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Inheritance of agronomic traits in the generations from the cross between Arta and Arg wheat cultivars under water deficit stress

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Abstract

Knowledge about the type of gene action involved in the expression of a trait is essential for conducting a proper breeding program. In this investigation the inheritance of grain yield and twelve important agronomic traits of wheat was studied through generations mean analysis. The experiment was carried out in the experimental station of Faculty of Agriculture, University of Tabriz, Iran, for two years (2016 and 2017). The generations were produced from the cross of Arg and Arta varieties. In each year, a split plot design was conducted based on randomized complete blocks with three replications. The irrigation conditions were arranged in the main plots and generations in the subplots. In the stress condition, irrigation was withheld after pollination. Analysis of variance showed significant differences among generations or significant generation × yearinteraction for majority of the traits under study. Generation mean analysis at both normal and water deficit conditions revealed that additive, dominance and epistatic effects were involved in the inheritance of majority of these traits, with the ranges of 0.16-5.57, 0.32-164.16 and -0.02-153.9, respectively. However, the dominance effects and dominance by dominance interaction (from 3.69 to 153.9) were more important than other types. The average degree of dominance for all traits in both normal and water deficit conditions was greater than unity (from 1.94 to 3.81), which indicated the existence of over-dominance gene action in controlling the traits under investigation. In conclusion, our results indicated the necessity of exploiting dominance gene action in wheat breeding programs.

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Introduction

Wheat (*Triticum aestivum* L.) is the first important and strategic crop in the world(Gustafson *et al.*, 2009). Wheat production is adversely affected by abiotic stresses like heat, cold, salinity and drought (Fischer and Maurer, 1978).Drought stress is probably the most important abiotic factor that limits wheat production (Srivastava *et al.*, 2016).

In cereal crops especially wheat, the flowering and grain-filling phases are more sensitive to drought stress than other phases (Farooq *et al.*, 2014). Therefore, breeding varieties in wheat tolerant to terminal drought stress, especially in the Mediterranean climate is very important.

Knowledge about the type of gene action in relation to the traits under consideration is regarded as a prerequisite for an efficient breeding program. Most methods estimate additive and dominance genetic effects assuming no epistasis. However, generation means analysis provides information not only on the relative importance of additive and dominance effects in populations created from two inbred lines, but also estimat esepistatic effects such as additive × additive, additive × dominance and dominance × dominance interactions (Mather and Jinks, 1982).

Ferrari *et al.* (2018) carried out generation mean analysis for the progenies derived from a cross of contrasting lines in triticale for some quantitative traits. In this study, epistatic effects were present for grains per spike and grain yield per plant. Gangopadhyay *et al.* (2018) used five generations (P_1, P_2, F_1, F_2, F_3) in wheat to study the gene effects for grain yield. In their research, additive × additive and dominance × dominance types of interaction were significant for plant height, spike length, 1000 grain weight and grain yield.The involvement of epistasis in the inheritance of traits in wheat have also been indicated by Asadi*et al.* (2015) under normal and water deficit conditions. Saleem *et al.*(2016) reported the role of both additive and dominance components in governing the inheritance of number of tillers, grain weight per spike and 1000 grain weight in wheat under normal condition, but duplicate epistasis was also present for 1000 grain weight under drought stress conditions. It seems that epistatic genetic effects also contribute to the inheritance of agronomic traits in wheat.

The purposes of this study were to provide information about genetic effects governing yield and its components in a bread wheat cross under water deficient stress and normal conditions.

Materials and methods

Plant material

The experimental material consisted of generations derived from a cross between two Iranian spring wheat cultivars. Parents were selected based on their tolerance and sensitivity to water deficit stress. The Arg cultivar, tolerant to drought stress (Anonymous, 2013) and Arta, sensitive to drought stress (Molla Heydari Bafghi *et al.,* 2017)were used as parents and subsequent generations such as F_2 (Second filial generation), F_4 (Fourth filial generation), BC_1S_2 and BC_2S_2 (Second selfed generations of backcrosses to Arg and Arta, respectively). The parents were provided by the Seed and Plant improvement Institute, Karaj, Iran.

Experimental layout

The experiments were carried out in the experimental station of Faculty of Agriculture, University of Tabriz, Iran during 2015/2016 and 2016/2017 growing seasons, using split plot design based on randomized complete blocks with three replications. Irrigation conditions (normal irrigation and water deficit stress) were arranged in the main plots and the generations in the sub-plots. Sowing was done in spring, with the plant to plant and row to row distances of 5 and 12 cm, respectively. Main plots in the normal condition received water whenever required, whereas, in the water stressed plots, irrigation was withheld after pollination. Data were collected on the well-guarded 20 plants of the parents, 119 plants from F_2 and 272 plants from F_4, BC_1S_2 and BC_2S_2 in each replication.

The following traits were recorded: grain yield (GY), 1000-grain weight (GW), number of spikes per plant (NS), spikes weight per plant (SW), spike length (SL), biomass (Bio), plant height (PH), peduncle length (PL), straw weight (STW), flag leaf length of the main tiller (FLL), flag leaf width of the main tiller (FLW) and harvest index (HI). Flag leaf area (FLA) was also calculated according to Muller (1991):

Flag leaf area = Flag leaf length × Flag leaf width × 0.74)

Statistical analyses

At first, combined analysis of variance for two years and mean comparisons of the generations by Duncan's multiple range test were performed. Then, generation mean analysis was conducted separately for each irrigation condition, averaged over years and replications, according to Mather and Jinks (1982). In this method the expected values of means for each character were defined as follows:

$$Y = m + \alpha[d] + \beta[h] + \alpha^2[i] + 2\alpha\beta[j] + \beta^2[l]$$

where, Y: generation mean, m: F_∞ metric, d: sum of additive effects, h: sum of dominance effects, i: sum of additive × additive interactions, j: sum of additive × dominance interactions, l: sum of dominance × dominance interactions and α, 2αβ and β^2 are the coefficients of genetic parameters.

To estimate the genetic parameters, the weighted least square method was employed (Mather and Jinks,1982). The genetic parameters (m, [d], [h], [i], [j], [l]) were tested for significance using *t*-test. Average degree of dominance ($\bar{a}$) was estimated by the following formula(Mather and Jinks, 1982):

$$\bar{a} = \sqrt{\frac{H}{D}}$$

Where, D= 2 × additive genetic variance and H= 4× dominance genetic variance. D and H were estimated by the least squares method using the relative coefficients in Table 1. All statistical analyses were carried out by the SAS software (SAS Institute, 2009).

Results and discussion

The combined analysis of variance revealed significant differences among generations or significant generation × year interaction for most traits. Significant generation × year interaction suggests that the differences between generations are not stable from one year to another.

Table 1. Coefficients of the genetic components of variances for the generations under study.

Variance of generations	D	H	Variance of generations	D	H
V_{F_2}	0.5	0.25	$V_{\overline{BC_1S_2}} + V_{\overline{BC_2S_2}}$	0.5	0.0312
$V_{\overline{F_4}}$	0.75	0.0469	$\bar{V}_{BC_1S_2}$	0.375	0.0938
$\bar{V}_{F_4}$	0.125	0.0625	$\bar{V}_{BC_2S_2}$	0.375	0.0938

The effect of irrigation condition was significant only on GY, GW, HI, and SL. However, the irrigation condition × year interaction was significant for other characters such as NS, Bio, PH, PL, STW, FLL, FLW and FLA. None of the traits showed generation × irrigation condition interaction. But the three-way interaction of generation × irrigation condition × year was significant for GW, PH, FLW and FLA. Significant differences were also observed between the two years for GY, GW, NS, SW, BIO, PH and Pl, indicating that environmental conditions were not similar in these years. (Table 2).

The coefficient of variation varied from 5.78% for FLW to 24.22% for SW. The coefficient of variation for GY (9.43%) was in the acceptable range. Arg had higher mean values than Art for all traits, averaged over years and irrigation conditions (data not shown).

Water deficit stress decreased the magnitude of all traits (averaged over years) as compared to the normal condition (Table 3). According to Gooding *et al.* (2003), drought stress reduced maturing period, grain yield and 1000grain weight.

Other researchers have also reported the reduction of grain yield and it's components at different growth stages of wheat in response to drought stress (Prasad *et al.*, 2011; Liu *et al.*, 2015; Saeidi and Abdoli, 2015).

Table 2. Combined analysis of variance for two years under normal and water stress conditions for the studied traits using different generations of a wheat cross.

		Mean Squares						
S.O.V	df	GY	GW	HI	NS	SW	SL	Bio
Year	1	1.63**	288.08*	0.40ns	19.95**	21.71**	13.84ns	45.58**
Rep (Year)	4	0.023ns	39.25ns	16.01ns	0.006ns	0.95ns	2.12**	2.06ns
Irrigation condition	1	10.37*	661.63*	54.44**	4.51ns	17.38ns	4.87**	90.83ns
Year × Irrigation condition	1	0.034ns	35.14ns	0.005ns	4.29*	5.06ns	0.50ns	58.30**
Irrigation condition × Rep(Year)	4	0.062*	27.02ns	7.52ns	0.067ns	2.75*	0.77ns	3.79ns
Generation	5	1.05ns	137.77ns	18.26ns	0.80ns	8.08**	6.49**	24.69*
Irrigation condition × Generation	5	0.034ns	52.88ns	5.05ns	0.094ns	0.69ns	0.055ns	2.22ns
Year × Generation	5	0.33**	177.70**	20.50*	0.86**	3.06**	0.58ns	5.39*
Year × Irrigation condition × Generation	5	0.06*	48.48ns	7.75ns	0.12ns	0.94ns	0.086ns	2.79ns
Error	40	0.019	44.09	6.52	0.22	0.62	0.41	1.96
Coefficient of variation (%)		9.43	22.68	11.45	16.38	24.22	7.16	19.69

Table 2 Continued.

		Mean Square					
S.O.V	df	PH	PL	STW	FLL	FLW	FLA
Year	1	925.71**	134.75**	4.57ns	5.05ns	0.066ns	2.87ns
Rep (Year)	4	71.27ns	5.14ns	1.53*	6.50ns	0.08ns	39.24ns
Irrigation condition	1	362.11ns	32.91ns	29.23ns	64.27ns	0.52ns	335.18ns
Year × Irrigation condition	1	486.25*	25.22**	29.49*	40.84*	0.48*	267.46*
Irrigation condition × Rep(Year)	4	45.51ns	1.81ns	0.21ns	2.63ns	0.051**	21.98**
Generation	5	355.71*	133.85**	7.22**	32.75*	0.071ns	82.09*
Irrigation condition × Generation	5	21.22ns	1.21ns	0.77ns	3.21ns	0.023ns	18.51ns
Year × Generation	5	98.55**	4.53ns	0.73ns	4.81*	0.063**	30.79**
Year × Irrigation condition × Generation	5	21.79*	2.55ns	0.94ns	2.14ns	0.026**	15.53**
Error	40	20.94	3.66	0.63	1.69	0.006	4.73
Coefficient of variation (%)		7.61	8.98	20.59	7.07	5.78	11.39

ns, *, **: non-significant and significant at 0.05 and 0.01 probability levels, respectively. The sources with similar expected mean squares were pooled

+GY= Grain yield, GW = 1000-grain weight, HI= Harvest index, NS= Number of seeds per spike, SW= 1000 seed weight, SL= Spike length, Bio= Biomass, PH= Plant height, PL= Peduncle length, STW= Straw weight, FLL= Flag leaf length, FLW= Flag leaf width, FLA= Flag leaf area.

The generation means analysis for both normal and water deficit conditions showed significant chi-square for the three-parameter model for all of the studied traits, except NS in the water deficit 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) was fitted for NS in the water deficit condition. For rest of the traits, the six-parameter model was used to estimate the genetic effects.

In both normal and water deficit conditions, the chi-square of the six-parameter model was not significant for these traits, suggesting the suitability of this model for explaining the generation means (Table 4). In the normal condition, all parameters([m] [d] [h] [i] [j] [l])were significant for GY, SW, Bio, PL, STW and FLA. The genetic models fitted for NS, SL and FLW consisted of five parameters([m] [d] [h] [i] [l]),for HI and PH comprised four parameters {([m] [h] [j] [l])and([m] [d] [h] [l]), respectively},and for GW composed of three parameters([m] [h] [i]).

Table 3. Means of different traits in wheat under normal and water deficit stress conditions.

Traits	Normal	Water deficit	Significance
GY (gr)	1.55	1.36	**
GW (gr)	32.31	26.24	**
HI (%)	23.16	21.42	**
NS	3.13	2.63	**
SW (gr)	3.73	2.75	**
SL (cm)	9.28	8.76	**
Bio (gr)	8.24	5.99	**
PH (cm)	62.36	57.87	**
PL (cm)	21.98	20.62	**
STW (gr)	4.51	3.24	**
FLL (cm)	19.34	17.45	**
FLW (cm)	1.45	1.29	**
FLA (cm2)	21.24	16.92	*

*,**Significant difference between normal and water deficit stress conditions at 0.05 and 0.01 probability levels, respectively, based on F test in the combined analysis of variance over two years.

In the water deficit condition, the generation means analysis revealed the fitting of the six- parameter model ([m] [d] [h] [i] [j] [l]) for GY, SW, SL, and PH. Furthermore, five-parameter models were fitted for Bio, STW and FLW ([m] [d] [h] [i] [l]), FLL ([m] [d] [h] [j] [l]), FLA ([m] [d] [h] [i] [j]), and HI ([m] [h] [i] [j] [l]). The four-parameter models of [m] [d] [h] [i] and [m] [d] [h] [l] were the best fit for GW and PL respectively (Table 4).

Additive gene effect (d) was significant for all studied traits in both normal and water deficit conditions, except GW in normal and HI in both conditions, indicating the potential of improving the performance of these characters by the population breeding methods. Additive gene effects were positive for all of the studied traits except HI in the water deficit condition (Table4). The positive value for additive effects revealed that the first parent had higher values than the second parent for the traits under study.

The estimated of dominance gene effects (h) were also significant for all traits in both normal and water deficit conditions (Table 4), however, the magnitude of dominant effects was higher than the additive effects.

In this study, epistatic effects were also important in controlling the agronomic traits in the bread wheat.As Table 4 shows, the dominance × dominance epistasis was significant for all of the studied traits in both normal and water deficit conditions, except for GW (in both conditions), FLL (in the normal condition) and FLA (in the water deficit condition), which confirm the important role of dominance × dominance interaction in the genetic system of these traits. Both additive × additive and additive × dominance effects were also significant for most of the traits under study. However, dominance × dominance gene effects were much greater than those of the additive × additive and additive × dominance effects, except FLL for which the additive × dominance interaction was higher than dominance × dominance epistasis.

Table 4. Estimates of geneticseffects obtained by generation mean analysisfor the studied traits in wheat under normal and water deficit stress conditions.

Trait	Irrigation condition	m	[d]	[h]	[i]	[j]	[l]	χ^2
GY	Normal	1.898±0.07**	0.44±0.02**	-2.46±0.0.7**	-0.28±0.07**	1.01±0.28**	3.69±1.12**	1.49E-21^{ns}
	Water deficit	0.52±0.06**	0.33±0.02**	6.8±0.62**	0.84±0.06**	1.81±0.26**	-10.35±1.01**	1.05E-21^{ns}
GW	Normal	36.38±2.68**	0.44±0.92^{ns}	-57.57±24.6**	-7.52±2.52**	12.91±10.82^{ns}	72.61±39.06^{ns}	4.05E-24^{ns}
	Water deficit	30.22±2.57**	2.74±0.71**	-49.34±23.7**	-4.99±2.47**	-8.09±9.82^{ns}	71.69±32.6^{ns}	1.64E-23^{ns}
HI	Normal	26.89±1.43**	0.29±0.48^{ns}	-42.19±13.1**	-1.08±1.35^{ns}	19.46±5.63**	72.92±20.67**	2.79E-23^{ns}
	Water deficit	26.3±1.72**	-1.09±1.04^{ns}	-45.99±16.3**	-3.48±1.37**	22.79±9.45**	79.31±26.14**	2.06E-24^{ns}
NS	Normal	3.82±0.21**	0.39±0.11**	-4.75±1.91**	-0.88±0.17**	-1.46±1.01^{ns}	7.56±3.07**	6.85E-25^{ns}
	Water deficit	2.56±0.04**	0.33±0.05**	0.32±0.26^{ns}	-	-	-	0.82^{ns}
SW	Normal	5.91±0.22**	1.34±0.04**	-16.11±2.15**	-2.54±0.22**	-7.85±0.85**	25.14±3.46**	3.47E-21^{ns}
	Water deficit	1.66±0.21**	0.94±0.06**	11.12±2.04**	0.74±0.2**	2.15±0.86**	-16.95±3.31**	6.71E-25^{ns}
SL	Normal	5.61±0.35**	0.81±0.12**	30.56±3.34**	3.38±0.33**	2.75±1.47^{ns}	-47.68±5.32**	3.02E-24^{ns}
	Water deficit	5.20±0.39**	0.74±0.17**	30.69±3.74**	3.11±0.35**	4.71±1.83**	-48.25±5.95**	6.55E-23^{ns}
Bio	Normal	12.06±0.44**	2.06±0.16**	-29.66±4.08**	-4.48±0.41**	-11.82±1.85**	47.85±6.61**	7.74E-24^{ns}
	Water deficit	2.98±0.43**	1.91±0.23**	29.51±4.11**	2.31±0.36**	1.45±2.23^{ns}	-45.74±6.62**	1.89E-24^{ns}
PH	Normal	54.93±2.8**	5.57±0.74**	98.31±25.56**	3.05±2.7^{ns}	-9.32±10.32^{ns}	-172.28±40.34**	7.54E-23^{ns}
	Water deficit	43.74±2.82**	4.27±1.2**	164.16±26.3**	10.74±2.55**	48.28±12.73**	-283.33±42.02**	4.73E-24^{ns}

Table 4 continued.

Traits	Irrigation condition	m	[d]	[h]	[i]	[j]	[l]	χ^2
PL	Normal	30.02±1.17**	4.44±0.38**	-42.44±10.92**	-10.16±1.11**	-17.94±4.75**	51.68±17.39**	1.11E-24^{ns}
	Water deficit	18.09±1.18**	4.27±0.52**	41.98±11.09**	0.58±1.06^{ns}	5.84±5.43^{ns}	-67.46±17.77**	4.63E-24^{ns}
STW	Normal	6.16±0.35**	0.72±0.15**	-13.64±3.25**	-1.95±0.32**	-3.98±1.55**	23.11±5.23**	1.16E-24^{ns}
	Water deficit	1.36±0.35**	0.97±0.22**	18.5±3.32**	1.59±0.27**	-0.69±1.96^{ns}	-28.97±5.35**	2.66E-24^{ns}
FLL	Normal	21.85±0.73**	3.09±0.19**	-16.25±6.92**	-2.79±0.71**	-34.01±2.87**	21.42±11.03^{ns}	3.72E-23^{ns}
	Water deficit	16.19±0.77**	2.02±0.29**	16.15±7.31**	0.84±0.71^{ns}	-9.53±3.39**	-28.14±11.67**	2.16E-24^{ns}
FLW	Normal	2.01±0.06**	0.2±0.02**	-4.25±0.67**	-0.46±0.06**	-0.51±0.31^{ns}	6.09±1.07**	5.99E-23^{ns}
	Water deficit	1.81±0.08**	0.16±0.04**	-3.31±0.77**	-0.48±0.06**	-0.02±0.43^{ns}	4.32±1.24**	4.65E-24^{ns}
FLA	Normal	34.66±1.52**	4.92±0.48**	-105.67±14.7**	-13.59±1.43**	-46.15±6.61**	153.9±23.59**	1.29E-22^{ns}
	Water deficit	21.61±1.62**	3.06±0.82**	-33.66±15.81**	-4.33±1.39**	-32.77±8.37**	48.62±25.27^{ns}	2.52E-23^{ns}

+GY= Grain yield, HI= Harvest index, NS= Number of seeds per spike, SW= 1000 seed weight, SL= Spike length, Bio= Biomass, PH= Plant height, PL= Peduncle length, STW= Straw weight, FLL= Flag leaf length, FLW= Flag leaf width, FLA= Flag leaf area, m= F_∞ metric, d= sum of additive effects, h= sum of dominance effects, i= sum of additive × additive interactions, j= sum of additive × dominance interactions, l= sum of dominance × dominance interactions.

The presence of epistasis in the inheritance of agronomic traits of wheat were also reported by several authors (Ijaz andKashif, 2013; Said, 2014; Ljubicic *et al.*, 2016; Ferrari *et al.*, 2018). However, the magnitude and type of the effects depend on the parents used and the evaluation site or environment (Fethi, 2010). In total, our results show that all types of genetic effects (additive, dominance, epistasis) were important in controlling the majority of studied traits, including grain yield, however, the role of dominance and dominance × dominance gene effects were more prominent than other types of genetic effects. This suggests the need for exploiting dominance gene action in the breeding programs if barrier of producing hybrid varieties can be overcome in the bread wheat. Reports show that hybrid varieties are higher in yield and more stable than pure lines, especially under adverse environmental conditions (Longin*et al.*, 2012).

Table 5. Estimates of average degree of dominance for the studied traits in wheat under normal and water deficit stress conditions using different generations.

Trait		GY+	HI	NS	SW	SL	Bio
Irrigation condition	Normal	2.47	1.94	3.14	2.39	2.89	3.39
	Water deficit	2.11	2.82	2.93	2.45	2.37	2.67
Trait		PH	PL	STW	FLL	FLW	FLA
Irrigation condition	Normal	3.15	3.26	2.79	3.38	2.99	3.46
	Water deficit	3.28	3.81	2.55	2.41	2.41	2.01

+GY= Grain yield, HI= Harvest index, NS= Number of seeds per spike, SW= 1000 seed weight, SL= Spike length,Bio= Biomass, PH= Plant height, PL= Peduncle length, STW= Straw weight, FLL= Flag leaf length, FLW= Flag leaf width, FLA= Flag leaf area.

The estimates of average degree of dominance under normal and water deficit stress conditions are presented in Table 5. The average degree of dominance for all of studied traits was greater than one in both normal and water deficit conditions, indicating the presence of the over-dominance type of gene action in the inheritance of these traits. However, it should be noted that linkage (especially repulsion type) may upwardly bias the estimates of dominance variance, so that the partial or complete dominance is represented as the pseudo-over-dominance type of gene action (Moll *et al.*, 1964).

Conclusion

The generation means analysis showed that all additive, dominance, and epistatic effects were involved in the inheritance of agronomic traits of wheat for the genetic materials under investigation. However, dominant and dominance × dominance components were more important than other effects. Furthermore, the degree of dominance in all of the traits was more than one, which indicates again the importance of the dominance effect in governing these t traits. These results indicate the necessity of exploiting dominance gene effects and improving yield by producing hybrid varieties in wheat, if pollination and male sterility constraints are overcome in the hybrid breeding programs.

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