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Impact of Environment on the Combining Ability of Bread Wheat Genotypes

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Abstract: To determine the impact of environment on the combining ability of bread wheat eight genotypes were crossed in a diallel fashion and the resulting material was grown under irrigated as well as drought stress conditions. Data collected on yield and related traits revealed highly significant differences among genotypes under both sowing conditions. Combining ability analysis revealed that GCA mean squares were significant for flag leaf area, plant height, grains per spike and 1000-grains weight under irrigated condition while GCA mean squares were significant for flag leaf area, plant height, tillers per plant and 1000-grains weight under drought stress condition. Mean squares due to SCA were highly significant for all the traits under both sowing conditions. It was revealed that additive effects were more important than the dominant for almost all the characters under both sowing conditions which indicated the importance of additive variation for the inheritance of these characters. The presence of both additive and non-additive variability suggested the utilization of certain genotypes and crosses to evolve new wheat genotypes for irrigated as well as drought environments e.g., parental genotypes like Parula, MH.97 and 87094 and specific crosses like 85205 H MH.97, Parula H MH.97, Parula H 87094, Crow H MH.97 and Chak.97 H Kohis.97.

Key words: Environment, combining ability, GCA, SCA, drought stress, variance, diallel, wheat

Introduction

Modification of the plant's internal environment, through breeding varieties particularly suited to specific locations, is likely to produce significant results by way of enhanced acre yields. Breeding wheat for such specific needs requires the evaluation of genotypes for their combining behaviour so that potential genotypes with good general and specific combining abilities (GCA and SCA) may be identified. The genetic architecture of character control in this respect is of prime importance. Scientists working at various parts of the globe have presented important results in this regard. Significant mean squares due to both GCA and SCA were recorded for flag leaf area (Prabhu and Sharma, 1987), plant height, tiller number, 1000-grains weight and grain yield (Asad *et al.*, 1992; Borghi and Perenzin, 1994). Similarly significant mean squares due to SCA for flag leaf area (Chaudhry *et al.*, 1994; Ali and Khan, 1998), plant height, 1000-grains weight (Li *et al.*, 1991; Chaudhry *et al.*, 1994), grains per spike (Asad *et al.*, 1992; Ali and Khan, 1998; Senapati *et al.*, 2000) and grain yield (Chaudhry *et al.*, 1994; Ali and Khan, 1998; Senapati *et al.*, 2000) have also been reported. Khan and Bajwa (1990) observed greater GCA variance for grains per spike and 1000-grains weight. Similarly additive genetic control for flag leaf area (Prabhu and Sharma, 1987; Ali and Khan, 1998; Mahmood and Chowdhry, 2000), plant height (Wagoire, 1998; Li *et al.*, 1991), tiller number (Mishra *et al.*,1994; Ali and Khan, 1998), grains per spike (Li *et al.*, 1991; Asad *et al.*, 1992; Mishra *et al.*, 1994; Ali and Khan, 1998), 1000-grains weight (Li *et al.*, 1991; Mishra *et al.*, 1994; Ali and Khan, 1998) and grain yield per plant (Asad *et al.*, 1992; Ali and Khan, 1998; Wagoire, 1998) was also reported. However, Senapati *et al.* (1994) observed non-additive genetic effects for tiller number, grains per spike and 1000-grains weight. Sangwan and Chaudhry (1999) indicated the importance of both additive and non-additive genetic effects for tiller number, grains per spike and grain yield per plant.

This study was planned to ascertain the effects of different environments on the various economic characters reflecting yield potential by making a comparative assessment of their performance under irrigated and drought stress conditions, in terms of combining abilities of some bread wheat genotypes.

Materials and Methods

The studies were conducted in the research area of the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, during the crop seasons 1998-99 and 1999-2000. Eight bread wheat genotypes viz., Parula, Crow, 87094, 85205, Chakwal 97 (Chak.97), Kohistan 97 (Kohis.97), Punjab 96 (Pb.96) and MH.97 were crossed in a diallel fashion (8 x8 full diallel) during the crop season 1998-99.

During the next crop season (1999-2000) two experiments; one under irrigated conditions and second under drought conditions were planted on November 15, 1999. Each of the experiment was laid out in a triplicated randomized complete block design. All of the F_1s (56) along with the parents were sown in rows of 30 cm apart. All agronomic treatments i.e., hoeing, weeding, fertilization, etc. were practiced uniformly, except irrigation which was applied only to experiment sown under irrigated conditions. Data for flag leaf area, plant height, tillers per plant, grains per spike, 1000-grains weight and grain yield per plant were collected and subjected to basic analysis of variance (Steel and Torrie, 1984). Combining ability analysis was conducted according to Griffing (1956) using method I model II i.e., including the parents, direct as well as reciprocals crosses.

Results and Discussion

After obtaining significant differences among genotypes for all the traits combining ability analysis was conducted. Total variation among the genotypes was partitioned into variation due to general and specific combining ability and reciprocal effects. Estimates of variance due to GCA ($\acute{o}^2_g$), SCA ($\acute{o}^2_s$) and reciprocal effects ($\acute{o}^2_r$) were also calculated.

Flag leaf area: Highly significant and greater mean squares due to GCA for flag leaf area (Table 1) under both sowing conditions were recorded. Mean squares due to SCA were also highly significant but smaller. Variation due to reciprocal effects was also found highly significant. Significant mean squares due to GCA were also reported by Chaudhry *et al.* (1994) and Ali and Khan (1998) while Prabhu and Sharma (1987) reported significant mean squares due to both GCA and SCA.

Computation of variation components (Table 2) also indicated the preponderance of non-additive effects for flag leaf area under both sowing conditions. Similarly a low GCA/SCA ratio also depicted importance of non-additive effects for the trait under study.

Flag leaf area is the most important yield contributing trait and positive combining ability effects for this trait are desirable. In case of irrigated condition (Table 3) three genotypes displayed maximum GCA effects being maximum (5.229) in Chak.97 followed by Pb.96 (3.506) and Parula (2.440). These genotypes were thus, considered the best general combiners while rest of the five parental genotypes with undesirable negative GCA effects were thought to be poor general combiners for flag leaf area (Table 3). In case of hybrids 12 cross combinations displayed positive SCA effects. The best specific combination for flag leaf area was Chak.97 x Kohis.97 (7.095) followed by 87094 x MH.97 (6.476) and 85205 x MH.97 (4.533). Negative SCA effects were maximum (-4.684) in Parula x 87094 hybrid. The cross between 85205 and Parula displayed the highest positive reciprocal effects.

Table 1: Analysis of variance for studied traits in an 8 x 8 diallel cross of wheat

		Mean squares*			
Characters	Condition	GCA	SCA	Reci	Error
Flag leaf area	I	167.67**	19.30**	17.36**	1.38
	D	19.29**	4.13**	2.59**	0.49
Plant height	I	200.60**	11.04**	9.28**	1.56
	D	46.53**	9.54**	1.83	1.90
Tillers per plant	I	1.25	0.92**	0.27	0.18
	D	1.78*	0.63**	0.12*	0.07
Grains per spike	I	59.73**	10.75**	18.08**	2.77
	D	35.22	15.22**	6.70**	1.95
1000-grains weight	I	91.97**	15.48**	0.67*	0.41
	D	30.80**	2.43**	1.66**	0.57
Grain yield per plant	I	12.98	9.27**	0.55	0.63
	D	2.32	1.48**	0.82**	0.21

* $P \leq 0.05$, ** $P \leq 0.01$, I = Irrigated condition, D = Drought condition, Rep = Replication, GCA = General combining ability, SCA = Specific combining ability, Reci = Reciprocal effects

* DF for replication, genotypes, GCA, SCA, reciprocal effects and error mean squares is 2, 63, 7, 28, 28 and 126 respectively

Table 2: Components of variation for general (σ^2_g) and specific (σ^2_s) combining ability, reciprocal effects (σ^2_r), error (σ^2_e) and GCA/SCA ratios in an 8 x 8 diallel cross of wheat

Characters	Condition	σ^2_g	σ^2_s	σ^2_r	σ^2_e	GCA/SCA ratio
Flag leaf area	I	9.29	10.06	7.99	1.38	0.92
		(33.97)	(36.80)	(29.22)		
	D	0.95	2.04	1.05	0.49	0.47
		(23.51)	(50.50)	(25.99)		
Plant height	I	11.86	5.32	3.86	1.56	2.23
		(56.31)	(25.28)	(18.35)		
	D	2.32	4.29	-0.04*	1.90	0.54
		(35.10)	(64.90)			
Tillers per plant	I	0.02	0.41	0.05	0.18	0.05
		(4.17)	(85.42)	(10.42)		
	D	0.07	0.31	0.02	0.08	0.23
		(17.50)	(77.50)	(5.00)		
Grains per spike	I	3.07	4.48	7.66	2.77	0.69
		(20.18)	(29.45)	(50.36)		
	D	1.26	7.45	2.37	1.95	0.17
		(11.37)	(67.24)	(21.30)		
1000-grains weight	I	4.80	8.46	0.13	0.41	0.57
		(35.85)	(63.18)	(0.97)		
	D	1.78	1.04	0.54	0.57	1.71
		(52.98)	(30.95)	(16.07)		
Grain yield per plant	I	0.24	4.85	-0.04*	0.63	0.05
		(4.72)	(95.28)			
	D	0.05	0.72	0.31	0.21	0.07
		(4.63)	(66.67)	(28.70)		

(values in parentheses represent percentage of respective variance)

I = irrigated condition and D = drought condition

* Negative estimates for which the most reasonable value is zero (Allard, 1960).

Under drought stress conditions (Table 3) maximum positive GCA effects (1.478) were recorded in the genotype Parula being the best general combiner for flag leaf area, followed by Chak.97 (1.255) and Pb.96 (1.038). Rest of the five parents displayed undesirable negative GCA effects being maximum (-1.234) in the genotype 85205. Number of hybrids showing positive SCA effects were greater (16 out of 28) and maximum figure (2.110) was recorded in the cross 85205 x Kohis.97 followed by Chak.97 x MH.97 (1.476). The hybrid 85205 x Chak.97 showed the highest negative SCA effects. Reciprocal effects were positive and highest (3.033) in the cross 87094 H Parula.

Plant height: Analysis of variance for plant height (Table 1) indicated highly significant and greater mean squares due to GCA than SCA mean squares which, however, were also highly significant under both sowing conditions. Reciprocal effects were found highly significant under irrigated condition but non-significant under drought stress. Highly significant and greater mean squares due to GCA were also reported by Li *et al.* (1991) and Chaudhry *et al.* (1994) while Asad *et al.* (1992) and Borghi and Perenzin (1994) reported significant means squares due to both GCA and SCA. Ali and Khan (1998) also reported significant reciprocal effects for plant height.

Importance of additive genetic effects for plant height was evident due to greater GCA mean squares. These results are in accordance with the findings of Wagoire (1998) and Li *et al.* (1991) who also reported additive genetic effects for plant height.

Variance components depicted that GCA variance was greater than SCA variance under irrigated condition with high GCA/SCA ratio (Table 2). This indicated the importance of additive genetic effects for the inheritance of plant height. However, under drought stress condition, non-additive genetic effects were more important as indicated by high SCA variance and low GCA/SCA ratio.

Although plant height has a positive association with grain yield but excessive plant height will result lodging of the plants and reduction in yield. Therefore, medium tall plants are desirable for wheat crop. Thus, negative combining ability effects are considered useful.

It was depicted (Table 3) that under irrigated condition five parental genotypes displayed negative GCA effects. The genotype Pb.96 with maximum (-3.813) negative GCA effects was the best general combiner for plant height. In contrast the genotype 85205 with maximum positive GCA effects (5.871) was the poorest general combiner for plant height. Out of 28 crosses 18 showed positive and 10 showed negative SCA effects. The best specific combination with maximum negative SCA effects (-3.575) was 85205 x MH.97. Reciprocal effects were negative in 12 crosses being maximum (-3.033) in 85205 x 87094 hybrid.

In case of drought stress condition (Table 3), the best general combiner for plant height with maximum (-2.825) negative GCA effects was the genotype 87094. While 85205 with highest positive GCA effects (2.023) was the poorest general combiner. Out of 28, 18 hybrids showed negative SCA effects and the best specific combination with maximum negative SCA effects (-4.038) was the hybrid Parula x 85205. Maximum negative reciprocal effects (-1.383) were recorded in the hybrid 85205 x Parula.

Tillers per plant: Highly significant mean squares due to SCA (Table 1) were recorded for tillers per plant under irrigated condition while mean squares due to GCA and reciprocal effects were non-significant. Under drought, mean squares due to GCA were significant and greater as compared to highly significant SCA mean squares. Reciprocal effects were also found significant. Significant mean squares due to both GCA and SCA were also reported by Asad *et al.* (1992), Borghi and Perenzin (1994) and Ali and Khan (1998). However, Li *et al.* (1991) found significant mean squares due to only GCA while Senapati *et al.* (2000) found significant means squares due to only SCA.

Variance due to SCA was much higher for tillers per plant as compared to variation due to GCA with a lower GCA/SCA ratio under both sowing conditions (Table 2) indicating the importance of non-additive genetic effects for tiller number per plant. Importance of non-additive genetic effects for tillers per plant was also reported by Li *et al.* (1991) and Senapati *et al.* (1994). However, additive genetic effects for the control of tillers per plant were reported by Mishra *et al.* (1994) and Ali and Khan (1998) while both additive and non-additive genetic effects were reported as important by Sangwan and Chaudhry (1999).

Four of the parental genotypes (Parula, Crow, Chak.97 and MH.97) displayed the positive GCA effects for tillers per plant under irrigated condition (Table 3). The best general combiner was the genotype Crow with highest (0.381) positive GCA effects. Greater number of crossess (16 out of 28) depicted positive SCA effects. The best specific combination with highest (1.173) positive SCA effects was Chak.97 x MH.97. The highest negative SCA effects were recorded in the cross Crow x MH.97. Reciprocal

Table 3: General combining ability (diagonal), specific combining ability (above diagonal) and reciprocal (below diagonal) effects of 8 wheat genotypes and their crosses for the studied traits

	Irrigated condition								Drought stress condition							
Genotypes	Parula	Crow	87094	85205	Chak. 97	Kohis. 97	Pb. 96	MH.97	Parula	Crow	87094	85205	Chak. 97	Kohis. 97	Pb. 96	MH.97
Flag leaf area																
Parula	2.440	-0.033	-4.684	-0.702	-0.109	0.713	2.025	0.053	1.478	-0.152	-0.356	0.211	-0.090	1.158	-0.776	1.285
Crow	3.373	-3.048	2.393	0.990	-0.002	0.100	-3.404	1.625	0.707	-0.414	-0.100	1.352	-0.626	-1.016	0.788	0.336
87094	4.352	-1.812	-1.032	-1.912	-0.777	-0.500	0.931	6.476	3.033	-0.803	-1.083	0.989	-0.379	-1.281	0.304	1.175
85205	6.350	-2.742	-1.978	-2.962	-1.089	-1.327	-0.933	4.533	0.517	1.988	-0.213	-1.234	-1.968	2.110	0.030	1.261
Chak. 97	-1.320	1.723	-2.292	-4.442	5.229	7.095	-1.949	-2.468	-0.280	-0.115	-1.600	-0.067	1.255	0.832	-0.220	1.476
Kohis. 97	3.365	-0.645	0.285	5.333	-0.017	-2.295	-2.724	-1.726	0.432	0.152	-1.518	-1.012	-0.478	-0.209	0.763	0.881
Pb. 96	0.378	1.032	5.033	1.718	-1.993	-5.212	3.506	2.357	0.048	0.097	-0.327	0.845	2.350	1.343	1.038	-0.845
MH.97	3.435	-0.933	1.993	1.073	0.067	2.995	-0.528	-1.839	1.200	-0.112	-0.815	1.293	1.593	0.598	-0.607	-0.831
	S.E(g_i)=	0.076		S.E (s_{ij}) =	0.540	S.E (r_{ij}) =	0.691		S.E(g_i)=	0.027	S.E (s_{ij}) =	0.191		S.E (r_{ij}) =	0.245	
Plant height																
Parula	4.158	1.767	-0.583	2.900	0.667	0.0167	0.750	0.971	-0.324	-0.762	-0.207	-4.038	-0.687	-0.191	-0.253	4.878
Crow	-0.633	-2.929	-1.329	1.354	-0.246	-0.429	-0.529	4.392	0.733	-1.903	-2.011	-0.575	2.959	1.422	-1.274	-1.308
87094	1.933	1.700	-2.879	0.071	-0.796	2.721	-0.479	1.475	0.300	0.317	-2.825	2.372	0.481	-1.690	-1.169	-1.238
85205	2.167	-1.800	-3.033	5.871	2.454	0.104	2.138	-3.575	-1.383	-0.733	-2.575	2.023	-2.384	3.296	2.383	1.781
Chak. 97	2.400	-1.067	-1.033	-1.167	1.604	-1.329	1.171	0.325	-0.933	0.467	-0.200	-0.517	1.955	-0.037	3.084	-0.985
Kohis. 97	-0.200	2.067	3.467	2.600	1.033	-1.013	-1.546	1.875	-0.967	-0.267	-1.100	-0.200	1.600	0.626	1.097	-1.322
Pb. 96	1.867	0.033	2.400	1.833	0.467	-2.267	-3.813	0.708	0.083	-1.650	-1.300	-0.433	-0.867	-0.783	0.572	-1.335
MH.97	4.833	-0.500	-0.367	4.467	2.433	-2.167	-0.067	-1.000	0.850	-0.452	-1.000	0.533	0.300	0.700	0.900	-0.126
	S.E(g_i)=	0.085		S.E (s_{ij}) =	0.609		S.E (r_{ij}) =	0.779	S.E(g_i)=	0.104		S.E (s_{ij}) =	0.944	S.E (r_{ij}) =	0.752	
Tillers per plant																
Parula	0.040	-0.402	0.190	-0.750	0.704	-0.940	0.617	0.275	-0.422	-0.042	-0.457	0.220	0.279	-0.738	-0.007	0.897
Crow	0.033	0.381	-0.352	0.625	0.313	-0.315	0.608	-1.033	-0.300	-0.300	-0.563	-0.069	-0.128	0.989	-0.296	0.508
87094	0.267	-0.200	-0.110	-0.383	-0.829	0.377	0.400	0.325	0.100	0.083	-0.152	0.283	0.008	0.658	0.606	-0.173
85205	-0.083	-0.167	-0.533	-0.388	0.115	-0.546	-0.990	0.702	-0.267	0.133	-0.167	0.038	-0.615	0.602	-0.351	0.137
Chak. 97	-0.050	0.200	0.033	0.033	0.292	0.408	-0.352	1.173	0.233	-0.317	-0.033	-0.400	-0.154	-0.107	0.891	0.629
Kohis. 97	0.000	-0.167	-0.567	-0.100	-0.400	-0.315	0.138	0.129	-0.300	-0.317	-0.167	-0.300	-0.200	0.530	-0.326	-0.488
Pb. 96	0.767	-0.100	0.467	-0.467	-0.017	0.933	-0.104	-0.681	0.333	-0.367	-0.117	-0.183	-0.300	-0.033	0.032	0.010
MH.97	0.733	-0.167	-0.233	0.400	0.017	0.367	0.100	0.204	0.167	-0.367	-0.167	-0.200	0.300	-0.133	-0.267	0.428
	S.E(g_i)=	0.010		S.E (s_{ij}) =	0.070		S.E (r_{ij}) =	0.090	S.E(g_i)=	0.004		S.E (s_{ij}) =	0.029	S.E (r_{ij}) =	0.037	
Grains per spike																
Parula	1.582	0.209	-0.591	1.826	-1.232	-0.974	0.318	2.493	-1.772	0.818	1.980	-0.907	4.980	-3.407	2.214	-0.103
Crow	-0.700	2.224	-0.299	1.851	0.926	-0.582	-2.691	0.318	-1.000	0.170	-0.561	-1.349	-1.962	1.684	0.672	2.689
87094	-0.033	0.033	-0.843	1.051	1.193	2.618	-1.191	1.351	2.100	-0.900	-0.492	3.014	0.368	-3.820	-0.899	2.118
85205	-1.600	4.600	2.533	-0.959	-2.857	0.334	-1.274	-2.632	-0.333	-0.700	-0.800	-1.505	0.380	3.626	0.014	0.130
Chak. 97	-0.133	3.800	4.267	2.433	2.432	6.176	-0.766	-2.424	-0.567	-4.167	-1.633	0.833	1.641	3.747	-4.466	0.818
Kohis. 97	3.367	-0.133	-1.200	0.600	-2.367	-2.793	0.193	-0.399	-0.833	3.600	-1.433	-1.333	-1.600	-1.305	-1.653	-2.937
Pb. 96	1.967	1.533	-1.367	-0.167	2.333	2.467	-1.818	0.659	1.000	-1.400	-2.167	0.333	1.400	2.133	1.574	2.118
MH.97	0.933	1.667	-3.433	-8.333	-1.667	-6.533	-3.900	0.174	-2.000	-2.533	-3.433	-1.833	1.800	-1.300	-0.700	1.691
	S.E(g_i)=	0.152		S.E (s_{ij}) =	1.083		S.E (r_{ij}) =	1.386		S.E(g_i)=	0.107	S.E (s_{ij}) =	0.763	S.E (r_{ij}) =	0.976	
1000-grains weight																
Parula	1.428	-0.110	0.845	-0.356	2.325	-3.862	3.315	3.399	1.058	-0.051	-0.138	0.027	-0.794	0.763	1.275	0.002
Crow	0.325	-3.249	0.689	1.909	-1.230	0.944	-3.455	2.410	-0.247	-2.062	-0.811	0.099	1.757	-0.801	-0.797	0.803
87094	0.353	0.347	2.215	0.254	3.210	1.601	2.275	-6.409	-0.280	1.613	1.476	0.713	-0.865	1.505	1.272	0.944
85205	0.042	0.240	-0.495	3.967	0.169	-0.372	0.652	3.218	-0.135	-0.977	-0.788	1.839	0.174	1.090	0.112	0.474
Chak. 97	0.915	-0.050	-0.023	-0.492	-1.741	2.427	-0.788	-0.312	0.992	-0.495	0.278	-1.507	-1.051	0.002	-0.359	1.665
Kohis. 97	0.918	0.513	-0.027	-0.367	0.588	-1.201	0.055	1.918	-0.345	-1.387	0.657	-1.488	-0.362	0.139	-0.798	-1.195
Pb. 96	-0.253	0.363	-0.170	-0.030	0.775	-0.482	0.162	0.386	-0.272	-0.822	-0.245	-0.138	-0.315	0.442	-0.230	0.034
MH.97	0.052	-0.522	1.250	0.537	0.565	0.532	-1.502	-1.581	-0.007	0.560	2.292	-0.658	1.547	0.683	0.700	-1.169
	S.E(g_i)=	0.022		S.E (s_{ij}) =	0.159		S.E (r_{ij}) =	0.203		S.E(g_i)=	0.031	S.E (s_{ij}) =	0.223	S.E (r_{ij}) =	0.285	
Grain yield per plant																
Parula	0.295	0.178	-1.385	-0.164	-0.137	-0.989	0.716	2.395	-0.134	-0.264	1.119	0.359	-0.958	0.348	-1.168	0.940
Crow	0.167	0.401	0.443	0.897	2.157	2.972	-0.723	-3.328	-0.383	0.637	0.382	0.621	-0.012	0.478	-0.339	0.453
87094	-0.967	-0.567	-0.370	2.351	2.228	1.609	-0.619	-4.007	0.533	-0.433	0.170	-0.545	0.221	-1.156	0.028	-0.264
85205	-0.333	0.367	-0.683	-0.490	-2.818	-1.07	-1.198	4.048	-1.567	0.333	-0.633	-0.636	-0.589	-0.316	0.667	-0.158
Chak. 97	0.333	-0.467	-0.567	0.533	-1.384	2.240	-1.805	-0.409	0.300	-1.583	0.550	0.500	-0.186	1.334	0.517	0.959
Kohis. 97	-0.267	0.200	0.600	-0.200	-1.450	-0.732	0.943	-2.278	0.167	0.400	-0.500	0.400	-0.633	-0.226	0.107	-0.002
Pb. 96	-0.233	-0.233	-0.367	-0.533	0.033	0.367	1.130	3.238	0.167	0.367	0.333	0.233	-0.267	-0.917	0.225	1.215
MH.97	-0.400	-0.417	-0.267	0.133	-0.583	-0.833	0.190	1.150	-0.067	0.550	-0.633	-0.667	-1.033	-0.100	-0.567	0.150
	S.E(g_i)=	0.034		S.E (s_{ij}) =	0.245		S.E (r_{ij}) =	0.314		S.E(g_i)=	0.011	S.E (s_{ij}) =	0.081	S.E (r_{ij}) =	0.104	

effects were positive in 13 crosses while 1 hybrid (Kohis.97 x Parula) showed no reciprocal effects.

Under drought (Table 3) Kohis.97 with highest (0.530) positive GCA effects was the best general combiner for tillers per plant. Four genotypes showed negative GCA effects which were maximum (-0.422) in Parula. Positive SCA effects were depicted in 50% of the crosses. The hybrid Crow x Kohis.97 showing highest (0.989) positive SCA effects was the best specific combination. Positive reciprocal effects were maximum in Pb.96 x Parula hybrid.

Grains per spike: Mean squares due to GCA were highly significant and greater than highly significant SCA mean squares for grains per spike under irrigated condition (Table 1) while mean squares due to GCA were non-significant and those of SCA were highly significant under drought. Mean squares due to reciprocal effects were found highly significant under both sowing conditions. Significant mean squares for GCA for grains per spike were also reported by Asad *et al.* (1992), Ali and Khan (1998) and Senapati *et al.* (2000) while significant means squares due to both GCA and SCA were reported by Borghi and Perenzin (1994). Asad *et al.* (1992), however, reported non-significant differences due to SCA and reciprocal effects for grains per spike.

It was revealed that SCA variance was greater than GCA variance for grains per spike under both sowing condition. (Table 2) which suggested that non-additive genetic effects were involved in the inheritance of grains per spike.

Findings in this study are in accordance with those of Khan and Bajwa (1990) who also reported higher GCA variance for grains per spike while Senapati *et al.* (2000) reported a higher SCA variance with a low GCA/SCA ratio. Present results are also in agreement with Senapati *et al.* (1994) who also reported non-additive genetic effects for grains per spike. However, results of this study differ from Li *et al.* (1991), Asad *et al.* (1992), Mishra *et al.* (1994) and Ali and Khan (1998) who indicated the importance of additive genetic effects for grains per spike. Evidence of both additive and non-additive genetic effects has been reported by Sangwan and Chaudhry (1999).

Under irrigated condition Chak.97 was the best general combiner (Table 3) for grains per spike with maximum positive GCA effects (2.432) followed by Crow (2.224) and Parula (1.582) while Pb.96 showed highest negative GCA effects (-1.818). Highest positive SCA effects (6.176) were recorded in the cross Chak.97 x Kohis.97 while these were negative and highest (-2.857) in the cross 85205 x Chak.97. A total of 15 crosses showed positive reciprocal effects being maximum (4.600) in 85205 x Crow.

Four of the parental genotypes were considered as the good general combiners for grains per spike which showed desirable positive GCA effects under drought (Table 3). These were MH.97 (1.691), Chak.97 (1.641), Pb.96 (1.574) and Crow (0.170). Other 4 genotypes displayed undesirable negative GCA effects. Best cross combinations showing high positive SCA effects were Parula x Chak.97 (4.980), Chak.97 x Kohis.97 (3.747) and 85205 x Kohis.97 (3.626). The hybrid Chak.97 x Pb.96 showed the maximum negative (-4.466) SCA effects. Only 8 crosses showed positive reciprocal effects which were highest (3.600) in Kohis.97 x Crow hybrid.

1000-grain weight: Analysis of variance of combining ability for 1000-grain weight under both sowing conditions (Table 1) revealed highly significant mean squares due to both GCA and SCA. Reciprocal effects were found significant under irrigated conditions but were highly significant under drought. Significant mean squares due to both GCA and SCA for 1000-grains weight were also reported by Asad *et al.* (1992), Borghi and Perenzin (1994) and Ali and Khan (1998) while Li *et al.* (1991) and Chaudhry *et al.* (1994) reported significant mean squares due to GCA.

Components of variation (Table 2) revealed high SCA variance and low GCA/SCA ratio for 1000-grains weight under irrigated conditions indicating the preponderance of non-additive genetic effects for the trait. However, SCA variance was smaller than GCA variance indicating the importance of additive genetic effects for the inheritance of 1000-grains weight under drought. High GCA variance for 1000-grains weight was also reported by Khan and Bajwa (1990). Similarly importance of additive genetic effects for 1000-grains weight was indicated by Li *et al.* (1991), Mishra *et al.* (1994) and Ali and Khan (1998) while Asad *et al.* (1992) and Senapati *et al.* (1994) indicated the importance of non-additive genetic effects for 1000-grains weight.

Under irrigated conditions (Table 3) the genotypes 85205 and 87094 showing high GCA effects (3.967 and 2.215, respectively) were thought to be the best general combiners for 1000-grains weight. The genotype Crow was the poorest general combiner with highest negative GCA effects (-3.249). SCA effects were positive in 19 crosses being maximum (3.399) in Parula x MH.97 followed by 85205 x MH.97 (3.218) and 87094 x Chak.97 (3.210). Reciprocal effects were positive in 16 crosses being maximum (1.250) in the cross MH.97 H 87094.

The same two genotypes (85205 and 87094) which were best general combiners under irrigated conditions, also came out to be the best under drought stress condition (Table 3). Similarly Crow with maximum negative (-2.062) GCA effects was again the poorest general combiner for 1000-grain weight. Eighteen cross combinations displayed positive SCA effects which were highest in Crow x Chak.97 (1.757) followed by Chak.97 x MH.97 (1.665) and 87094 x Kohis.97 (1.505). Maximum positive reciprocal effects (2.292) were recorded in MH.97 x 87094 hybrid.

Grain yield per plant: Highly significant mean squares due to SCA were recorded for grain yield per plant under both sowing conditions (Table 1) while mean squares due to GCA were non-significant. Reciprocal effects were non-significant under irrigated conditions but highly significant under drought. Significant mean squares due to both GCA and SCA for grain yield per plant were also reported by Asad *et al.* (1992) and Borghi and Perenzin (1994) while Chaudhry *et al.* (1994), Ali and Khan (1998) and Senapati *et al.* (2000) reported significant mean squares due only to GCA and Li *et al.* (1991) reported significant mean squares due to only SCA.

Estimation of variance components (Table 3) revealed that SCA variance was much greater than GCA variance for grain yield per plant under both sowing conditions. Similarly GCA/SCA ratio was also low. This suggested the importance of non-additive genetic effects for the inheritance of grain yield per plant under irrigated as well as drought stress conditions. Significant and greater SCA variance for grain yield per plant was also reported by Mishra *et al.* (1994) and Senapati *et al.* (2000), however, significant and greater GCA variance for grain yield was reported by Khan and Bajwa (1990).

Results of this study are also in accordance with the findings of Li *et al.* (1991), Mishra *et al.* (1994) and Sangwan and Chaudhry (1999) who reported non-additive genetic effects for grain yield per plant. However, Asad *et al.* (1992), Ali and Khan (1998) and Wagoire (1998) reported additive genetic effects for grain yield per plant.

Under irrigated conditions (Table 3) 4 of the parents showed positive GCA effects for grain yield per plant. Maximum value (1.150) was indicated in MH.97 followed by Pb.96 (1.130). Parula and Crow displayed positive GCA effects of low magnitude. Highest negative GCA effects (-1.384) were indicated by the genotype Chak.97. Positive SCA effects were recorded in 50% of the crosses which were maximum (4.048) in 85205 x MH.97 hybrid. Highest negative SCA effects (-4.007) were displayed by the cross 87094 x MH.97. Positive reciprocal effects were recorded in only 10 crosses all with low values. However, negative effects were highest (-1.450) in Kohis.97 x Chak.97 hybrid.

The genotype Crow with maximum positive GCA effects (0.637) was the best general combiner for grain yield per plant under drought stress conditions (Table 3). Genotypes showing high negative GCA effects in descending order were 85205, Kohis.97, Chak.97 and Parula. SCA effects were positive in 16 cross combinations. Useful combinations with high positive SCA effects were Chak.97 x Kohis.97, Pb.96 x MH.97 and Parula x 87094 in descending order. Reciprocal effects were positive in 13 crosses.

It became evident that mean squares due to both GCA and SCA were significant for all the traits, with a few exceptions where GCA mean squares were only significant or non-significant, under irrigated as well as drought stress conditions. The relative magnitude of variation due to GCA and SCA indicated the importance of additive effects for all the characters under both sowing conditions, except tillers per plant and grain yield under irrigated condition and grains per spike under drought where importance of dominant genetic effects was indicated.

It was also revealed that additive effects were more important than the dominant for almost all the characters under both sowing conditions which indicated the importance of additive variation for the inheritance of these characters. Thus, it is speculated that certain crosses may produce transgressive segregants in the early generations which could be of great significance.

Greater SCA effects obtained in crosses involving both parents with high GCA (high x high) indicated the possibility of genetic improvement for those particular characters through pedigree selection. For example the cross 87094 x 85205 may produce transgressive recombinants for 1000-grain weight under both sowing conditions and Pb.96 x MH.97 for grains per spike under drought.

Similarly crosses showing high SCA and involving both parents as low general combiner (low x low) for a trait indicated the presence of epistasis or non-allelic interaction at the heterozygous loci. This suggested to utilize these crosses through single plant selections in the later generations. These type of crosses under irrigated condition include Parula x MH.97 for grains per spike and 1000-grain weight; 87094 x MH.97 for flag leaf area; Crow x MH.97 for plant height and 1000-grain weight. Chak.97 x Kohis.97 for 1000-grain weight and grain yield per plant; 87094 x 85205 for grain yield. Under drought this situation was found in 85205 x Kohis.97 for flag leaf area; Parula x MH.97 for plant height, tillers per plant and grain yield per plant; Chak.97 x Pb.96 for tillers per plant and grain yield; 87094 x MH.97 for flag leaf area and grains per spike; 85205 x Pb.96 for grain yield; Chak.97 x MH.97 for 1000-grain weight and grain yield per plant.

Crosses presenting high SCA and involving at least one parent with high GCA (Low x high) indicated the involvement of additive x dominance gene interaction for the expression of that particular trait. This situation under irrigated condition was indicated in Parula x MH.97and Pb.96 x MH.97 for grain yield per plant; Crow x Pb.96 and Chak.97 x MH.97 for tillers per plant; Chak.97 x Kohis.97 for flag leaf area and grains per spike; 85205 x MH.97 for 1000-grain weight and grain yield. This situation under drought was found in crosses like Parula x Pb.96, Chak.97 x Kohis. 97 and Parula x Chak.97 for grains per spike; Crow x Kohis.97 for tillers per plant and grain yield per plant; Parula x 87094 for grain yield per plant.

The presence of both additive and non-additive variability suggested the utilization of certain genotypes and crosses to evolve new wheat genotypes for irrigated as well as drought environments. Use of diallel mating with recurrent selection and integration with pedigree selection will yield new recombinations with accumulation of desirable genes. This can be done by using parental genotypes like Parula, MH.97 and 87094 and specific crosses like 85205 x MH.97, Parula x MH.97, Parula x 87094, Crow x MH.97 and Chak.97 x Kohis.97.

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