Combining Ability of Biological Yield and Harvest Index in Diallel Cross of Wheat Cultivars under Drought and Non-drought Stress Conditions

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Summary

In order to determine the mode of inheritance, genes action, general and specific combining abilities and effect of various environmental conditions on genetic parameters of harvest index and biological yield in bread wheat, diallel crosses design with eight parents was used. Parents and F_1 progenies were sown in a randomized complete block design with three replications under drought stress and non-stress conditions in experimental field of Shahrekord Agricultural Research Center during 2011-2013 growing season. The data were analyzed according to method of Hallauer and Miranda as well as fixed model of Griffing's method II. Jinks-Hayman model was used to estimate broad and narrow-sense heritabilities and mean degree of dominance. There were significant differences between genotypes for mentioned traits in both conditions. Studying mean square of general combining ability (GCA) and specific combining ability (SCA), the ratio of GCA to SCA mean square and portion of additive and dominance variances showed importance of both additive and non-additive genes effects for harvest index in both conditions, but in biological yield heredity, additive effect was more important. Estimating broad-sense and narrow-sense heritabilities showed low efficiency of harvest index and high efficiency of biological yield for selection programs in both conditions.

Key words

bread wheat, diallel crosses, harvest index, biological yield, combining ability, gene effects and heritability

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Introduction

Breeders are usually interested to introduce new varieties for various environments. Crossing new cultivars and selection of superior genotypes in their progenies for desirable traits is one of the methods that is frequently used by breeders. Finding cultivars that have good combining ability with other cultivars is one of the aspects of quantitative genetic. Various methods have been created in order to estimate general and specific combining ability of parents and crosses. Diallel crosses theory and the way of their analysis has been described by many researches (Griffing, 1956 a; Hallauer and Miranda, 1982; Hayman, 1954; Jinks, 1954; Jinks and Hayman, 1953).

Diallel crosses analysis is one of the most important mating design methods to estimate genetic parameters (theoretical aspect of diallel crosses) and combining ability of lines (practical aspect of diallel crosses). Griffing (1956 a,b) expressed analysis of diallel crosses in four various methods including complete diallel with parents, half diallel with parents, complete diallel without parents, and half diallel without parents. He explained every of these methods in four statistical models: randomized, constant, mixed A and mixed B (Griffing, 1956 a,b). Half diallel method (without reciprocal crosses) has the most use because of easiness in conduct. In Jinks and Hayman method, phenotypic variance is divided to genotype and environmental components and then genotypic variance is divided to additive and dominance components (Jinks and Hayman, 1953). Thus, lots of information could be obtained about genetic nature of evaluating trait. Anyway, before designing every breeding plan, wide knowledge about genetic control nature of evaluating trait is necessary (Kamaluddin *et al*., 2007). Examining various traits in different environmental conditions showed that with changing living environment of plant, changes the way of genes action and therefore estimation of genetic parameters and even combining ability of cultivars and crosses (Dagustu, 2008; Kaya *et al*., 2006).

It is known because of high interaction that usually exists between genotype and environment for most of polygenic traits (Koemel *et al*., 2004; Quarrie *et al*., 1999; Richards, 1996). Golparvar *et al.* (2011) and Chowdhry *et al.* (1999) in a study about some quantitative traits in bread wheat found that the way of gene action and estimation of genetic parameters are very different for all those traits in both stress and non-stress environments and for this reason presented different breeding strategies for improving each of evaluating traits in both environments. Dagustu (2008) and Hassan (2004) also studied genetic of day to heading, grain number in ear, grain yield of ear, thousands grain weight, harvest index and grain yield traits over different environments using diallel crosses analysis (Jinks-Hayman method) so reported changing in genetic parameters in different environments.

The goal of this study was comparing the mode of inheritance, combining ability, gene action as well as genetic control of harvest index and biological yield in bread wheat under drought stress and non-stress conditions.

Materials and methods

In this study, eight winter wheat cultivars entitled: ‘Sardaari’, ‘Zarrin’, ‘Zagros’, ‘Alamoot’, ‘Vee-Nac’, ‘M75-7’, ‘C75-5’ and ‘Sakha-8’ were sown as parents of diallel crosses in research site of Iran Seed and Plant Certification and Registration Institute (November 2011). In 2012 spring, half diallel crosses were done among parents in half diallel method to produce F_1 seeds. Produced seeds were harvested in same summer. In autumn 2012 sterilized seeds of parents (8 parents) and their half diallel crosses (28 crosses), totally 36 treatment, were sown in a randomized complete block design with three replications under both drought stress (rain fed) and non-stress (irrigated) conditions with 25 m distance in experimental field of Shahrekord Agricultural Research Center. Plots had two rows with 20 cm inter rows distance and distances between plants in rows were 5 cm. Ammonium phosphate, 300 kg/ha, was used before planting and 300 kg/ha of urea fertilizer was divided to two parts: 1/3 before planting and 2/3 as top dressing in 2-3 leaves stage. In stress condition only one irrigation was done for seeds germination and plants used saved water of soil (from precipitation), but non-stress condition plots were irrigated also every 10 days in 2013 spring. After maturity, ten normal plants were harvested from each plot.

After plant harvesting and drying them for 48 hours at 60ºC in oven, biological yield was determined. Harvest index was calculated from grain yield to biological yield ratio. Obtained data were analyzed according to the method proposed by Hallauer and Miranda (1982). So, sum square of genotypes (parents and crosses) was divided to three components: parents, crosses and parents versus crosses. Also using method II formulas (half diallel with parents) in Griffing’s fixed model sum of squares of crosses was divided to two components: general combining ability (GCA) and specific combining ability (SCA), and GCA effects for each parent and SCA for each cross were calculated (Griffing, 1956a). In F test, the experimental error was used in genotypes analysis of variance to determine which source of variances was significant.

Calculating of additive and dominance genetic variances and their percentage were also done using sum of squares of GCA and SCA and related formulas (Griffing, 1956a). T-test was used to test the general and specific combining abilities (Griffing, 1956a).

Early test of Jinks-Hayman model was done to estimate broad-sense (H_b) and narrow-sense (H_n) heritabilities and mean degree of dominance $(H_1/D)^{1/2}$ in both conditions as well as for both traits. In cases where early test included that model assumptions were observed, estimation of genetic parameters was done (Jinks and Hayman, 1953). Estimation of genetic parameters and statistical indices were conducted using Diallel and D2 softwares.

Results and Discussion

Non-stress condition

Parents and crosses were significantly different for harvest index (Table 1). Also, mean square of parents versus crosses was highly significant that showed the existence of heterosis for HI in non-stress condition (Hallauer and Miranda, 1982). Significant difference of GCA and SCA mean square (Table 2) as well as non-Significant difference of GCA to SCA mean square ratio, showed importance of both additive and non-additive components in genetic control of HI. On the other hand, belonging more than 79% of genetic variance to dominance variance (Table 3) confirmed higher portion of non-additive effects. Hannachi *et al.*

Table 1. Diallel analysis of variance f for harvest index and biological yield using Hallauer and Miranda method

Source of variations	Degree of freedom	Mean square			
		Non-stress condition		Stress condition	
		Harvest index	Biological yield	Harvest index	Biological yield
Genotypes	35	11.32**	7.28**	22.52**	6.44**
Parents	7	14.85**	13.27**	14.98**	15.50**
Crosses	27	10.80**	5.99**	25.15**	4.32**
Parent *crosses	1	0.65**	0.02	4.03**	0.26
Error	70	0.04	0.28	0.06	0.29
CV (%)		0.55	4.91	0.84	6.75

** - significant at 1% probability level

Table 2. Analysis of variance of combining ability for harvest index and biological yield using fixed model of Grifing's method 2

Source of variances	Degree of freedom	Mean square			
		Non-stress condition		Stress condition	
		Harvest index	Biological yield	Harvest index	Biological yield
GCA	7	20.39**	30.97**	12.94**	28.88*
SCA	28	9.05**	1.35**	24.91**	0.83**
Error	70	0.04	0.28	0.06	0.29
GCA/ SCA		2.25	22.94**	0.52	34.8**

** - significant at 1% probability level

Table 3. Estimation of the portion of dominance and additive variances (Griffing's method), degree of dominance, broad and narrow-sense heritabilities of harvest index and biological yield (Jinks-Hayman model)

Genetic parameters		Non-stress condition		Stress condition	
		Harvest index	Biological yield	Harvest index	Biological yield
Dominance variance	6^{2}_{D}(%)	79.8	15.45	100	16.2
Additive variance	6^{2}_{A}(%)	20.2	84.55	0	83. 8
Degree of dominance	$(H_1/D)^{1/2}$	1.65	0.64	2.76	0.44
Broad-sense heritability	H_b(%)	99.7	96	96.4	95
Narrow-sense heritability	H_n(%)	32	81	12	86

Table 4. Mean[1] of harvest index for 8 parents (above diagonal) and 28 crosses (below diagonal) and their specific combining ability (above diagonal) and general combining ability effects in non-stress condition

	Specific combining ability (SCA)								(GCA)
Parent	Sardaari	Zarrin	Zagros	Alamoot	Vee-Nac	M 75-7	C75-5	Sakha-8	
Sardaari	37.2	0.72**	0.91**	-0.21*	0.08	-4.37**	-0.09	0.14	0.78**
Zarrin	36.13	34.30	0.25*	-0.40**	0.46**	2.74**	-1.59**	-0.68**	0.40**
Zagros	37.23	36.20	35.80	1.13**	-1.35**	0.30**	1.97**	-1.09**	1.31**
Alamoot	34.50	33.93	36.37	32.20	-2.33**	0.45**	1.92**	2.29**	-0.31**
Vee-Nac	35.13	35.13	34.23	31.63	36.40	2.67**	-2.15**	-1.55**	0.04
M 75-7	30.07	36.80	35.27	33.80	36.37	32.80	-0.57**	-0.64**	-0.58**
C75-5	33.60	31.73	36.20	34.53	30.80	31.77	30.80	2.11**	1.32**
Sakha-8	34.83	33.62	34.13	35.90	32.40	32.70	34.70	33.3	-0.32**

[1] - means are not compared in this table; * and ** - significant at 5% and 1% probability levels, respectively

(2013) and Kamaluddin *et al.* (2007) emphasize higher portion of non-additive gene effects in genetic control of harvest index in non-stress conditions.

'Zagros', 'Sardaari' and 'Zarrin' parents had the most positive significant GCA effects, respectively (Table 4). Then increasing in portion of additive gene effects in progenies of these parent's crosses as well as in genetic efficiency of selection is expectable. Crosses of these three parents also had positive and significant SCA effects (Table 4) that is another reason for efficiency of selection among progenies of these crosses. Mean degree of dominance (Table 3) showed that harvest index was affected by over dominance gene effects in non-stress condition. In these circumstances, non-additive gene effects have higher portion than additive effects that is in agreement with the results given

Table 5. Mean[1] of biological yield for 8 parents (above diagonal) and 28 crosses (below diagonal) and their specific combining ability (above diagonal) and general combining ability effects in non-stress condition

	Specific combining ability (SCA)								(GCA)
Parent	Sardaari	Zarrin	Zagros	Alamoot	Vee-Nac	M 75-7	C75-5	Sakha-8	
Sardaari	8.40	0.16	0.41	0.18	0.22	-0.04	-0.01	0.20	-1.01**
Zarrin	8.45	7.88	0.11	0.15	-0.35	0.12	-0.55	0.30	-1.46**
Zagros	10.14	9.40	11.20	0.20	0.34	0.46	-1.28**	-0.79**	-0.02
Alamoot	9.95	9.47	10.56	11.14	0.36	0.24	-1.77**	0.36	0.01
Vee-Nac	9.21	8.64	10.77	10.82	9.23	0.13	1.11**	0.43	-0.32**
M 75-7	11.30	11.02	12.80	12.61	12.16	13.53	1.06**	-1.13**	1.59**
C75-5	9.75	8.77	9.47	9.02	11.56	13.42	11.31	0.36	0
Sakha-8	11.16	10.81	11.16	12.34	12.08	12.43	12.34	13.3	1.20**

[1] - means are not compared in this table; * and ** - significant at 5% and 1% probability levels, respectively

by Griffing's method. Ahmed *et al.* (2011) and Imanullah *et al.* (2006) also reported the existence of over dominance gene effect for harvest index.

Estimations of broad-sense and narrow-sense heritabilities of this trait (Table 3), high difference of these two estimations and higher portion of non-additive gene effects, expresses that with broad-sense heritability alone, we cannot reason an appropriate breeding strategy to improve a trait. Considering average narrow-sense heritability and high importance of non-additive gene effects in genetic control of harvest index in non-stress condition it is better to postpone selection for improving this trait until advanced breeding generations. For this goal, we emphasize use of 'Zagros', 'Sardaari' and 'Zarrin' cultivars and their progenies. Differences between genotypes (parents and crosses) were highly significant for biological yield (Table 1). Mean square of parents versus crosses was not significant that shows lack of heterosis for this trait (Jinks and Hayman, 1953). Mean squares of GCA and SCA were highly significant that explains importance of both additive and non-additive gene effects on genetic control of biological yield in non-stress condition.

Comparison of GCA sum of squares and mean square of parents versus crosses, signification of GCA to SCA mean square ratio and belonging more than 84% of genetic variance to additive variance (Table 3) shows that portion of additive gene effects in genetic control of biological yield is really higher than non-additive effects. But some researchers emphasized non-additive gene effects as more important component in genetic control of this trait (Dere and Yildirim, 2006; Heydari, 2001).

Cultivars 'M75-5' and 'Sakha-8' were the best general combinators to increase biological yield in non-stress condition (Table 5), however their cross showed significant negative SCA. On the other hand, 'M75-5' * 'C75-5' cross had positive significant SCA. Considering positive GCA of 'M75-7' cultivar and GCA=0 for 'C75-7' it seems that the only way to increase the portion of additive effects and also genetic efficiency of selection is using progenies of this cross and selection among them. Mean degree of dominance (Table 3) denotes partial dominance gene effects for biological yield. In this situation, portion of additive gene effects is higher than non-additive, which is in agreement with results of Griffing's method. Imanullah *et al.* (2006) and Heydari (2001) emphasized existence of over dominance effects for this trait.

Drought stress condition

Analysis of variance showed that there was highly significant difference between genotypes (parents and crosses) for harvest index trait under stress (Table 1). Mean square of parents versus crosses was also significant and that shows heterosis existence for harvest index under stress (Jinks and Hayman, 1953). Signification of GCA and SCA mean squares (Table 2) expresses portion of both additive and non-additive effects in genetic control of this trait. It is inferred that additive gene effects have higher portion here by comparing mean square of GCA and parents versus crosses. But non significant ratio of GCA to SCA mean square and belonging all of genetic variance to dominance variance (Table 3) shows that non-additive gene effects are more important than additive effects in genetic control of harvest index under stress. Golparvar *et al.* (2011), Dere and Yildirim (2006) and Menon and Sharma (1995) emphasized higher portion of non-additive gene effects on harvest index under stress and believed that selection for improving this trait must be delayed until later breeding generations.

Whenever in analysis of variance table of combining ability mean of square of SCA is higher than GCA, amount of additive variance will be negative. This has been reported by many researchers (Golparvar *et al.*, 2011; Pourdad and Sachan, 2002; Dana and Dasgupta, 2001). Roy (2000) announced inappropriate statistical model, inappropriate sampling from population, sampling errors and inappropriate statistical designs as reason of negative estimation of variance components. In this situation, all of genetic variances belonged to dominance variance. Parents Sakha8, Sardaari and Zarrin had the highest significant and positive GCA effects, respectively (Table 6). Then considering high means of these cultivars and their GCA effects for harvest index under stress, selection from progenies of these cultivars crosses, not only improves this traits, but also increases contribution of additive gene effects and will increase genetic efficiency of selection. On the other hand, negative significant effect of SCA for crosses of these three parents shows that selection among progenies of these crosses may have ambiguous and unpredictable results. In this regard, we can only emphasize on 'Sakha-8' * 'Zagros' and 'Sardaari' * 'Zagros' crosses. Mean degree of dominance (Table 3) shows that harvest index under stress is affected by over dominance effects of genes. In this situation portion of non-additive gene effects will be higher than

Table 6. Mean[1] of harvest index for 8 parents (above diagonal) and 28 crosses (below diagonal) and their specific combining ability (above diagonal) and general combining ability effects under stress condition

	Specific combining ability (SCA)								(GCA)
Parent	Sardaari	Zarrin	Zagros	Alamoot	Vee-Nac	M 75-7	C75-5	Sakha-8	
Sardaari	31.37	-0.75**	1.82**	3.30**	-0.78**	-1.62**	-4.05**	-1.88**	0.74**
Zarrin	28.40	27.37	-0.12	1.46**	2.38**	3.80**	-1.59**	-2.06**	0.52**
Zagros	30.43	28.27	28.27	1.07**	0.25	-1.09**	-3.15**	0.35**	-0.13**
Alamoot	31.20	29.13	28.20	29.30	-4.89**	-3.72**	-2.10**	-0.86**	-0.73**
Vee-Nac	27.20	30.13	27.47	21.62	26.20	-2.48--	2.67**	3.62**	-0.65**
M 75-7	26.40	31.60	26.17	22.83	24.15	24.27	6.66**	3.24**	-0.61**
C75-5	24.43	26.67	24.57	24.91	29.76	33.79	29.47	-2.17**	-0.15**
Sakha-8	27.67	27.27	29.13	27.22	31.78	31.43	26.49	29.60	0.92**

[1] - means are not compared in this table; * and ** - significant at 5% and 1% probability levels, respectively

Table 7. Mean[1] of biological yield for 8 parents (above diagonal) and 28 crosses (below diagonal) and their specific combining ability (above diagonal) and general combining ability effects under stress condition

	Specific combining ability (SCA)								(GCA)
Parent	Sardaari	Zarrin	Zagros	Alamoot	Vee-Nac	M 75-7	C75-5	Sakha-8	
Sardaari	8.29	0.02	-0.02	0.32	-0.62	0.40	0.14	0	0.21*
Zarrin	7.36	6.41	0.06	-1.48**	0.22	0.43	-0.04	0.54	-0.85**
Zagros	7.11	6.14	5.38	0.58*	0.47	-0.17	0.11	-0.06	-1.05**
Alamoot	10.10	7.25	9.10	11.79	0.23	-0.56	0.01	-0.37	1.59**
Vee-Nac	7.95	7.73	7.77	10.18	9.43	-0.06	-1.26**	-0.37	0.38**
M 75-7	7.94	6.91	6.10	8.36	7.65	6.45	0.36	0.05	-0.65**
C75-5	9.43	8.19	8.14	10.68	8.20	8.79	10.31	0.40	1.10**
Sakha-8	7.44	6.93	6.12	8.45	7.24	6.63	8.74	6.40	-0.74**

[1] - means are not compared in this table; * and ** - significant at 5% and 1% probability levels, respectively

additive effects, which is in agreement with Griffing's method (Griffing, 1956b). Majeed *et el.* (2011), Dagustu (2008) and Dere and Yildirim (2006) also reported existence of over dominance effects for harvest index under stress. Estimation of broad-sense and narrow-sense heritability for this trait (Table 3), high difference between this estimates and higher portion of non-additive effect expresses that selection for improving harvest index doesn't have proper genetic efficiency under stress and specifically in early generations.

Comparing mode of inheritance and gene effects for harvest index in both stress and non-stress conditions shows that with changing in environment genetic parameters of this trait will not change a lot and there is only a little increase in heritability and portion of additive effects in non-stress conditions. The reason can be more interaction between genotype and environment under stress condition. Dere and Yildirim (2006) and Kaya *et al.* (2006) reported similar results. Analysis of variance showed highly significant difference between parents and crosses for biological yield (Table 1). Mean square of parents versus crosses was not significant that expresses that there is no heterosis for this trait (Hallauer and Miranda, 1982). Mean square of GCA and SCA was significant that shows importance of both additive and non-additive effects in genetic control of biological yield under stress (Table 2). Significant GCA/SCA mean square, comparing GCA mean square and parent versus crosses mean square and belonging more than 83% of genetic variance to additive variance (Table 3) shows that portion of additive gene effects is considerably higher than non-additive effects in genetic control of biological yield. Golparvar *et al.* (2011) and Nazeer *et al.* (2004) reported that non-additive gene effects are more important than additive effects in genetic control of biological yield under stress. Parents GCA effects (Table 7) showed that 'Alamoot', 'C75-5' and 'Vee-Nac' cultivars had the best general combining ability for biological yield under stress and then, in progenies of their crosses some genotype can be selected for higher amounts of this trait plus increase in portion of additive gene effects. But considering SCA effects of these parents' crosses, it seems that using these crosses and selection from their progenies can have unfavorable and unpredictable results.

Mean degree of dominance (Table 3) is an explainer of relative dominance effect extent for this trait. In these cause additive effects have more portion than non-additive, which is in agreement with Griffing's method. Imanullah *et al.* (2006) and Heydari (2001) emphasized existence of over dominance for biological yield under stress that is opposite with results of this study. Estimations of broad-sense and narrow-sense heritabilities (Table 3), little difference between them and more importance of additive effects for this trait confirms that selection to improve biological yield under stress has a good genetic efficiency and selection the superior genotypes can be done from early generations. Comparing mode of inheritance, gene effects, combining ability and estimating genetic parameters of biological yield trait in both stress and non-stress conditions showed that genetic parameters of this trait didn't change a lot with changing in environment and just its narrow-sense heritability was higher under stress, whereas contribution of additive effects was less under stress. Hennach *et al.* (2013), Golparvar *et al.* (2011), Joshi *et al.* (2004) and Riaz and Chowdry (2003) in their studies found that genetic parameters were sensitive to changes of environment and this was because of high extent of interaction between environment and genotype, specifically under stress.

Conclusion

Estimations of broad-sense and narrow-sense heritabilities, little difference between these estimates and higher portion of additive gene effect showed that selection for biological yield improving in non-stress conditions is possible from early breeding generations as well as have proper genetic efficiency. For this, using 'M75-5' and 'C75-5' cultivars is highly emphasized. Furthermore, using biological yield as an indirect selection criterion to improve grain yield in drought stress conditions lead to favorable results. Yield heritability is low because of high interaction between genotype and environment especially under stress and in early generations which evaluations were done with no replication designs. Indirect selection via traits that have high heritability and also have high genetic correlation with grain yield can be advisable breeding strategy. Therefore, in early generations of breeding programs, genetic efficiency of indirect selection is much higher than direct selection for yield.

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