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Inheritance of agronomic and physiological traits in wheat under water deficit stress and normal conditions

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Abstract

To study the inheritance of several agronomic and physiological traits, an experiment was conducted in the research station of the University of Tabriz, Iran, under water deficit stress and normal conditions using the generation mean and generation variance analyses. The generations were produced from the cross of Arg and Moghan3 varieties. The experiment was conducted as a split-plot design based on randomized complete blocks with two replications. The irrigation conditions were arranged in the main plots and generations in the subplots. In the stress condition, irrigation was withheld after pollination. Based on the results of generation means analysis for flag leaf length in the normal condition and flag leaf width, flag leaf area and leaf chlorophyll content in both conditions, the additive-dominance model explained variation among generation means. For other traits, including flag leaf length under water stress condition and plant height, peduncle length, spike length, fertile tillers, days to heading, number of grains per spike, head weight, straw weight, biomass, grain yield and harvest index in both water-stress and normal conditions, the six-parameter model was fit for the generation means implying the presence of non-allelic interactions in the inheritance of these traits. Broad-sense heritability and narrow- sense heritability for the traits were estimated as 0.70 - 0.99 and 0.03 - 0.30 in the water-stress conditions and 0.60 - 0.99 and 0.10 - 0.55 in the normal conditions, respectively. At both conditions, the dominance genetic variance was higher than the additive genetic variance for most of the traits under study. The average degree of dominance for all characters at both water-stress and normal conditions was greater than unity which showed the existence of over-dominance gene action in controlling the traits under study. These results suggest the need for exploiting non-additive gene action by producing hybrid varieties in wheat if breeders overcome the barriers of producing hybrid seed.

Keywords: Gene action; Generation mean analysis; Genetic variance components; Heritability; Water deficit stress.

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Introduction

Drought is the second important factor for the crop yield loss after pathogens and insects (Mahajan and Tuteja 2005). Drought adversely affects growth and yield of wheat; however, it's effect is more pronounced at flowering and grain-filling period (Farooq *et al*. 2014). Terminal drought in wheat is common in the Mediterranean area, and a prolonged mild drought at flowering and grain filling reduces the grain yield of wheat by about 58-92% (Farooq *et al*. 2014). The adverse effect of terminal drought on wheat will presumably increase in the future due to climate change.

The wheat plant shows various morphological, physiological, biochemical and molecular adaptive responses when subjected to water stress (Nezhadahmadi *et al*. 2013). Stomata closure, production of toxic metabolites and a decrease in photosynthesis activity are among the important physiological responses to water stress

(Bray 2002). Drought stress after anthesis reduces grain filling period (Kaur and Behl 2010), 1000-seed weight and grain yield (Kaur and Behl 2010; Koocheki *et al*. 2014). Saeidi and Abdoli (2015) showed that terminal drought decreases chlorophyll content, 1000-seed weight, biomass, grain yield and harvest index but increased leaf temperature.

Improvement of drought tolerance in wheat is the main goal of breeding programs in arid and semi-arid regions. In this regard, knowledge about the type of gene action is necessary to determine the breeding strategy of the crop under improvement.

Several genetic methods have been developed to study the type of gene action, but most of the genetic models are additive-dominance models and the epistatic or non-allelic interactions are largely ignored. However, it has been shown that epistatic effects occur frequently in the control of traits (Hallauer and Miranda 1988). Among these methods, generation mean analysis is a biometrical technique that estimates all types of gene effects including epistasis (Kearsey and Pooni 1996). Additive and dominance genetic effects have been detected in many studies (e.g., Nanda *et al.* 1982; Moussa 2010) for several traits in bread wheat. In the study of Erkul *et al*. (2010) on wheat, variation in generation means was explained by the additive-dominance model for the number of fertile tillers, the number of spikelets per spike, 1000-grain weight and grain yield, and by the six-parameter model for the number of grains per spikelet and the number of grains per spike, suggesting the role of epistatic gene action in controlling these traits. Novoselovic *et al*. (2004) studied gene effects in two winter wheat crosses via generation mean analysis in the normal conditions. For most traits a digenic epistatic model explained the variation in generation means.

Based on Abbasi *et al*. (2013), additive, dominance and additive × additive effects were responsible for the inheritance of the majority of the traits related to grain yield in wheat under drought stress conditions. Although both types of additive and dominance effects were involved in the control of the studied traits, the dominant component was more prominent than the additive component. In another experiment, the genetics of grain yield and its components were studied under water stress conditions in bread wheat using generation mean analysis. The additive-dominance model didn’t explain all of the variation among generations for characters under study. Therefore, different models consisting of four to six parameters were fitted to generation means. These indicated the importance of epistasis in controlling grain yield and its components under the terminal drought conditions (Zanganeh Asadabadi *et al*. 2012). Abedi *et al*. (2015) used generation mean analysis to study the inheritance of some morphological traits in bread wheat under drought stress conditions. The additive-dominance model provided the best fit for all traits except harvest index, grain weight of the main spike, number of grains per plant and total spike weight of the plant. Although both additive and dominance effects were responsible for controlling the traits under study, dominance gene action was more prominent than additive effects for the number of tillers, main spike weight, seed number per the main spike and grain yield. Said (2014) used generation mean analysis to study the inheritance of several agronomic and physiological traits in two wheat crosses under normal irrigation and drought stress conditions. He indicated the importance of dominance gene action plus additive × additive and dominance × dominance interactions in the genetic control of most of the studied traits under both conditions. Sheikh *et al*. (2009) also reported the importance of dominance gene effects as compared to additive effects for yield and yield components in wheat under normal and high-temperature stress environments. The differences among experiments for types of gene action can be mainly attributed to the type of plant materials, sample size and experimental conditions.

This study was aimed to estimate gene effects, genetic variances and heritability of several agronomic and physiologic traits in bread wheat via generation mean and generation variance analyses.

Materials and Methods

Plant materials and experiment

Plant materials consisted of 12 generations as F_2, RF_2, F_3, RF_3, F_4, RF_4, BC_1, BC_2, BC_1S_1, BC_2S_1, BC_1S_2 and BC_2S_2, derived from the cross of Arg (tolerant to salinity and drought) and Moghan3 (sensitive to drought) (Anonymous 2013). The seeds of parents were provided by Seed and Plant Improvement Institute, Karaj, Iran. The experiment was carried out at the research station and greenhouse of the University of Tabriz, Iran in the 2015-2016 growing season. This station is located at 38°52 N latitude, 46°172 E longitude and altitude of 1360 m above the sea level. The experiment was carried out as a split-plot design based on randomized complete blocks with two replications. It should be noted that F_1 and RF_1 seeds were not used due to the low seed amount. F_1 and RF_1 plants were selfed to produce F_2 and RF_2 seeds, respectively, and backcrossed to their parents to produce BC_1 ($P_1 \times F_1$) and BC_2 ($P_2 \times F_1$) seeds. The irrigation conditions (normal and water deficit stress) were arranged in the main plots and generations in the subplots. Each plot consisted of 60 plants in 3 rows for each of the parents and backcrosses, 1400 plants in 70 rows for F_3, 1160 plants in 58 rows for RF_3, 1260 plants in 63 rows for the F_4, 840 plants in 42 rows for RF_4, 700 plants in 35 rows for BC_1S_1, 660 plants in 33 rows for BC_1S_2, 600 plants in 30 rows for BC_2S_1, 640 plants in 32 rows for BC_2S_2 and 160 plants in 8 rows for F_2 and RF_2 generations. Rows were 1 m long and 15 cm apart with 5 cm between plants in each experimental unit. In the normal condition, plants were irrigated throughout the cropping period. However, in the water deficit stress condition, irrigation was withheld after pollination till harvest. To estimate the within generation variance, data were recorded on all individual plants in all traits.

Traits

The following traits were measured during the growing season: plant height, peduncle length, spike length, flag leaf length, flag leaf width, flag leaf area, fertile tillers, chlorophyll content, leaf temperature, days to heading, number of seeds per spike, 1000 seed weight, head weight, straw weight, biomass, grain yield and harvest index. Chlorophyll content was measured using a SPAD chlorophyll meter (James *et al*. 2002). For this character, the average of three leaves per plant was taken. Leaf temperature was measured using a hand-held infrared thermometer (Reynolds *et al.* 1998). To measure the flag leaf length and width, the maximum length and width of fully developed leaves were measured in the main spikes. Flag leaf area (FLA) was calculated by the following equation (Muller 1991):

FLA = Flag leaf length × Flag leaf width × 0.74

Statistical analysis

At first, assumptions of analysis of variance (i.e. normal distribution of residuals, homogeneity of error variances and independence of errors) were tested. Then, generation mean analysis for each character was carried out separately for the two irrigation conditions by the weighted least squares method; the weight was the inverse of the variance of the means within each generation (Mather and Jinks 1982). In this method, the overall average for each trait is shown as follows:

$$Y = m+\alpha[a]+\beta[d]+\alpha^2[aa]+2\alpha\beta[ad]+\beta^2[dd]$$

where, Y: the generation mean, m: F_∞ metric, a: additive effect, d: dominance effect, aa: additive × additive interaction, ad: additive × dominance interaction, dd: dominance × dominance interaction and α, 2αβ and β^2 are the coefficients of the genetic parameters.

The expectation of generation means and coefficients of genetic components for each generation are given in Table 1. At first, a three-parameter model (m, a, d) was tested using means of 14 generations for each trait as described by Mather and Jinks (1982). To test for the validity of the additive-dominance model, the concordance between expected and observed mean values for each generation was determined by the joint scaling test (Cavalli 1952). When chi-square was significant, a six parameter model (m, a, d, aa, ad, dd) was fitted to the data. Again, the goodness of fit for the six-parameter model was verified by the joint scaling test. A t-test was used for the significance test of all genetic parameters. Since the sample sizes for the segregating generations were very large, we may have robust estimates of genetic parameters.

To estimate the additive (A) and dominance (D) variance components, analysis of generation variances for each trait was carried out separately for the two conditions by the least squares method using the coefficients in Table 2. Then, additive variance (V_A) and dominance variance (V_D) were obtained as follows (Mather and Jinks 1982):

$$V_A = \frac{A}{2} \text{,} \quad V_D = \frac{D}{4}$$

Environmental variance (V_E), genetic variance (V_G), broad sense (h^2_{bs}) and narrow sense (h^2_{bs}) heritability and average degree of dominance ($\bar{a}$) were estimated using the following equations:

$$V_E = \sqrt{V_{P_1} \times V_{P_2}}$$

$$V_G = V_A + V_D$$

$$h^2_{bs} = \frac{V_G}{V_G + \frac{V_E}{r}}$$

$$h^2_{ns} = \frac{V_A}{V_G + \frac{V_E}{r}}$$

$$\bar{a} = \sqrt{\frac{2V_D}{V_A}}$$

Where r, V_{P_1} and V_{P_2} represent the number of replications and variances within the first and second parents, respectively.

All statistical analyses were carried out by Excel, Quattro Pro 6 and SAS 9.2 software.

Table 1. Expected generation means and the coefficients of the genetic parameters.

Generations	m	[a]	[d]	[aa]	[ad]	[dd]
$\bar{P}_1 = m + [a] + [aa]$	1	1	0	1	0	0
$\bar{P}_2 = m - [a] + [aa]$	1	-1	0	1	0	0
$\bar{F}_2 = m + {}^{1}/_{2}\ [d] + {}^{1}/_{4}\ [dd]$	1	0	0.5	0	0	0.25
$\overline{RF}_2 = m + {}^{1}/_{2}\ [d] + {}^{1}/_{4}\ [dd]$	1	0	0.5	0	0	0.25
$\bar{F}_3 = m + {}^{1}/_{4}\ [d] + {}^{1}/_{16}\ [dd]$	1	0	0.25	0	0	0.0625
$\overline{RF}_3 = m + {}^{1}/_{4}\ [d] + {}^{1}/_{16}\ [dd]$	1	0	0.25	0	0	0.0625
$\bar{F}_4 = m + {}^{1}/_{8}\ [d] + {}^{1}/_{64}\ [dd]$	1	0	0.125	0	0	0.015625
$\overline{RF}_4 = m + {}^{1}/_{8}\ [d] + {}^{1}/_{64}\ [dd]$	1	0	0.125	0	0	0.015625
$\overline{BC}_1 = m + [a] + {}^{1}/_{2}{}^{1}/_{2}\ [d] + {}^{1}/_{4}\ [aa] + {}^{1}/_{4}\ [ad] + {}^{1}/_{4}\ [dd]$	1	0.5	0.5	0.25	0.25	0.25
$\overline{BC}_2 = m - {}^{1}/_{2}\ [a] + {}^{1}/_{2}\ [d] + {}^{1}/_{4}\ [aa] - {}^{1}/_{4}\ [ad] + {}^{1}/_{4}\ [dd]$	1	-0.5	0.5	0.25	-0.25	0.25
$\overline{BC_1S_1} = m + {}^{1}/_{2}\ [a] + {}^{1}/_{4}\ [d] + {}^{1}/_{4}[aa] + {}^{1}/_{8}\ [ad] + {}^{1}/_{16}\ [dd]$	1	0.5	0.25	0.25	0.125	0.0625
$\overline{BC_2S_1} = m - {}^{1}/_{2}\ [a] + {}^{1}/_{4}\ [d] + {}^{1}/_{4}[aa] - {}^{1}/_{8}\ [ad] + {}^{1}/_{16}\ [dd]$	1	-0.5	0.25	0.25	-0.125	0.0625
$\overline{BC_1S_2} = m + {}^{1}/_{2}\ [a] + {}^{1}/_{8}\ [d] + {}^{1}/_{4}[aa] + {}^{1}/_{16}\ [ad] + {}^{1}/_{64}\ [dd]$	1	0.5	0.125	0.25	0.0625	0.015625
$\overline{BC_2S_2} = m - {}^{1}/_{2}\ [a] + {}^{1}/_{8}\ [d] + {}^{1}/_{4}[aa] - {}^{1}/_{16}\ [ad] + {}^{1}/_{64}\ [dd]$	1	-0.5	0.125	0.25	-0.0625	0.015625

m: F_∞ metric, a: additive effect, d: dominance effect, aa: additive × additive interaction, ad: additive × dominance interaction, dd: dominance × dominance interaction.

Results and Discussion

Tests for normality of residuals, homogeneity of variances and independence of errors showed that these assumptions were valid concerning all traits (data not shown).

Analysis of variances

There were significant differences among generations for all of the traits except 1000 seed weight (data not shown) and, thus, the analysis of generation means was justified. Furthermore, since the generation by irrigation condition was significant for grain yield, the genetic parameters were estimated in each irrigation condition separately for all of the traits.

Effect of water stress on the studied traits

Water stress increased leaf temperature and reduced other traits except for plant height, peduncle length and number of grains per spike significantly (Table 3). Significant reduction of grain yield due to terminal water deficit stress can be attributed to the reduction of the grain filling period and the assimilates needed for grain filling (Saeidi *et al*. 2010).

Table 2. Coefficients of genetic variance components for the wheat generations under study.

Generations	A	D	AD
P_1	0	0	0
P_2	0	0	0
F_2	1/2	1/4	0
RF_2	1/2	1/4	0
F_3 (Between)	1/2	1/16	0
F_3 (Within)	1/4	1/8	0
RF_3 (Between)	1/2	1/16	0
RF_3 (Within)	1/4	1/8	0
F_4 (Between)	3/4	3/64	0
F_4 (Within)	1/8	1/16	0
RF_4 (Between)	3/4	3/64	0
RF_4 (Within)	1/8	1/16	0
BC_1	1/4	1/4	-1/2
BC_2	1/4	1/4	1/2
BC_1S_1 (Between)	1/4	1/16	-1/4
BC_1S_1 (Within)	1/4	1/8	0
BC_2S_1 (Between)	1/4	1/16	1/4
BC_2S_1 (Within)	1/4	1/8	0
BC_1S_2 (Between)	1/4	1/64	-1/8
BC_1S_2 (Within)	3/8	3/32	0
BC_2S_2 (Between)	1/4	1/64	1/8
BC_2S_2 (Within)	3/8	3/32	0

A: additive variance component; D: dominance variance component; AD; additive by dominance covariance component.

Estimates of genetic parameters

Estimates of genetic effects based on three- or six-parameter models for the studied characters under normal and water stress conditions are given in Table 4. The results revealed that the inheritance of all traits except flag leaf width, flag leaf area and chlorophyll content could not be explained by the additive-dominance model. For several traits, including grain yield and harvest index, the chi-square for the six- parameter model was significant, implying the presence of higher-order non-allelic interactions and linkage or maternal effects in the inheritance of these traits (Mather and Jinks 1982).

Both additive and dominance effects were significant in the inheritance of all characters under investigation, except for flag leaf area at the water deficit condition and the number of grains per spike at both conditions. However, for almost all characters the dominance genetic effects were greater in magnitude than the additive gene effects at both conditions.

Epistatic effects (additive × additive, additive × dominance and dominance × dominance) were also present for most of the characters under study at both irrigation conditions, whereas dominance × dominance and additive × dominance interactions more important than additive × additive component for most of the traits including grain yield (Tables 4).

In general, both main effects and epistasis

Table 3. Means of the two irrigation conditions for the characters under investigation in wheat.

Irrigation condition	PH	PL	SL	FLL	FLW	FLA	FT	Chl	LT
Normal	54.765a	19.560a	8.926a	15.606a	1.307a	15.264a	3.502a	47.424a	30.599b
Water deficit	47.124a	16.974a	8.395b	14.571b	1.201b	13.183b	2.761b	44.145b	35.066a

Table 3 continued

Irrigation condition	DH	NS	SW	HW	STW	Bio	GY	HI
Normal	71.255a	22.509a	25.45a	5074.437a	4039.015a	9113.452a	2996.905a	32.884a
Water deficit	68.918b	18.001a	23.32b	3736.681b	3093.430b	6830.111b	1754.121b	25.682b

- PH: plant height, PL: peduncle length, SL: spike length, FLL: flag leaf length, FLW: flag leaf width, FLA: flag leaf area, FT: fertile tillers, Chl: chlorophyll content, LT: leaf temperature, DH: days to heading, NS: number of grains per spike, SW: 1000-grain weight, HW: head weight, STW: straw weight, Bio: biomass, GY: grain yield and HI: harvest index.
- Means with different letters in each column are significantly different at the 0.01 probability level (based on the F-test).

governed the studied traits. Because both dominance gene effects and dominance type of epistasis were significantly involved in the inheritance of the traits under study. This indicates the necessity of exploiting dominance effects in wheat breeding programs if hybrid varieties could be produced in the wheat plant. However, linkage disequilibrium may bias the estimates of genetic parameters, especially epistasis (Mather and Jinks 1982). The occurrence of bias in the estimates of epistasis in our study is possible, because, we have evaluated some early segregating generations, such as F_2 and F_3. Therefore, a portion of the epistatic effects may be due to linkage disequilibrium.

Saleem *et al*. (2016) used generation mean analysis in wheat and showed that additive, dominance and epistatic effects were responsible in governing morpho-physiological traits but physiological traits, such as chlorophyll content, leaf carotenoids content, osmotic potential, turgor potential and canopy temperature were governed by lower epistatic effects as compared to agronomic and yield-related traits. In a study, dominance, additive × additive and dominance × dominance effects were significant for most agronomic and physiologic characters at both normal and drought stress conditions in two bread wheat crosses (Mohamed 2014). Prakash *et al*. (2006) reported that dominance effects together with additive effects and additive × dominance and additive × additive interactions had a role in controlling the wheat traits under study. In another investigation, several yield-related traits were analyzed using generation means analysis and the results showed that additive, dominance and epistatic gene effects played a role in the inheritance of all characters in two bread wheat crosses (Akhtar and Chowdhry 2006). Based on Abd EL-Rahman (2013) the additive, dominance and epistatic gene effects were important in controlling the inheritance of the number of kernels per spike, days to heading and kernel weight in bread wheat. Ljubicic *et al*. (2016) studied the type of gene action involved in the inheritance of yield-related traits in four bread wheat crosses and showed the presence of digenic epistasis for most of the studied traits. The additive × additive and dominance × dominance non-allelic interactions were observed in most of the cross combinations. They suggested that selection for some traits should be postponed to advanced segregating generations due to epistasis. Aykut Tonk *et al*. (2011) studied the inheritance of some agronomical traits in wheat using generation mean analysis and reported that the additive, dominance and epistatic gene effects were significant for all of the measured traits.

Asadi *et al*. (2015) examined the genetics of some physiological traits in wheat by generation mean analysis under normal and water deficit conditions and concluded that the mode of gene action depends upon the water regime. The dominance effect was significant for all traits in the normal condition but in the water deficit stress condition it was not significant for flag leaf area and relative water content. The additive effect was also significant for most of the traits at both irrigation conditions. Furthermore, epistasis was responsible for governing the inheritance of physiological traits under both normal and water deficit conditions. Bilgin *et al*. (2016) by carrying out generation mean analysis for several yield and quality traits in two winter wheat crosses (Pehlivan × Bezostaja, Sana × Krasunia) found that the additive-dominance model didn't explain the variation among generations for most of the traits under investigation. Similar to our results, the estimates of dominance genetic effects and dominance × dominance interaction were higher than additive genetic effects and other epistatic types.

In this study, genetic variance and heritability were also estimated assuming no epistasis. However, these estimates should be regarded to have an upward bias because epistasis was present in controlling the traits under study using generation mean analysis. Estimates of genetic components of variance and other parameters for each character under normal and water-deficit stress conditions are shown in Table 5. In both conditions the dominance genetic variance was higher than the additive genetic variance for all traits, except flag leaf length, flag leaf area and days to heading in the normal condition. The results indicated again that dominance variance played an important role in the inheritance of these traits. Larger dominance variance than the additive genetic variance for grain yield and harvest index in wheat was reported also by Abbasi *et al*. (2013). Also, based on Mohamed (2014), dominance variance was higher than the additive variance for the number of spikes per plant, grain yield and chlorophyll content in bread wheat. However, Abd EL-Rahman (2013) by using three bread wheat crosses, stated that additive genetic variance was larger than dominance variance for the number of days to heading, days to physiological maturity, plant height, number of spikes per plant, number of kernels per spike, 100 kernel weight and grain yield per plant in most crosses. Furthermore, in another study, the additive genetic variance was higher than the dominance genetic variance for

Table 4. Estimates of genetic parameters for the studied characters of wheat under normal and water-deficit stress conditions using generation mean analysis.

Trait	Irrigation condition	m	[a]	[d]	[aa]	[ad]	[dd]	x^2
PH	Normal	$62.9^{**}\pm1.0$	$2.6^{*}\pm1.0$	$-36.6^{**}\pm7.7$	$0.61^{ns}\pm1.2$	$-6.3^{ns}\pm5.9$	$70.2^{**}\pm13.4$	16.7^{*}
	Water deficit	$49.2^{**}\pm1.0$	$2.5^{**}\pm1.0$	$-77.2^{**}\pm7.8$	$-5.8^{**}\pm1.2$	$-7.6^{ns}\pm5.7$	$137.4^{**}\pm14.1$	13.3^{ns}
PL	Normal	$22.8^{**}\pm0.5$	$1.3^{*}\pm0.6$	$-15.9^{**}\pm4.2$	$0.05^{ns}\pm0.71$	$-4.8^{ns}\pm3.4$	$28.3^{**}\pm6.8$	13.0^{ns}
	Water deficit	$18.0^{**}\pm0.5$	$0.89^{*}\pm0.44$	$-27.4^{**}\pm4.1$	$-3.41^{**}\pm0.66$	$-1.7^{ns}\pm2.7$	$48.5^{**}\pm7.2$	27.5^{**}
SL	Normal	$9.3^{**}\pm0.2$	$0.95^{**}\pm0.19$	$-2.8^{*}\pm1.4$	$-0.13^{ns}\pm0.23$	$-3.5^{**}\pm1.0$	$3.3^{ns}\pm2.3$	23.4^{**}
	Water deficit	$8.4^{**}\pm0.2$	$0.43^{*}\pm0.18$	$-4.6^{**}\pm1.2$	$-0.88^{**}\pm0.21$	$-0.43^{ns}\pm1.0$	$9.9^{**}\pm2.2$	23.0^{**}
FLL	Normal	$14.5^{**}\pm1.4$	$3.3^{*}\pm1.6$	$9.9^{**}\pm3.6$	-	-	-	3.3^{ns}
	Water deficit	$14.2^{**}\pm0.6$	$-1.6^{**}\pm0.4$	$-11.0^{*}\pm5.2$	$2.1^{**}\pm0.7$	$6.5^{*}\pm2.5$	$26.6^{*}\pm10.7$	2.9^{ns}
FLW	Normal	$1.2^{**}\pm0.1$	$0.28^{**}\pm0.09$	$0.36^{*}\pm0.15$	-	-	-	1.6^{ns}
	Water deficit	$1.1^{**}\pm0.04$	$0.15^{**}\pm0.05$	$0.77^{**}\pm0.29$	-	-	-	2.1^{ns}
FLA	Normal	$14.2^{**}\pm1.7$	$-3.9\pm1.9^{*}$	$7.0^{*}\pm3.2$	-	-	-	3.5^{ns}
	Water deficit	$12.4^{**}\pm0.6$	$1.9^{*}\pm0.8$	$3.4^{ns}\pm1.0$	-	-	-	4.7^{ns}
FT	Normal	$4.0^{**}\pm0.2$	$0.73^{**}\pm0.16$	$-2.5^{*}\pm1.3$	$-0.69^{**}\pm0.22$	$-3.6^{**}\pm0.9$	$2.7^{ns}\pm2.0$	15.4^{ns}
	Water deficit	$3.0^{**}\pm0.2$	$0.32^{*}\pm0.16$	$-3.81^{*}\pm1.56$	$-1.4^{**}\pm0.2$	$-0.95^{ns}\pm0.94$	$8.0^{**}\pm2.7$	57.0^{**}
Chl	Normal	$48.5^{**}\pm4.6$	$11.2^{*}\pm4.6$	$12.0^{*}\pm5.0$	-	-	-	2.6^{ns}
	Water deficit	$45.5^{**}\pm1.2$	$4.8^{**}\pm1.8$	$-21.3^{*}\pm10.3$	-	-	-	4.7^{ns}
DH	Normal	$66.0^{**}\pm0.5$	$6.1^{**}\pm0.2$	$10.5^{**}\pm3.4$	$-5.3^{**}\pm0.5$	$-4.4^{**}\pm1.2$	$-31.8^{**}\pm5.2$	538.2^{**}
	Water deficit	$73.0^{**}\pm0.5$	$3.5^{**}\pm0.1$	$43.2^{**}\pm3.2$	$-3.1^{**}\pm0.5$	$9.0^{**}\pm1.0$	$-76.7^{**}\pm5.0$	259.9^{**}
NS	Normal	$22.1^{**}\pm1.4$	$3.4^{**}\pm1.0$	$-4.4^{ns}\pm14.6$	$3.2^{*}\pm1.4$	$-53.9^{**}\pm6.0$	$-28.1^{ns}\pm38.0$	97.5^{**}
	Water deficit	$15.6^{**}\pm0.9$	$2.6^{**}\pm0.4$	$-6.3^{ns}\pm6.2$	$2.9^{**}\pm0.9$	$-32.1^{**}\pm4.3$	$15.4^{ns}\pm9.7$	135.2^{**}
HW	Normal	$7277^{**}\pm384$	$1119^{**}\pm230$	$-3826^{*}\pm1912$	$-698^{*}\pm340$	$-4140^{**}\pm1400$	$8338^{*}\pm3422$	35.8^{**}
	Water deficit	$3804^{**}\pm296$	$502^{*}\pm251$	$-15270^{**}\pm2840$	$-3429^{**}\pm441$	$-730^{ns}\pm1585$	$31953^{**}\pm4860$	104.3^{**}
STW	Normal	$6322^{**}\pm359$	$1440^{**}\pm257$	$-6294^{**}\pm1950$	$-1731^{**}\pm333$	$-1466^{ns}\pm1474$	$8506\pm3140^{**}$	69.6^{**}
	Water deficit	$5461^{**}\pm270$	$729^{*}\pm310$	$-2851^{*}\pm1391$	$-2612^{**}\pm425$	$8300^{**}\pm1772$	$6493^{ns}\pm4667$	96.0^{**}
Bio	Normal	$13594^{**}\pm676$	$2661^{**}\pm300$	$-8905^{*}\pm3516$	$-2648^{**}\pm541$	$-8760^{**}\pm2140$	$13639^{*}\pm5742$	40.8^{**}
	Water deficit	$9308^{**}\pm490$	$1401^{**}\pm504$	$-16639^{**}\pm5103$	$-5858^{**}\pm776$	$6692^{*}\pm2909$	$37726^{**}\pm8734$	55.3^{**}
GY	Normal	$4157^{**}\pm189$	$819^{**}\pm118$	$-1892^{*}\pm916$	$23^{ns}\pm152$	$-5908^{**}\pm677$	$2312^{ns}\pm1502$	56.9^{**}
	Water deficit	$1557^{**}\pm 129$	$642^{**}\pm130$	$-12835^{**}\pm1408$	$-1827^{**}\pm218$	$-5999^{**}\pm843$	$24581^{**}\pm2600$	63.2^{**}
HI	Normal	$28.5^{**}\pm0.9$	$2.8^{**}\pm0.8$	$-9.5^{*}\pm4.7$	$11.1^{**}\pm1.2$	$-38.1^{**}\pm6.5$	$17.1^{ns}\pm12.8$	250.6^{**}
	Water deficit	$16.9^{**}\pm0.9$	$-1.5^{ns}\pm1.3$	$-54.2^{**}\pm6.7$	$1.0^{ns}\pm1.0$	$-67.7^{**}\pm4.4$	$99.8^{**}\pm13.4$	264.0^{**}

- PH: plant height, PL: peduncle length, SL: spike length, FLL: flag leaf length, FLW: flag leaf width, FLA: flag leaf area, FT: fertile tillers, Chl: chlorophyll content, DH: days to heading, NS: number of grains per spike, HW: head weight, STW: straw weight, Bio: biomass, GY: grain yield, HI: harvest index.

- m: F_∞ metric, a: additive effect, d: dominance effect, aa: additive × additive interaction, ad: additive × dominance interaction, dd: dominance × dominance interaction.

plant height, number of kernels per spike, number of spike per plant, kernel weight and grain yield per plant in four crosses of bread wheat under two water regimes (Sultan *et al.* 2011).

The degree of dominance was greater than unity in two conditions for all traits (Table 5), indicating the existence of possible over-dominance gene action in controlling these traits or the result of the accumulation of many genes effects with partial or complete dominance. However, the estimates may be upwardly biased due to linkage disequilibrium and/or epistasis.

Table 5. Estimates of genetic variances, broad-sense heritability, narrow-sense heritability and average degree of dominance for the studied traits of wheat under normal and water-deficit stress conditions using different generations.

Trait	Irrigation condition	A	D	V_A	V_D	h^2_{bs}	h^2_{ns}	$\bar{a}$
PH	Normal	24.1	187	12.1	46.8	0.70	0.14	2.79
	Water deficit	20.6	291	10.3	72.7	0.79	0.10	3.75
PL	Normal	4.68	46.2	2.34	11.6	0.60	0.10	3.14
	Water deficit	4.50	60.3	2.25	15.1	0.77	0.10	3.66
SL	Normal	2.36	4.76	1.18	1.19	0.71	0.35	1.42
	Water deficit	1.99	5.32	1.00	1.33	0.70	0.30	1.64
FLL	Normal	25.4	40.3	12.7	10.1	0.81	0.45	1.26
	Water deficit	3.65	55.7	1.83	13.9	0.87	0.10	3.91
FLW	Normal	0.82	1.73	0.41	0.43	0.99	0.48	1.45
	Water deficit	0.45	3.39	0.23	0.85	0.99	0.21	2.75
FLA	Normal	36.3	57.2	18.1	14.3	0.80	0.45	1.26
	Water deficit	4.36	81.7	2.18	20.4	0.89	0.09	4.33
FT	Normal	0.99	6.98	0.49	1.74	0.86	0.19	2.66
	Water deficit	0.66	8.43	0.33	2.11	0.84	0.11	3.57
Chl	Normal	97.5	747	48.8	187	0.89	0.18	2.77
	Water deficit	76.2	977	38.1	244	0.91	0.12	3.58
DH	Normal	6.89	8.91	3.44	2.23	0.90	0.55	1.14
	Water deficit	1.35	14.1	0.68	3.53	0.86	0.14	3.23
NS	Normal	35.6	351	17.8	87.6	0.91	0.15	3.14
	Water deficit	25.8	518	12.9	130	0.97	0.09	4.48
HW	Normal	5960777	14525666	2980388	3631417	0.87	0.39	1.56
	Water deficit	2270555	22357549	1135277	5589387	0.82	0.14	3.14
STW	Normal	1811390	25004632	905695	625115	0.87	0.11	3.72
	Water deficit	898517	31703898	449258	7925975	0.86	0.05	5.94
Bio	Normal	10815688	68492239	5407844	17123060	0.90	0.22	2.52
	Water deficit	3149663	87111077	1574832	21777769	0.86	0.06	5.26
GY	Normal	562522	7846305	281261	1961576	0.88	0.11	3.74
	Water deficit	284544	16352041	142272	4088010	0.92	0.03	7.58
HI	Normal	21.9	145	11.0	36.3	0.73	0.17	2.57
	Water deficit	20.6	732	10.3	183	0.88	0.05	5.40

- PH: plant height, PL: peduncle length, SL: spike length, FLL: flag leaf length, FLW: flag leaf width, FLA: flag leaf area, FT: fertile tillers, Chl: chlorophyll content, DH: days to heading, NS: number of grains per spike, HW: head weight, STW: straw weight, Bio: biomass, GY: grain yield, HI: harvest index.

- A, D, V_A, V_D, h^2_{bs}, h^2_{ns}, $\bar{a}$: Additive variance component, dominance variance component, additive genetic variance, dominance genetic variance, broad sense heritability, narrow sense heritability and average degree of dominance, respectively.

Estimation of the degree of dominance may be biased by linkage disequilibrium, especially in the early segregating generations, so that an incomplete or complete dominance is estimated as an overdominance genetic effect (Marzooghian *et al*. 2014; Hill and Maki-Tanila 2015). Similar results in bread wheat were reported also by several authors for some agronomic traits including grain yield (Zanganeh Asadabadi *et al*. 2012; Mohamed 2014; Said

2014; Abedi *et al*. 2015). Abd EL-Rahman (2013) studied three bread wheat crosses (Giza 168 × Sids 13, Gemmeiza 9 × Misr 2, Sids 12 × Misr 2) and reported that the average degree of dominance was more than unity for plant height, the number of kernels per spike, kernel weight and grain yield per plant in the first cross as well as grain yield in the third cross. On the contrary, the same parameter was less than one for days to heading, plant height and grain yield per plant in the second cross as well as for kernel weight in the third cross. Also, it was less than one for days to physiological maturity in the first and third crosses, the number of kernels per spike in the last two crosses and the number of spikes per plant in the three crosses. Furthermore, Sultan *et al*. (2011) evaluated the progeny of four crosses in wheat under both normal and water stress conditions and indicated partial dominance or over-dominance for the number of spikes per plant, number of kernels per spike, kernel weight and grain yield depending on the type of cross and irrigation condition. Akhtar and Chowdhry (2006) reported a partial dominance for biomass, spike number and 1000- kernel weight.

For most of the traits, which were significantly influenced by generations, dominance effects, dominance × dominance epistasis effects, and for all traits, dominance variance and average degree of dominance were higher under water deficit stress condition as compared to normal condition. It looks like the dominance gene action is more important in stressed environments than non-stressed conditions. On the other hand, additive effects for most traits, and additive genetic variance and narrow-sense heritability for all traits were higher under the normal condition as compared to the water-deficit stress condition. This indicates that selection for additive effects in drought stress conditions will be less effective than normal environments.

Estimating the heritability of plant traits is important in breeding programs. Broad-sense heritability estimates the genetic portion of the total phenotypic variation, while narrow-sense heritability estimates only the additive part. However, heritability estimates are influenced by several factors such as estimation method, type of genetic material, sample size and type of experiment (Sharma 2003). In the present study, broad-sense heritability was high and narrow-sense heritability was relatively low in both environmental conditions. Estimates of broad-sense heritability and narrow-sense heritability for the traits under study ranged between 0.60 (peduncle length) - 0.99 (flag leaf width) and 0.10 (peduncle length) 0.55 (days to heading) in the normal condition and between 0.70 (spike length) - 0.99 (flag leaf width) and 0.03 (grain yield) - 0.30 (spike length) in the water stress condition, respectively (Table 5). The flag leaf width had the highest broad-sense heritability in both conditions. The difference between broad-sense and narrow-sense heritability is due to the existence of a large dominance effect in governing these characters at both water regimes. Moderate to high broad-sense heritability and low to moderate narrow-sense heritability for most of the traits in wheat under normal and water-deficit conditions were also reported by Mohamed (2014), Said (2014) and Asadi *et al*. (2015). Based on Dvojkovic *et al*. (2010) the estimated values of narrow-sense heritability and broad-sense heritability varied for the number of grains per spike (0.43 - 0.71 and 0.35 -0.42), grain weight per spike (0.62 - 0.71 and 0.51 - 0.53) and single grain weight (0.65 - 0.67 and 0.30 - 0.41) in two winter wheat crosses, respectively. However, Abbasi *et al*. (2013) described that broad-sense heritability estimates were between 0.50 to 0.98 and those of narrow-sense heritability rate between 0.46 to 0.88 for the majority of the traits related to grain yield in wheat under drought-stress condition indicating the importance of additive genetic variance in governing the traits on their study.

In general, dominance and epistatic gene effects together with additive effects governed the inheritance of agronomic traits such as grain yield at both normal and water-deficit stress conditions. Also, genetic analyses showed over-dominance gene action in the inheritance of all studied characters under normal and drought conditions. Thus, hybrid production is justified in wheat if breeders can overcome the hybridization barriers (transfer of pollen and male sterility). It has been stated that hybrid varieties are potentially superior to pure lines in terms of grain yield, yield stability and abiotic and biotic stress resistance (Schnable *et al.* 2014). However, the commercial hybrid seed production is currently very limited in the world (Longin *et al*. 2012; Whitford *et al*. 2013; Kempe *et al*. 2014; Florian Mette *et al*. 2015). The main limitations for the extensive use of wheat hybrid varieties are seed production capacities and costs, but reports show the progress in improving the economic use of hybrid wheat (Whitford *et al*. 2013; Florian Mette *et al*. 2015). According to Whitford *et al*. (2013), rapid progress in wheat genomics, increasing the knowledge about gene function and the genetic modification technologies to modify plant phenotypes may improve the hybridization efficiency and therefore help in the development of more cost-effective hybrid seed production systems. According to some reports, wheat hybrid varieties will be available at affordable prices over the next few years (Ledbetter 2016).

In conclusion, non-additive genetic effects (dominance and epistatic) were present in the cross of Arg with Moghan3 varieties, suggesting the exploitation of non-additive effects in breeding programs if hybridization barriers were overcome in wheat.

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وراثت صفات زراعی و فیزیولوژیک در گندم نان تحت شرایط تنش کم‌آبی و عادی

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چکیده

به منظور بررسی وراثت برخی صفات زراعی و فیزیوبولوژیک در گندم نان، تجزیه میانگین نسل‌ها و تجزیه واریانس نسل‌ها در ایستگاه تحقیقاتی دانشگاه تبریز در شرایط عادی و تنش آبی انجام شد. نسل‌ها از تلاقی دو رقم ارگ (متحمل به خشکی) و مغان۳ (حساس به خشکی) حاصل شدند. آزمایش به صورت طرح کرت‌های خرد شده در قالب بلوک‌های کامل تصادفی در دو تکرار صورت گرفت. شرایط آبیاری در کرت‌های اصلی و نسل‌ها در کرت‌های فرعی قرار داده شدند. در شرایط تنش، آبیاری پس از گرده‌افشانی متوقف شد. بر اساس نتایج تجزیه میانگین نسل‌ها، مدل افزایشی - غالبیت برای طول برگ پرچم (شرایط آبیاری عادی) و برای عرض برگ پرچم، مساحت برگ پرچم و میزان کلروفیل برگ (در دو شرایط تنش کم‌آبی و عادی) برازش یافت. برای سایر صفات (طول برگ پرچم در شرایط تنش کم‌آبی و ارتفاع بوته، طول پدانکل، طول سنبله، تعداد پنجه‌های بارور، روز تا ظهور سنبله، تعداد دانه درسنبله، وزن سنبله، وزن کاه، بیوماس، عملکرد دانه و شاخص برداشت در هر دو شرایط)، مدل شش پارامتری بهترین برازش را داشت که بیانگر وجود اثرهای متقابل غیرآللی در کنترل صفات مورد بررسی بود. دامنه وراثت پذیری عمومی و خصوصی برای صفات مورد مطالعه در شرایط تنش کم‌آبی به ترتیب ۰/۹۹ - ۰/۷۰ و ۰/۳۰ - ۰/۰۳ و در شرایط عادی به ترتیب ۰/۹۹ - ۰/۶۰ و ۰/۵۵ - ۰/۱۰ به دست آمد. در هر دو شرایط، واریانس غالبیت بزرگ‌تر از واریانس افزایشی برای اکثر صفات بود. متوسط درجه غالبیت نیز برای کلیه صفات در هر دو شرایط بیش‌تر از یک بود که وجود پدیده فوق غالبیت را در کنترل این صفات نشان داد. این نتایج نیاز به بهره‌برداری از اثرهای ژنی غیرافزایشی را از طریق تولید واریته‌های هیبرید در گندم، در صورت رفع موانع تولید بذر هیبرید، گوشزد می‌کند.

واژه‌های کلیدی: اجزای واریانس ژنتیکی؛ تجزیه میانگین نسل‌ها؛ تنش کم‌آبی؛ عمل ژن؛ وراثت پذیری.