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Original Research Article

Diallel Cross Study for Estimating Genetic Components Underlying Wheat Grain Yield

Mahdiyeh Zare-Kohan and Bahram Heidari*
Department of Crop Production and Plant Breeding, College of Agriculture, Shiraz University, 7144165186, Shiraz, IRAN

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ABSTRACT

In order to analysis genetic control of grain yield, five cultivars and their F_2 diallel crosses were sown in two locations of Shiraz and Zarghan, Iran. The traits of interest were number of grains per spike (GN), weight of grains per spike (GW), number of spikelet per spike (SN), spike length (SL), 1000-grain weight (TGW) and grain yield per plant (GY). The significant variances due to general (GCA) and specific (SCA) combining abilities indicated that both additive and non-additive components were involved in genetic control of traits. The GCA × location was only significant for GW. The Baker ratio implied the higher importance of additive variances. Graphical analysis of Hayman showed that gene action for all the traits was of partial dominance type. The environmental sensitivity analysis indicated heterogeneity among cultivars and their progenies for GW and that except Marvdasht, most of cultivars were relatively sensitive to the environmental conditions. The SCAs revealed that selection among progenies of Crossadl × Darab2 cross would be efficient for increasing GY. The GCA estimates revealed that the cultivars Cross adl and Marvdasht for GY, Cross adl and Shiraz for SN and SL and Cross adl for all traits were the best combiners.

Key Words: Combining Ability, Diallel, Environmental Sensitivity, Gene Action, Grain Yield, Wheat

INTRODUCTION

Wheat, being the most valuable staple food, is estimated for feeding about two third of the world population (Rahman *et al.,* 2008). Iran is one of the most important wheat producer countries in Asia and wheat consumption is widely seen in many parts of the country. In most parts of Iran, wheat production and grain filling has been affected by low precipitations over growing season and water limited resources. Iran has experienced more than two consecutive years of drought and reduced winter grain harvests. As a result, the country has had to resort to record-level grain imports to satisfy domestic demand for food and feed grains and to rebuild stocks. In Iran, wheat growing regions are widely dispersed climatically. It is uncommon to have favorable conditions in virtually all primary grain growing areas. The national wheat harvest normally occurs from May to August, with crops at the higher elevations maturing the latest. Widespread drought conditions appear to affect the majority of agricultural areas of Iran. The state of Fars is in the first rank of wheat production in Iran which is due to high cultivation area. Fars has experienced long time drought stress due to low precipitation. Average grain yield of wheat in Fars has been around 2 t ha^{-1} (FAO 2012). The best varieties for a specific location are those that fully explored the potential growing season fitting the constraints of the local environment (Andrade *et al.,* 1999; Capristo *et al.,* 2007). At low latitudes, temperature and radiation do not significantly vary throughout the year but different locations may vary environmentally. Therefore, to minimize the adverse effects of environmental conditions on wheat production, it is necessary to produce high yielding cultivars adapted to wheat cultivation areas.

For producing high yielding cultivars under wide range of agro- climatic conditions, it is necessary to evolve new wheat varieties with wide genetic base (Chowdhry *et al.,* 2002). As a part of wheat breeding programs, the Institute of Agricultural Research of Iran, one of important representative and pilot of CIMMYT at south west Asia, every year evaluates elite introduced wheat cultivars in order to be crossed with local cultivars and used in breeding programs for different climates of the country. One of the important strategies for increasing wheat production is crossing the lines with that of showing good general combining ability (GCA), access to the information of gene actions that influence grain yield and selection for transgressives segregated in the progeny generations. In addition, information of general and specific (SCA) combining ability of wheat genotypes is prerequisites to launch an efficient wheat breeding program (Kumar *et al.* 2011). Among genetic designs, diallel cross is an appropriate scheme to obtain genetic information of interested traits in a short period

* Corresponding author: bheidari@shirazu.ac.ir

of time. Mode of gene action, number or cluster of genes that control the traits of interest and the frequency of dominant and/or recessive genes can be used for a better planning of breeding programs. Information of GCA and SCA are important for plant breeders for selection of suitable genotypes and developing new high yielding varieties (Siddique *et al.,* 2004; Joshi *et al.,* 2004; Inamullah *et al.,* 2006; Rahim *et al.,* 2006; Ajmal *et al.,* 2011; Kumar *et al.,* 2011).

Given the importance of estimating genetic parameters in better programming a breeding scheme, the present study was conducted to obtain information about (1) the relative importance of the GCA to SCA variances in controlling grain yield and some of its related components using F_2 wheat diallel crosses under two geographically different locations, (2) to identify the best combiners that can be used in crossing plans for increasing grain yield, (3) to perform graphical analysis for determination of gene action responsible for the traits of interest, and (4) to identify environmental sensitivity of cultivars and their progenies.

MATERIALS AND METHODS

Five winter wheat cultivars (Cross adl, Marvdasht, Chamran, Shiraz and Darab2) originated from different pedigrees (Table 1) were selected to be crossed for production of 10 one-way F_1 diallel entries. Spike emasculation was done manually and pollination of the emasculated cultivars was performed via goo-goo method for producing F_1 grains at the research greenhouse of the College of Agriculture, Shiraz University, Iran. In order to increase number of seeds, 10 F_1 seeds from each of crosses were selected for producing F_2 progenies. The seeds of F_2 progenies and the parental cultivars were sown in 2010-2011 growing season in two locations of Zarghan Agricultural Research Center (29^o 47' N, 52^o 43' E, 1600 m alt), Zarghan, Fars, and the Research Farm of the College of Agriculture, Shiraz University (29^o 50 N', 52^o 46' E, 1810 m alt), Shiraz, Fars, Iran.

Table 1. The pedigree of wheat cultivars used as parental genotypes for producing diallel crosses.

Cultivar	Origin	Pedigree
Cross adl	Zarghan, Iran	Turkey/Shahpasand
Marvdasht	Zarghan, Iran	HD2172/BLoudan//Azadi
Chamran	CIMMYT, Mexico	CM85836-5OY-OM-OY-3M-OY
Shiraz	Zarghan, Iran	Gv/D630//ALd"s"/3/Azd
Darab2	CIMMYT, Mexico	Maya"s"/Nac

In each location, a randomized complete block design (RCBD) with three replications was arranged as the experimental design. At winter, 2010-2011, the seeds of each of parental cultivars and F_2 entries were manually sown in three rows 2 m long spaced 5 cm with row spacing of 15 cm. In each block, 30 plants from each of F_2 entries and 10 plants in parental plots were selected for traits measurement. The traits of interest were number of spikelet per spike (SN), spike length (SL), number of grains per spike (GN), grain weight per spike (GW), thousand- grain weight (TGW) and grain yield per plant (GY).

Data were subjected to analysis of variance for a randomized complete block design and also a combined analysis of variance of two locations. Genetic analyses were performed for individual and combined analyses of diallel crosses based on Griffing's method II, model I (Griffing 1956 a, b). In this model, genotypes and locations were respectively considered as fix and random effects. To estimate the GCA and SCA effects, a general linear model (GLM) procedure was used in SAS software (SAS Institute 2003). The combining ability ratio was calculated according to Baker (1978) as below:

$$\text{Baker ratio} = \frac{2MS_{GCA}}{2MS_{GCA} + MS_{SCA}}$$

where, MS_{GCA} and MS_{SCA} are the mean squares for GCA and SCA, respectively. Average degree of dominance, the frequency ratio of dominant to recessive alleles and the broad and narrow-sense heritabilities were estimated using a model proposed by Hayman (1954 a, b) and Jinks (1954). In this model, a graphical analysis was performed to determine the frequency of dominant and recessive alleles in the cultivars evaluated in both locations. The adequacy of the assumptions of the model was tested using the analysis of variances of (Wr + Vr) and (Wr - Vr) and the regression coefficients of Wr/Vr in Dial 98 (Ukai, 2006) and SAS (SAS Institute 2003) software's.

Genotypic correlation (r) coefficients of the traits and correlations between mid-parent (MP), F_2 means and the SCA effects were calculated using SAS statements (SAS Institue 2003). Some of the genotype by environment interactions could be ascribed to the differences of the sensitivity of genotypes (Falconer and McKay, 1996). In order to determine the environmental sensitivity of each genotype, the specific environments have to be quantified by the mean performance of all genotypes. To do this, the mean of a parent and its own progenies in different crosses in each location was regressed on the mean of all 15 genotypes as the environmental value of each location (Falconer and McKay, 1996). The slope of the regression lines for each parent and their progenies was considered as the environmental sensitivity of that parent.

RESULTS

Traits mean and genetic effects

The means of traits were higher in Zarghan as compared with Shiraz (Table 2). The means of F_2 entries were lower for GN, GW and GY as compared with their parents while for other traits, F_2s had higher means than their ancestral cultivars (Fig. 1). Variations between parents and F_2 means are being linked to the genetic and transgressive segregation.

Table 2. Traits mean in five parents and F_2 progenies of wheat in two locations of Shiraz and Zarghan.

	GN		GW (g)		SN		SL (cm)		TGW (g)		GY (g)	
Cultivar/Cross	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
Cross adl (1)	70.2	68.4	3.51	3.25	24.0	24.2	14.1	12.7	49.1	46.6	23.9	22.1
Marvdasht (2)	70.8	68.1	2.79	2.58	20.8	19.29	10.3	9.6	39.1	34.6	24.0	21.7
Chamran (3)	68.0	65.4	2.83	2.72	22.3	20.88	11.0	9.58	40.8	37.7	21.4	19.7
Shiraz (4)	60.5	58.7	2.6	2.17	20.9	20.45	11.9	11.3	41.8	37.4	19.7	17.5
Darab2 (5)	60.4	56.8	2.42	3.12	19.9	19.31	9.5	8.6	38.5	35.4	17.9	16.3
1×2	68.9	67.1	3.16	3.21	22.43	20.99	11.4	9.9	45.9	41.3	22.7	21.1
1×3	63.9	62.3	3.09	2.92	22.37	22.62	12.8	12.1	47.2	44.5	21.1	18.5
1×4	64.3	61.9	3.17	3.18	23.0	21.74	13.4	11.8	48.5	43.8	19.9	17.3
1×5	63.5	61.5	2.9	2.56	20.3	20.96	12.1	11.5	45.7	42.7	23.7	22.1
2×3	65.5	64.3	2.75	2.93	20.53	19.32	10.0	8.5	41.0	36.2	18.1	16.3
2×4	69.6	67.8	2.81	2.68	23.07	21.85	11.4	10.6	41.2	38.8	19.3	17.2
2×5	60.5	60.4	2.53	2.84	20.9	20.57	10.9	9.4	41.1	36.7	18.7	16.5
3×4	61.9	61.0	2.71	1.98	23.2	22.11	12.2	11.6	43.7	40.3	17.6	15.9
3×5	52.8	56.5	2.22	2.45	19.7	19.37	9.7	8.4	41.5	36.8	17.6	15.6
4×5	62.8	61.2	2.72	2.99	20.7	19.85	11.8	10.3	42.3	39.9	16.2	16.3
Mean± SEM	64.2±1.2	62.7±1.0	2.81±0.08	2.77±0.09	21.60±0.35	20.90±0.36	11.5±0.34	10.4±0.35	43.2±0.86	39.5±0.93	20.1±0.65	18.3±0.62

GN: number of grain per spike, GW: grain weight per spike, GY: grain yield per plant, SEM: standard error of the mean, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight,

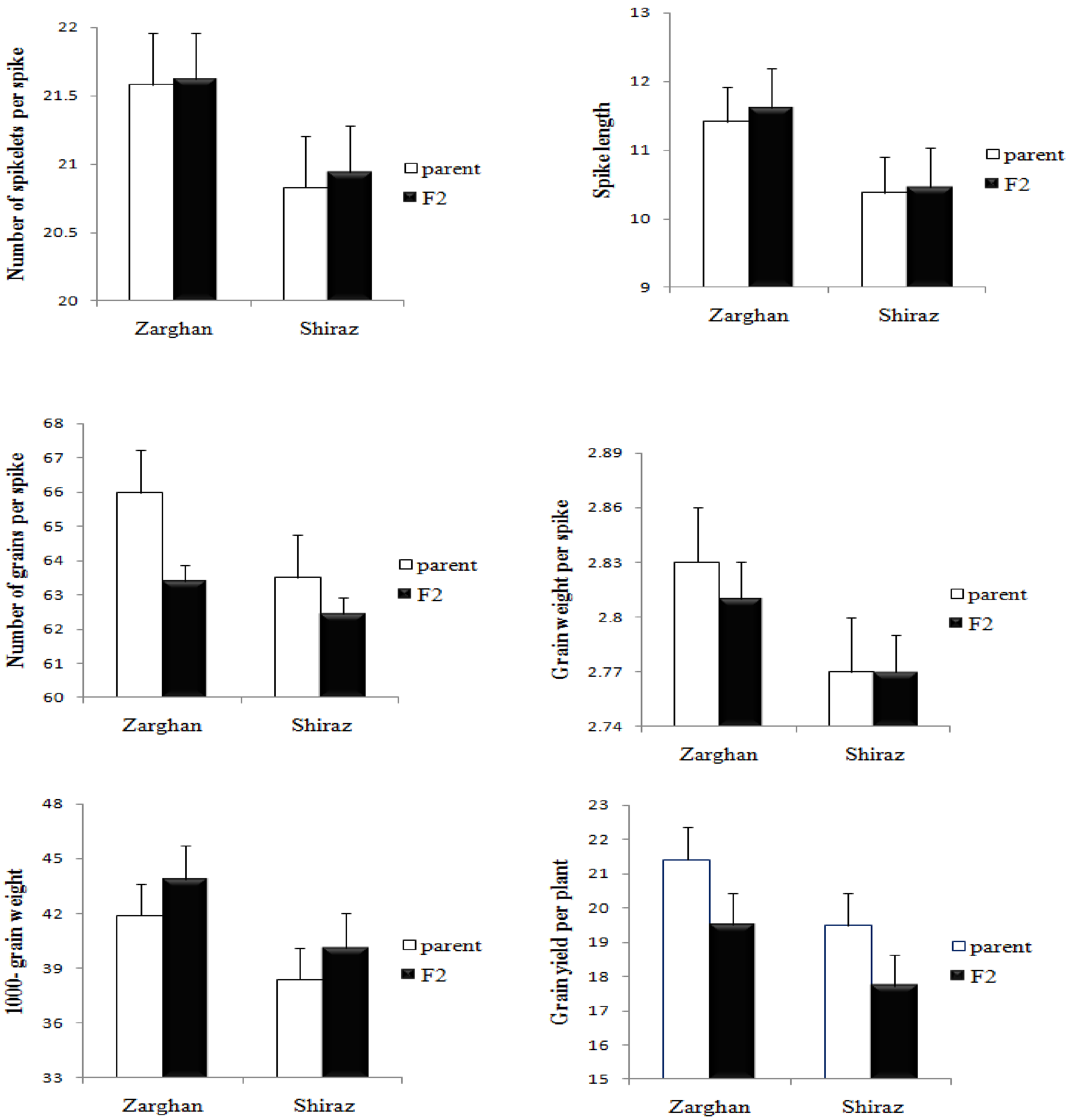


Figure 1. Traits mean for parents and their F_2 progenies in Shiraz and Zarghan locations.

Among parental cultivars, Cross adl (23.92 and 22.11 g plant^{-1} in Zarghan and Shiraz respectively) and Marvdasht (24.04 and 21.76) had the highest GY in both locations (Table 2). Cross adl had also the highest SL, SN, GW, and TGW. The average GY in the crosses involved either Cross adl or Marvdasht was relatively higher than in crosses involved other cultivars. The cross Chamran × Darab2 had the lowest GN in Zarghan (52.8) and in Shiraz (56.53) experiments. Among diallel crosses, the lowest (8.4 cm) and highest (14.1 cm) SL belonged to Chamran × Darab2 and Cross adl respectively.

Table 3. Combined analysis of variances for general (GCA) and specific (SCA) combining abilities in five wheat cultivars and their crosses.

		Mean square					
Effect	Df	GN	GW (g)	SN	SL (cm)	TGW (g)	GY (g)
Location (L)	1	48**	0.038	11.21**	27.95**	299.43**	75.88**
Genotype (G)	14	113.2**	0.56**	10.91**	10.83**	71.61**	36.55**
GCA	4	267.52**	1.29**	26.22**	31.87**	228.43**	78.55**
SCA	10	51.47**	0.27**	4.79**	2.41**	8.88**	19.74**
G×L	14	4.04**	0.18**	$0.71^{n.s}$	$0.23^{n.s}$	$1.33^{n.s}$	$0.58^{n.s}$
GCA×L	4	$1.42^{n.s}$	0.36**	$1.29^{n.s}$	$0.06^{n.s}$	$0.89^{n.s}$	$0.37^{n.s}$
SCA×L	10	5.09**	0.11**	$0.49^{n.s}$	$0.3^{n.s}$	$1.5^{n.s}$	$0.67^{n.s}$
Error	56	1.27	0.037	0.49	0.27	1.42	1.59

GN: number of grain per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant, * and ** respectively significant at 0.05 and 0.01 probability levels

The combined analysis of variances showed significant mean square for the effect of genotype in both locations (Table 3). The mean squares for genotype × location were significant for GN and GW. On the other hand, for SN, SL, TGW and GY, the non-significant genotype by location variances showed that the behavior of the genotypes was relatively similar in both locations.

Analysis of variances for combining abilities revealed that the variances due to GCA and SCA were significant for all the traits in both locations (Table 4). Therefore, both additive and non-additive gene effects attributed to genetic control of the traits. The GCA × location mean square was significant for GW, reflecting the effect of environment on additive gene actions. Except GN and GW, the SCA × location interactions were not significant indicating the insensitivity of the non-additive genetic effects to the environmental conditions.

Table 4. Mean squares for general (GCA) and specific (SCA) combining abilities and the Baker ratio in two locations of Shiraz and Zarghan.

		GN		GW(g)		SN		SL (cm)		TGW (g)		GY (g)	
Effect	Df	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
GCA	4	145.97**	122.97**	0.98**	0.67**	12.42**	15.08**	16.08**	15.9**	105.51**	123.8**	43.2**	35.73**
SCA	10	39.69**	16.87**	$0.05^{n.s}$	0.33**	2.82**	2.45**	1.02**	1.7**	4.76**	5.62**	10.1**	10.32**
Error	28	0.012	0.83	0.023	0.001	0.14	0.19	0.0053	0.18	0.068	0.88	0.32	0.74
Baker ratio		0.88	0.93	0.97	0.80	0.90	0.92	0.97	0.95	0.98	0.98	0.89	0.87

GN: number of grain per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant, * and ** respectively significant at 0.05 and 0.01 probability levels, ns: not significant

The Baker ratios (Baker, 1978) were larger than 0.80 indicating the higher contribution of the additive gene effects in the genetic control of traits (Table 4). The same results were reported in the works conducted on wheat for SL, SN and GY (Anwar *et al.,* 2011; Nazir *et al.,* 2005; Masood and Kronstard, 2000; Mahmood and Chowdhry, 2002; Chowdhry *et al.,* 1999), GN (Joshi *et al.,* 2004; Hassan *et al.,* 2007) and GW (Hassan *et al.,* 2007; Petrovic and Cermin, 1994; Bebyakin and Starichkova, 1992). Additive variances are linked to heritability and efficiently respond to selection for increasing the traits of interest. Some of previous works conducted on wheat indicated that 1000-grain weight was predominantly controlled by additive (Anwar *et al.,* 2011; Li *et al.,* 1991; Singh and Paroda 1988) or non-additive effects (Joshi *et al.,* 2004; Hassan *et al.,* 2007; Nazir *et al.,* 2005).

Environmental sensitivity

The amount of variance due to the interaction of parents and progenies with the effect of location was obtained from the heterogeneity of regression slopes (Fig. 2). For GN, the regression slopes for Darab2 and Chamran were lower than the slopes for other cultivars. Therefore, it can be concluded that these cultivars and their progenies had lower sensitivity to environmental conditions. Regression lines for GW indicated considerable heterogeneity among genotypes and that except Marvdasht, most of cultivars were relatively sensitive to the environmental conditions. This was confirmed by the results of GCA × location interactions for GW (Table 4). The regression lines for TGW indicated that cultivars and their progenies had sensitivity to environmental conditions of two locations. As compared with other cultivars, Darab2 had the lowest slope over two locations indicating grain yield of this cultivar and it′s progenies was less affected by the environmental conditions.

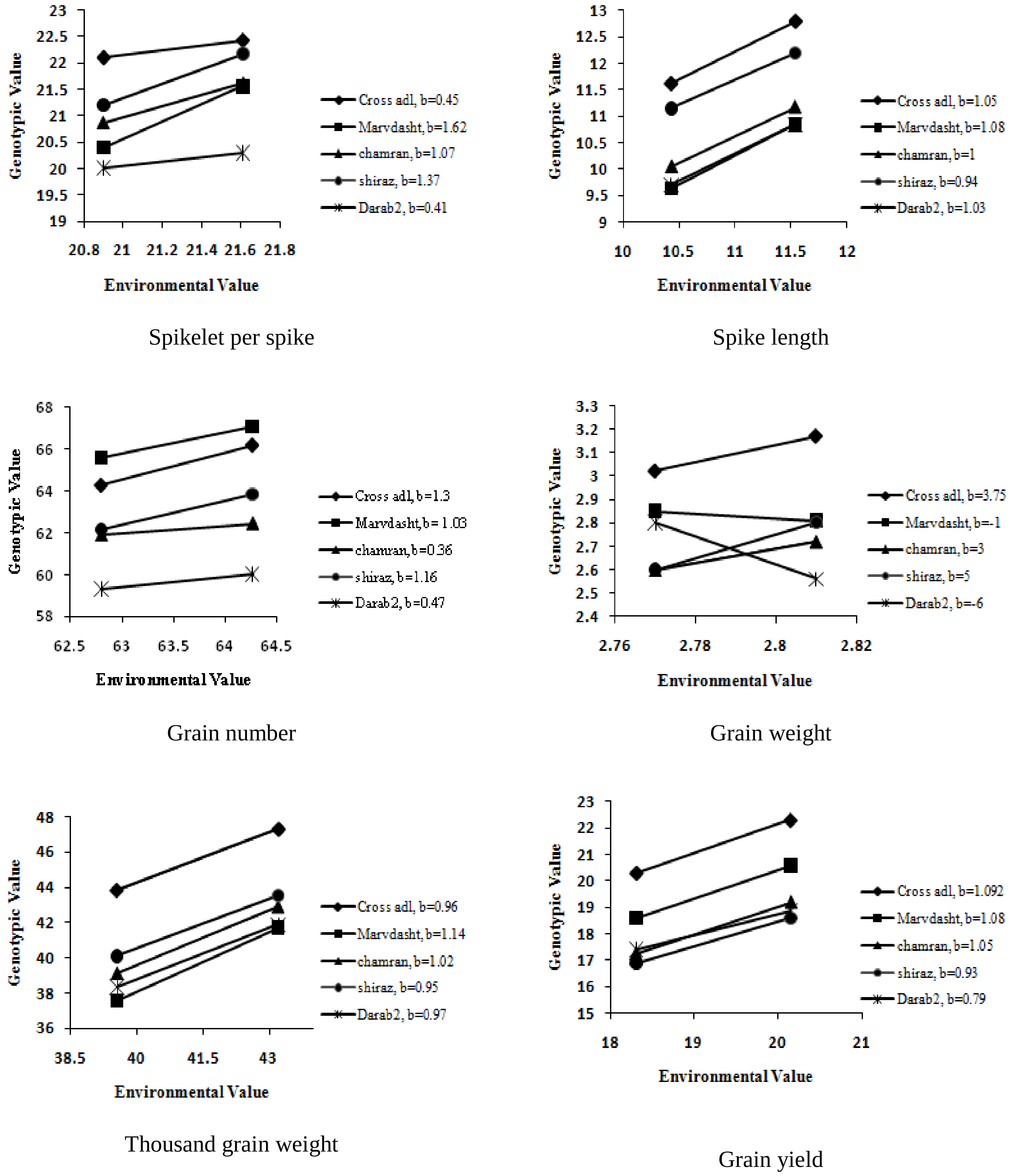


Figure 2. Regression of genotypic effects of parents and their progenies on environmental values in Shiraz and Zarghan experiments.

Correlation analysis

Genetic correlation coefficients are presented in Table 5. GY was significantly correlated with GN (r= 0.66** and 0.72** in Zarghan and Shiraz respectively), while its correlation with GW ($r_{Zarghan}$= 0.76**) was only significant in Zarghan. The correlations of SN and SL were significantly positive ($r_{Zarghan}$= 0.78**, r_{Shiraz}= 0.90**) in both locations.

Table 5. Genetic correlation coefficients among traits in wheat cultivars and crosses in the locations of Shiraz and Zarghan

	GW(g)		SN		SL(cm)		TGW(g)		GY(g)	
Trait	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
GN	0.82**	0.30	0.61**	0.43	0.33	0.24	0.21	0.26	0.66**	0.72**
GW(g)			0.9**	0.15	0.89**	-0.04	0.92**	0.34	0.76**	0.26
SN					0.78**	0.90**	0.66**	0.94**	0.33	0.40
SL(cm)							0.88**	0.90**	0.38	0.46
TGW(g)									0.42	0.46

GN: number of grain per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant, * and ** respectively significant at 0.05 and 0.01 probability levels

Correlation (r) coefficients indicated that r (MP and SCA) was not significant for all traits (Table 6). This shows that there was no significant relationship between mean of each pair of parents and their specific combining ability and that mid-parent values could not be predicted via the SCA effects. r (MP and F_2) was significant for GW (r= 0.83** at Zarghan), TGW (r= 0.98** and 0.92** at Zarghan and Shiraz respectively) and GY (r= 0.61** at Zarghan), showing that parents with higher performance had higher F_2 means for the trait of interest in a specific cross.

Table 6. Correlation coefficients among F_2 means, mid-parent (MP) and specific combining ability (SCA) effects in two locations of Shiraz and Zarghan

	GN		GW(g)		SN		SL(cm)		TGW(g)		GY(g)	
	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
r (F_2, MP)	0.45	0.58	0.83**	0.22	0.40	0.58	0.81**	0.78**	0.98**	0.92**	0.61*	0.52
r (F_2, SCA)	0.52	0.28	0.68*	0.75**	0.74**	0.66	0.42	0.58	0.47	0.42	0.24	0.36
r (MP, SCA)	-0.24	-0.34	0.17	-0.27	0.04	-0.11	-0.08	0.02	0.39	0.21	-0.54	-0.52

GN: number of grain per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant, * and ** respectively significant at 0.05 and 0.01 probability levels

Table 7. The general (GCA) and specific (SCA) combining abilities effects of wheat cultivars and their crosses in the locations of Shiraz and Zarghan.

	GN		GW(g)		SN		SL(cm)		TGW(g)		GY(g)	
Cultivar/Cross	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
Cross adl (1)	2.22**	1.86**	0.35**	0.25**	0.92**	1.33**	1.27**	1.18**	3.8**	4.07**	2.07**	1.95**
Marvdasht (2)	2.95**	2.76**	-0.007	0.027*	-0.158	-0.58*	-0.67**	-0.7**	-1.65**	-2.14**	0.86**	0.69*
Chamran (3)	-0.76**	-0.24	-0.065	-0.13**	0.108	-0.032	-0.33**	-0.38*	-0.57**	-0.55	-0.51*	-0.56
Shiraz (4)	-0.83**	-1.04*	-0.039	-0.21**	0.3*	0.15	0.52**	0.64**	0.04	0.08	1.18**	-1.15*
Darab2 (5)	-3.58**	-3.3**	-0.24**	0.064**	-1.2**	-0.9**	-0.78**	-0.8**	-1.62**	-1.46**	-1.24**	0.93*
1×2	-0.47**	-0.29	0.003	0.16**	0.06	-0.66	-0.7**	-1.03*	0.62*	-0.176	-0.37	0.22
1×3	-1.79**	-2.07*	-0.01	0.03	-0.27	0.42	0.34**	0.88*	0.84*	1.48	-0.56	-1.13
1×4	-1.35**	-1.70*	0.04	0.36**	0.17	-0.64	0.065	-0.44	1.45**	0.167	-1.08*	-1.74*
1×5	2.10**	2.16*	-0.03	-0.54**	-0.5	0.23	0.22*	0.66	-1.3**	-0.46	2.39**	2.75*
2×3	-0.93**	-0.99	0.008	0.26**	-1.03*	-0.97*	-0.54**	-0.8*	0.015	-0.65	-2.39**	-2.09*
2×4	3.24**	3.37*	0.043	0.09*	1.32*	1.38*	0.097	0.27	-0.31	1.35	-0.52	-0.66
2×5	-2.48**	-1.93*	-0.046	-0.27**	0.14	0.68	0.99**	1.03*	0.46	0.13	1.12*	0.48
3×4	-0.69**	-0.51	0.04	-0.45**	1.18*	1.09*	0.55**	0.93*	-1.06**	1.24	-0.85	-0.65
3×5	-1.85**	0.45	-0.14	-0.046	-0.36	-0.59	-0.53**	-0.93*	-0.68*	-1.38	1.51*	1.36
4×5	0.89**	0.84	0.048	0.18**	-1.35*	-1.09*	-0.07	-0.36	-0.73*	-0.52	0.51	1.56*
SEg_i	0.036	0.31	0.052	0.01	0.127	0.146	0.025	0.143	0.088	0.32	0.192	0.29
SEs_{ij}	0.094	0.8	0.13	0.028	0.33	0.376	0.064	0.37	0.23	0.82	0.496	0.75

GN: number of grains per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant, * and ** respectively significant at 0.05 and 0.01 probability levels, SEg_i and SEs_{ij} denote for standard error for general and specific combining ability effects respectively

Combining abilities

The GCA effects revealed that Cross adl and Marvdasht were the best combiners that increased GY in both locations (Table 7). Cross adl and Shiraz with significantly positive GCA effects increased SN and SL in F_2 entries. Among cultivars, Cross adl was a significant combiner for all traits, while Chamran and Darab2 had negative GCA for most of traits. The GCA effects are related to the frequency of favorable alleles in a genotype, therefore, cultivars with positive GCAs increase selection efficiency in breeding programs (Gardner and Eberhart 1966). Cross adl, Marvdasht and Shiraz with positive GCA could be used in hybridization programs in order to accelerate the pace of genetic improvement of wheat grain yield.

Almost similar results were observed for the specific combining ability in both environments. The SCA of diallel crosses revealed that Cross adl × Darab2 for GN, GY and SL, Marvdasht × Shiraz for GN and SN, Chamran × Shiraz for SN and SL, the crosses Cross adl × Chamran, Marvdasht × Darab2 and Chamran × Shiraz for SL, Cross adl × Shiraz for GW and TGW were the best specific combiners. In self-pollinated crops such as wheat, crosses with high SCA effects are useful genetic materials for the selection of superior recombinants segregated in their progenies (Table 7).

Graphical analysis and genetic parameters

Diallel assumptions underlying the genetic model for analysis of diallel crosses were adequate for SN, SL, TGW and GY in both locations and for GN in Shiraz location. Assumptions for GW in Shiraz were not adequate; therefore, removing one of cultivars that biased the genetic model aided the assumptions to be fulfilled. For GN and GW in Zarghan, even eliminating parents or data transformation was not sufficient for the adequacy of assumptions and consequently the analysis of Hayman (1954 a, b) and Jinks (1954) model was not performed for these traits.

The H_1-H_2 parameter indicated the unequal distribution of dominant and recessive alleles for all traits in parents, a result that was strengthened by the $H_2/4H_1$ ratio that was lower than 0.25 under both locations (Table 8). The negative F value and small $[(4DH_1)^{1/2} + F/ (4DH_1)^{1/2} – F]$ ratio indicated the predominance of recessive alleles in genetic control of SL in Shiraz and TGW in both locations. For other traits, the positive F values in both locations implied the higher frequency of dominant alleles. The correlation of (Wr + Vr) and Yr showed the increasing effects of dominant alleles on GN, GW and GY, but recessive alleles increased SL, SN and TGW.

The Wr/Vr graph showed that the interceptions of all regression lines were positive that was an indication for the incomplete or partial dominance gene action (Fig. 3). This result was confirmed by dominance ratio $(H_1/D)^{0.5}$ that was less than 1 (Table 8). Similar results indicated that partial dominance was responsible for SL and SN (Hussain *et al.,* 2012; Gurmani *et al.,* 2007; Ullah *et al.,* 2010; Malik *et al.,* 2005), GN (Ojaghi and Akhundova, 2010; Nazeer *et al.,* 2011; Farooq *et al.,* 2010), GW (Nazeer *et al.,* 2011) and TGW (Hakizimana *et al.,* 2004; Farooq *et al.,* 2010). Grain yield has been reported to be controlled by additive (Ullah *et al.,* 2010; Hakizimana *et al.,* 2004; Farooq *et al.,* 2010) or over dominance effects (Hussain *et al.,* 2012; Ojaghi and Akhundova, 2010; Nazeer *et al.,* 2011).

Table 8. Estimated genetic parameters for the traits in wheat diallel crosses evaluated in two locations of Shiraz and Zarghan

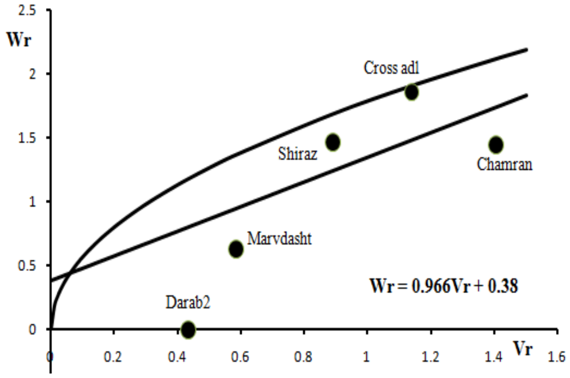
Parameters	GN	GW (g)	SN		SL		TGW (g)		GY (g)	
	Shiraz	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz	Zarghan	Shiraz
D	28.5	0.236	2.43	3.86	3.12	2.44	18.23	22.3	6.73	5.80
H_1	22.73	0.63	4.02	3.02	1.44	1.88	4.18	3.92	11.97	11.60
H_2	15.83	0.54	2.68	2.58	1.17	1.76	4.03	3.71	9.24	9.15
F	12.67	0.15	1.14	1.82	0.282	-0.599	-2.45	-1.038	0.084	0.81
h^2	2.42	0.04	-0.074	-0.076	0.099	-0.093	9.79	7.18	8.89	7.49
$(H_1/4D)^{0.5}$	0.45	0.82	0.64	0.44	0.34	0.44	0.24	0.21	0.67	0.71
$\frac{K_D}{K_R}=\frac{\sqrt{4DH_1}+F}{\sqrt{4DH_1}-F}$	1.66	1.48	1.44	1.73	1.14	0.75	0.75	0.89	1.0	1.10
R (Wr + Vr), Yr	-1.72	-0.2	0.064	0.178	0.32	0.114	3.14	2.77	-3.01	-2.80
$H_2/4H_1$	0.17	0.21	0.17	0.21	0.2	0.23	0.24	0.24	0.19	0.20
H_1- H_2	6.90	0.09	1.34	0.44	0.27	0.12	0.15	0.203	2.73	2.45
h^2_b	0.93	0.99	0.9	0.89	0.99	0.89	0.99	0.93	0.93	0.84
h^2_n	0.86	0.73	0.78	0.81	0.95	0.83	0.96	0.91	0.80	0.71

D:additive effect, H_1 and H_2: dominance effects, F: frequency of dominant to recessive alleles in parents, h^2: overall dominance effect due to heterozygous loci, $(H_1/4D)^{0.5}$: average degree of dominance, $[(4DH1)^{1/2} + F/(4DH1)^{1/2} – F]$: proportion of dominant and recessive genes in the parents, $4h^2/H_2$: number of effective factors (genes), $H_2/4H_1$: proportion of genes with positive and/or negative effects in the parents, h^2_b : broad - sense heritability, h^2_n : narrow- sense heritability, GN: number of grain per spike, GW: grain weight per spike, SN: number of spikelet per spike, SL: spike length, TGW: thousand grain weight, GY: grain yield per plant

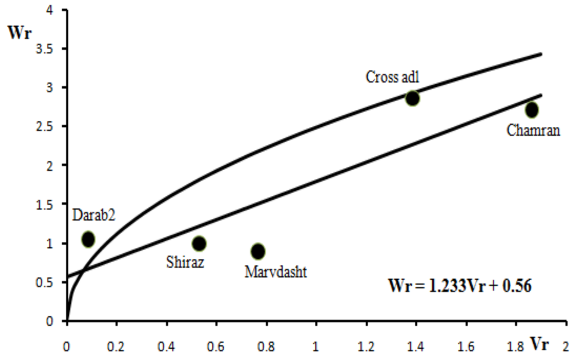
*: Assumptions for Hayman (1954a, 1954b) and Jinks (1954) models were not valid for GN and GW at Zarghan, therefore, parameters were not estimated

Based on graphical analysis for distribution of the parental lines, the closer cultivar to the interception has higher dominant alleles for a trait; while the farthest has more frequent recessive alleles (Hayman 1954 a, b, Jinks 1954). Our study indicated that Darab2, based on its position on the regression line, had the highest dominant alleles that decreased SN in both locations, while Chamran and Cross adl had the highest frequencies of recessive genes for increasing SN (Fig. 3). Chamran, being relatively the farthest from interception, had higher frequency for recessive alleles that increased SL, SN and TGW in both locations. Distribution of cultivars over the curve indicated higher frequency of dominant alleles with increasing effects for GW in Cross adl and for GY in Marvdasht, Chamran and Cross adl.

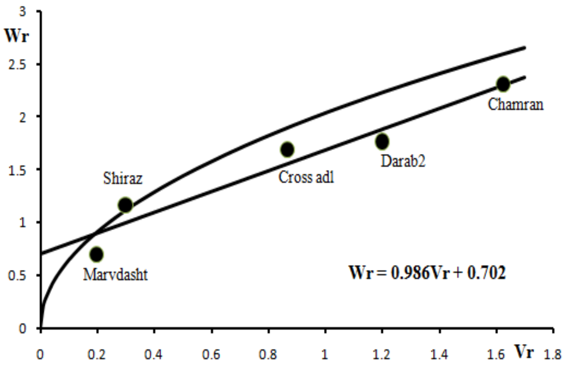
The broad and narrow-sense heritabilities of all traits were relatively high (Table 8). Therefore, strategies based on selection of the best combiners with positive GCA effects would be efficient in breeding programs of interested traits.



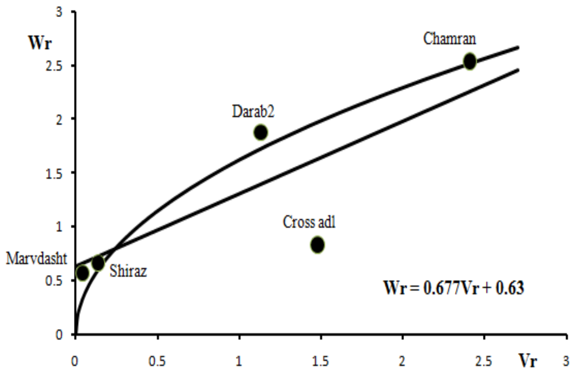
Spikeletes per spike (Zarghan)



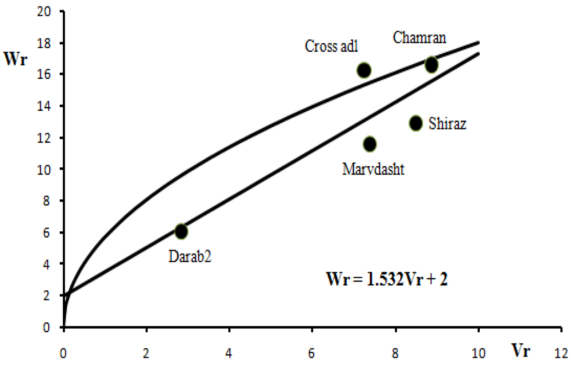
Spiklete per spike (Shiraz region)



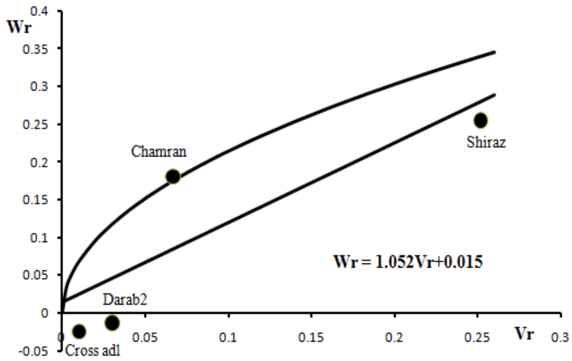
Spike length (Zarghan)



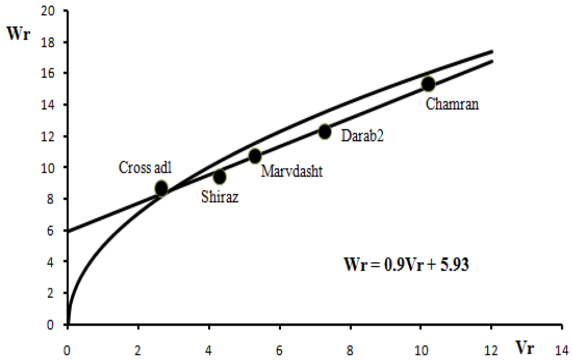
Spike length (Shiraz region)



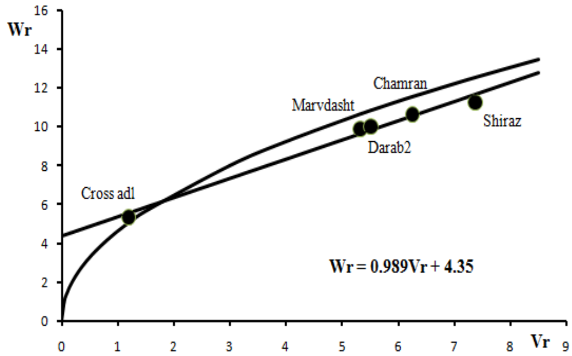
Grain number (Shiraz region)



Grain weight (Shiraz region)



Thousand grain weight (Shiraz region)



Thousand grain weight (Zarghan)

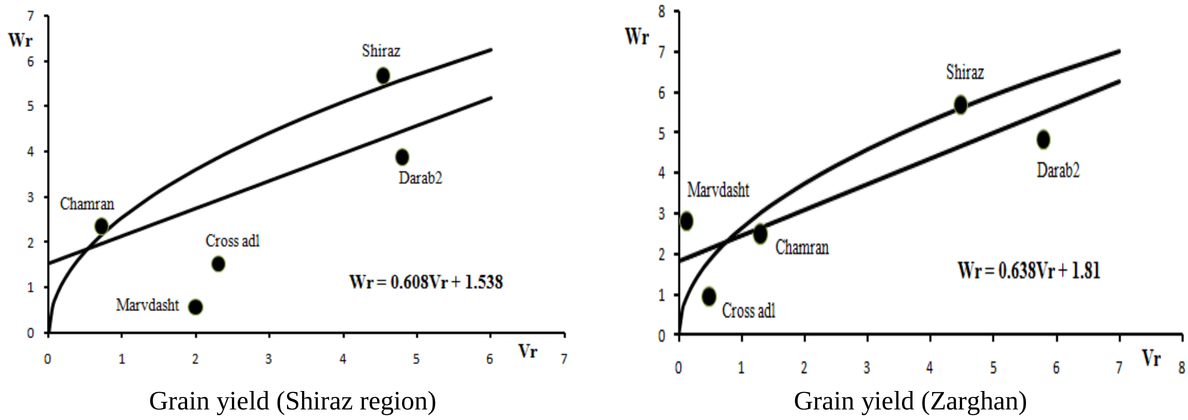


Figure 3. Graphical analysis for distribution of parental cultivars over the regression line in Shiraz and Zarghan locations.

DISCUSSION

Regression analysis showed stronger relations between grain weight and grain number and between grain weigh and yield in Zarghan compared with their relations in Shiraz. Correlation between GW and GN in Zargan was significantly positive although this relation was not significant in Shiraz experiment. This may possibly due to the fact that in Zarghan, plants experienced efficient remobilization and longer grain filling that resulted in grains with larger size, matured and fully developed and also lower immature grains. Analysis for environmental sensitivity indicated that cultivars and their progenies had sensitivity to environmental effects for grain weight. Therefore, it can be concluded that grain filling and/or weight as the most important components of grain yield was highly sensitive to environmental conditions. As a consequence, breeding methods for selection of higher grain weight along with better agronomical attentions at grain filling is necessary for increasing grain weight and grain yield. Analysis of variances for GCA and SCA showed significant effects of environmental conditions on additive and non-additive genetic variances for grain weight and grain yield. For other traits there was no interaction between genetic effects and environment.

The results of both Griffing (1996 a, b) and Hayman and Jinks (1954 a, b) models were in agreement. Griffing results showed that additive (fixable) and non-additive (non-fixable) components of genetic variances were not equally contributed to governing the inheritance of interested traits. Therefore, bi-parental and /or diallel mating design that allow inter-mating the selected plants in different cycles and exploit both the additive and non-additive gene effects could be useful in the genetic improvement of wheat. The Baker ratio indicated that additive effects had higher contribution to genetic variances. The higher importance of additive variances implies that selection of agronomic traits in early generations is preferred and postponing that to advanced generations is not recommended. Rashid *et al.* (2012), using 6 × 6 wheat dialell crosses, indicated that grain yield was controlled by additive gene effects. They also emphasized that selection of genotypes in early generations has higher efficiency in breeding programs. The same results were reported for wheat SL, SN and GY (Anwar *et al*. 2011, Nazir *et al*. 2005, Mahmood and Chowdhry 2002) and GN and GW (Joshi *et al*., 2004; Hassan *et al*., 2007).

The estimated narrow sense heritabilities were relatively high in both locations. Results of Hayman (1954 a, b) and Jinks (1954) model and graphical analysis indicated that gene action for all traits was partial dominance that was confirmed by Griffing (1956) model analysis. Therefore, selection-based strategies that are highly responsive to additive effects increase genetic improvement of grain yield and its components in early generations in a breeding program initiated with a hybridization.

Among cultivars, Cross adl for all traits, Marvdasht for grain yield and grain number, Shiraz for spike number and length had significantly positive GCA effects and therefore were the best combiners that would increase favorable alleles in their progenies. The SCA effects are tightly linked to dominance or non-additive genetic effects. High SCA effects were observed in the progenies of Cross adl × Darab2 for grain number, grain yield and spike length, Marvdasht × Shiraz for grain and spike number, Chamran × Shiraz for spike number and length, Cross adl × Chamran, Marvdasht × Darab2 and Chamran × Shiraz for spike length. Higher contribution of dominance or non-additive effects in cross pollinated plants means that strategies towards hybrid cultivar production would be beneficial. But, in self-pollinated crops such as wheat higher SCA or non-additive effects means that it is possible to select superior plants in the progenies of a cross for a trait of interest.

CONCLUSIONS

Analysis for environmental sensitivity indicated that grain weight as the most important components of grain yield was affected by the effect of location and it was highly sensitive to environmental conditions. As a consequence, breeding methods for selection of higher grain weight along with better agronomical practices at grain filling are necessary for increasing grain weight and grain yield.

Our results indicated that diallel crosses provide comprehensive information about genetic components underlying grain yield and its components in a very short time via F_2 generation. The Baker ratio indicated that selection-based strategies that are highly responsive to additive effects increase genetic improvement of grain yield and its components in early generations in a breeding program initiated with a hybridization. The estimated SCAs revealed that segregated progenies of Cross adl × Darab2 would be valuable for selection of superior plants to be used for breeding of grain number, grain yield and spike length. Among cultivars, Cross adl for all traits, Marvdasht for grain yield and grain number, Shiraz for spike number and length had significantly positive GCA effects and therefore are the best general combiners that would increase favorable alleles in wheat cultivars. In general, the results of both experiments indicated that there are great variations among combining abilities of wheat cultivars for increasing grain yield and its components.

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