronomic characters must therefore be delayed until the F3 or F4 generations. This delay permits the reduction of non-additive genetic variances through inbreeding, so that the additive genetic variance can be more efficiently exploited (Said, 2014).

Conclusion

The results of this study indicated that all additive, dominance, and epistatic effects were involved in the inheritance of agronomic traits of wheat for the genetic materials under investigation. In concordance with the results from the generation mean analysis, both additive and dominance variance components explained the total genetic variation for the measured traits.

However, dominant and dominance \times dominance components were more important than others, but it is difficult to exploit them due to the presence of duplicate epistasis, likewise, it would be advisable to relegate the selection to more advanced families (e.g. F3, F4) replicated in multiple environments. Furthermore, the degree of dominance for most of the traits was more than one, which indicates the importance of the over-dominance effect in governing the traits under study.

Acknowledgment

Authors duly acknowledge the Department of Plant Breeding, University of Tabriz, Iran, for financial support of the work.

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