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Combining ability analysis for yield and protein content in bread wheat (*Triticum aestivum*)

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ABSTRACT

The experiment was conducted with 10 parents and their 45 F_1s (half diallel) during crop seasons (2008/09 and 2009/10) under normal and heat-stress environment to find out combining ability effects. The analysis of variance showed highly significant differences for all the traits at genotypic level under both normal and heat-stress environment. The significant additive variance (D) and dominance variance (H_1) indicated that, expression of these traits is controlled by both additive and non-additive gene action. Among the parents, there was asymmetrical distribution of positive and negative dominant genes and preponderance of over-dominance gene action for all the traits under both the environment. Estimates of narrow-sense heritability were higher for days to 50% flowering; days to maturity; plant height and spike length. Our results also indicated that only three parents (HD 2285 for grain filling duration and thousand grains weight; PBW 373 for the days to maturity and plant height and UP 2425 for number of tillers and grain yield) had favorable general combining ability (GCA) effects under normal sown environment. While under heat-stress environment, cultivar HD 2285 showed highest GCA effect for days to 50% flowering, grain filling duration and thousand grain weight; HD 2733 for plant height and protein content; and PBW 373 for number of tillers and grain yield. Five cross combinations showed contrasting favorable specific combining ability (SCA) effect for more than one trait under both normal and heat-stress environment. Attempting combinations involving parents with high GCA for desirable yield components could be useful. The traits showing more than 35 percent narrow-sense heritability could be rewarding for further improvement of grain yield and protein content in wheat (*Triticum aestivum* L.).

Key words: Combining ability analysis, Gene action, Grain yield, Protein content, Wheat

Wheat (*Triticum aestivum* L.) is second most important cereal crop after rice in the context to its antiquity and use as a major crop food in India and also at global level. The manifold increase of wheat production in India has mainly been attributed to the development and cultivation of semi dwarf, input responsive and disease resistant varieties. Although, the production of wheat in India has gone up tremendously, hence the productivity enhancement is still an issue. Heat tolerance is an important breeding target under warmer wheat growing areas. Improvement of the wheat yield is possible by knowing the gene action and combining ability of the parents with wider adaptability. The general and specific combining ability effects are very effective genetic parameters in deciding, next phase of the breeding programme. Diallel analysis also provides a unique opportunity to test a number of lines in all possible combinations. In view of this, objective of present study was to identify the best combining parents on the basis of their general and specific combining ability for various traits for further improvement in bread wheat.

MATERIALS AND METHODS

Field experiment was conducted during winter (*Rabi*) seasons of 2008/09 and 2009/10 at the Research Farm of Department of Genetics and Plant Breeding, CCS University, Meerut. For this experiment, 10 bread wheat diverse cultivars (HD 2733, PBW 373, HD 2687, PBW 343, UP 2382, WH 542, PBW 226, UP 2425, HUW 468 and HD 2285) were obtained from DWR, Karnal. Based on the available passport data these cultivars were selected as they differed with respect to parentage and performance for various traits, such as grain yield, grain size, protein content, heat tolerance, plant height, days to maturity, adaptation zone and cultivation condition. Among these, cultivar PBW 343 was used as a standard check variety for the purpose of comparison. The details of these genotypes are given below in Table 1.

Each genotype was planted in two row plot of 2.0 m length spaced at 23 cm apart. Hybridization programme was attempted to obtain a total 45 F_1 cross combinations following half diallel mating design. The complete set of 45

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Table 1 List and passport data of parental lines used for diallel crosses

Genotype	Pedigree/Parentage	Area of adoption	Production condition
HD 2733	ATTILA/3/TUI/CARC//CHEN/CHTO/4/ATTILA	NEPZ	TS, IR
PBW 373	ND/VG9144//KAL/BB/3/YCO“S’/4/VEE#5“S’	NWPZ	LS, IR
HD 2687	CPAN 2009/HD2329	NWPZ	TS, IR
PBW 343	ND/VG9144//KAL/BB/3/YCO“S’/4/VEE##5“S”	NWPZ	TS, IR
UP 2382	CPAN2004/HD2204	UP	LS, IR
WH 542	JUP/BJY“S”//URES	NWPZ	TS, IR
PBW 226	C591/RN//JN/3/CHR/HD1941	NWPZ	LS, IR
UP 2425	HD2320/UP2263	NWPZ	LS, IR
HUW 468	CPAN1962/TONI//LIRA‘S’/RRL‘S’	NEPZ	TS, IR
HD 2285	249/HD2150//HD2186	NWPZ	LS/VLS, IR

NEPZ- North Eastern Plains Zone, NWPZ- North Western Plain Zone, U.P. -Uttar Pradesh, TS-Timely sown, LS-Late sown, VLS-Very late sown and IR-Irrigated.

F_1s along with ten parents was evaluated in a RCBD with three replications over the two year (2008/09 and 2009/10) over two dates of sowing as timely sown (15 November) and late sown (20 December), respectively. The timely sown crop environment was considered as non-stress (normal environment) and late sown crop as the heat-stress environment. The data were pooled for normal (timely sown 2008/09 and 2009/10) and similarly for heat stress environment (late sown-2008/09 and 2009/10) environment, respectively. Data were recorded on days to 50% flowering, plant height, tillers per plant, days to maturity, grain filling duration, spike length, number of grains per spike, grain yield per plant, 1000-grain weight and protein content.

Data recorded on parental line and F_1s for all the traits under study averaged and utilized for statistical analysis by software SAS version 9.2 (SAS Institute, 2008). The data were first subjected to the usual analysis followed by a RCBD (Panse and Sukhatme 1984), then pooled analysis for g × e interaction have been made following Comstock and Robinson (1952a) model. Combining ability analysis was carried out following the model II of method 2 (Parents and one set of F_1’s) for combining ability analysis of Griffing (1956a). The various genetic components were calculated based on the formulae of Hayman (1954 a, b) as demonstrated by Aksel and Johnson (1963).

RESULTS AND DISCUSSION

First of all, the analysis of variance was carried out separately for each of the four environments. It suggested significant differences among treatments for all the traits over the entire four environments. Then, the analysis of variance was carried out involving data of all the four environment together (i.e. ANOVA of pooled data) to examine whether significant differences exist between the data of normal and heat-stress environment and between two years data. There were significant differences between normal and heat-stress environment with respect to all the traits. The differences between two years data for the treatments are non-significant for all the traits invariably. Therefore, the data of two years were pooled to get average. Using the average of the two years data (mean values obtained from two years data), analysis of variance was carried out separately for normal and heat-stress environment. Analysis of variance indicated highly significant differences for all the characters at genotypic level under both normal and heat-stress environment (Table 2).

Diallel analysis was carried out by method described by Mather and Jinks (1982) and genetic parameters by method described by Hayman (1954a). The combining ability analysis was done following method 2- model II of Griffing (1956). Analysis of variance for parents and F_1s indicating significant differences among parents for all the traits invariable. Similarly the differences among hybrids were also significant for all the studying traits. It indicates the presences of diversity among the material under both environment. There were significant differences between parents and F_1s versus parent for all the studying traits under both environment, excepting for the trait- days to maturity and number of tillers in normal environment. It indicates that there was wider genetic variability existing among the studying material. Significant genotypic variation for all the ten traits under normal/heat-stress environment was further partitioned into variation due to GCA and SCA effects. The significance of GCA/SCA variance indicated that both kinds of gene effects are important in controlling the inheritance of all the studied traits. However the GCA/SCA ratio tilted in favor of GCA for all studying traits under both environment, excepting for number of tillers per plant, number of grains per spike and grain yield under heat-stress environment, indicating preponderance of additive gene effects in the genetic control of most of the traits. The number of tillers, number of grains per spike and grain yield was primarily controlled by non-additive component of genetic variance (Table 3).

Similarly to our findings, the estimates of the genetic components of variation as well as ratio of GCA/SCA showed that all the characters were predominantly controlled by additive gene action (Yao *et al*. 2011). Plant height and its components were governed by partial dominance with additive type of gene action (Yao *et al*. 2011). The roles of both additive and non-additive effects were also reported for grain yield and its component character by Sheikh *et al*. (2000) and Singh (2003).

The analysis of variance components indicates that both additive variance (D) and dominance variance (H_1) are significant for all the studying traits in both normal and heat-stress environment, indicating that the expression of all the traits is conditioned by both additive and dominance (non-additive) gene action. However, dominance component (H_1) was more predominant than additive component (D)

Table 2 ANOVA for analysis of variance under normal/heat-stress environments and G × EI for yield and protein content in bread wheat

Source of variation	DF	Environment	Traits									
			Days to 50% heading	Number of tillers/plant	Plant height (cm)	Spike length (cm)	Grain filling duration	Days to maturity	Number of grains/spike	Grain yield/ plant (g)	1000-grain weight (g)	Protein content (%)
Treatments	54	NEY-1	157.14**	21.54**	121.29**	4.23**	127.25**	102.09**	194.66**	35.39**	83.02**	7.11**
		NEY-2	165.03**	16.82**	121.67**	4.32**	135.33**	100.67**	189.49**	34.68**	83.32**	4.31**
		NE(Pooled)	152.63**	18.02**	120.35**	4.32**	87.34**	117.19**	182.99**	31.79**	86.99**	0.21**
		HEY-1	32.31**	20.93**	206.74**	1.61**	30.46**	22.94**	58.19**	26.30**	92.01**	14.25**
		HEY-2	49.19**	17.04**	196.06**	1.62**	30.74**	19.85**	65.15**	24.45**	97.52**	15.13**
		HE(Pooled)	34.89**	18.18**	201.74**	1.63**	31.19**	32.31**	51.15**	22.78**	86.57**	1.08**
Error	108	NEY-1	1.04	1.04	1.49	0.07	1.19	2.28	1.45	0.45	0.45	0.15
		NEY-2	1.55	1.56	1.96	0.06	1.07	1.94	2.59	0.47	0.37	0.20
		NE(Pooled)	0.62	0.72	0.94	0.03	1.34	0.73	0.95	0.27	0.25	0.04
		HEY-1	1.00	1.03	1.43	0.05	1.28	1.86	1.71	0.42	0.40	0.01
		HEY-2	1.14	1.16	1.66	0.06	1.25	1.89	3.18	0.44	0.41	0.01
		HE(Pooled)	0.56	0.59	0.64	0.03	1.56	0.65	1.28	0.21	0.28	0.03
Replication (r)	2	G × EI over 4 environment	1.96^{ns}	0.20^{ns}	3.90^{ns}	0.07^{ns}	1.63^{ns}	1.91^{ns}	1.07^{ns}	0.06^{ns}	0.23^{ns}	2.29**
Locations (l)	1		21238.69**	1657.75**	34430.74**	451.59**	53568.05**	5024.30**	3314.30**	2569.59**	7165.63**	127.82**
Year (y)	1		0.73^{ns}	3.21^{ns}	5.64^{ns}	0.06^{ns}	0.29^{ns}	0.01^{ns}	6.80^{ns}	0.14^{ns}	0.08^{ns}	0.008^{ns}
(l × y)	1		254.69**	2.93^{ns}	3.07^{ns}	0.04^{ns}	2.42^{ns}	5.27^{ns}	10.95**	4.23*	0.02^{ns}	0.002^{ns}
Treatments (t)	54		233.68**	38.08**	416.53**	7.22**	145.03**	138.81**	246.02**	64.08**	185.38**	4.90**
(t × l)	54		141.35**	34.29**	223.66**	4.39**	175.04**	96.86**	248.45**	52.83**	169.17**	2.02**
(t × y)	54		15.53**	1.83**	2.61**	0.07^{ns}	1.51^{ns}	4.86**	6.12**	1.91**	0.67**	0.03^{ns}
(t × l × y)	54		13.12**	2.13**	2.98**	0.08*	2.21**	5.03**	6.90**	1.99**	0.66**	0.030^{ns}
Error (e)	438		1.22	1.99	1.62	0.06	1.19	1.99	2.24	0.45	0.41	0.11

*, ** Significant at 5% and 1% probability level respectively; NS, non-significant; DF, degree of freedom; NEY-1/HEY-1, normal/heat-stress environment of the year 2008/09; NEY-2/HEY-2, normal/heat-stress environment of the year 2009/10 and NE/HE (Pooled), normal/heat-stress environment pooled over the year (2008/09 and 2009/10)

Table 3 Analysis of variance for parents, F_1's and parents vs F_1's and GCA/SCA effect in 10 x 10 diallel set of wheat under normal/heat-stress environment

Source of variation	DF	Traits									
		Days to 50% flowering	Number of tillers/ plant	Plant height (cm)	Spike length (cm)	Grain filling duration	Days to maturity	Number of grains/ spike	Grain yield/ plant (g)	1000-grain weight (g)	Protein content (%)
						Normal environment					
Parents	9	228.54**	21.03**	168.13**	5.59**	41.19**	286.71**	113.38**	23.25**	74.58**	1.62**
F_1's	44	125.85**	17.81**	98.33**	4.02**	96.75**	85.15**	198.06**	30.61**	89.00**	2.19**
P vs F_1's	1	107.48**	0.07	658.99**	6.36**	82.49**	2.68	146.44**	160.95**	110.25**	2.43**
Error	108	0.62	0.72	0.94	0.03	1.34	0.73	0.95	0.27	0.24	0.04
GCA	9	128.79**	11.32**	82.22**	2.66**	51.03**	46.31**	93.42**	17.48**	64.92**	1.43**
SCA	45	35.29**	4.94**	31.69**	1.19**	24.73**	37.63**	54.51**	9.22**	21.81**	0.55**
Error	108	0.20	0.24	0.31	0.01	0.45	0.24	0.32	0.09	0.08	0.01
						Heat-stress environment					
Parents	9	107.71**	35.71**	255.39**	4.13**	14.55**	135.75**	32.68**	18.48**	67.25**	1.31**
F_1's	44	19.58**	14.54**	137.78**	1.13**	28.06**	9.26**	54.61**	23.09**	91.85**	0.99**
P vs F_1's	1	52.82**	20.29**	2533.36**	0.76**	319.09**	116.01**	65.33**	47.96**	28.33**	2.32**
Error	108	0.56	0.59	0.64	0.03	1.06	0.65	1.28	0.21	0.28	0.03
GCA	9	46.59**	4.15**	159.16**	1.05**	19.46**	14.73**	12.56**	4.56**	50.01**	0.72**
SCA	45	4.64**	6.44**	48.87**	0.44**	8.59**	9.98**	17.94**	8.20**	24.63**	0.28**
Error	108	0.19	0.20	0.21	0.01	0.35	0.21	0.43	0.07	0.09	0.01

*, ** Significant at 5% and 1% probability level respectively and DF, degree of freedom

for almost all the traits under study for both normal and heat-stress environment (Table 4). Similar to this analysis of genetic components revealed significant additive (D) and dominant (H) genetic variations for days to heading, productive tillers plant, number of grains spike, 1000-grain weight and grain yield plant under early planting, while under normal planting both additive (D) and dominant (H) genetic components were significant for days to heading, productive tillers plant, grain yield/plant and 1000-grain weight as reported by (Farhad *et al.* 2011). Other authors as Saml *et al.* (2011) reported, additive type of gene action with partial dominance for flag leaf area, stomatal frequency, leaf venation, days to heading and spike density, while for 100-grain weight over dominance type of gene action. Additive type of gene action with partial dominance for days to maturity was as reported by Saml *et al.* (2010).

The additive gene effects for spike length and peduncle length reported by Yucel *et al.* (2009) and Dagustu (2008) respectively. The involvement of additive effects in the inheritance of heading/maturity time in spring wheat was previously reported by Sheikh *et al.* (2000) and Singh *et al.* (2003). Prevalence of additive genetic effects in winter × spring wheat crosses were also suggested by Kant *et al.* (2001).

The proportion of dominant genes $H_2/4H_1$ with positive or negative effects in parents was less than 0.25 for all the traits under both normal and heat-stress environment, indicating asymmetrical distribution of positive and negative dominant genes in parents. Asymmetrical distribution of dominant and recessive alleles in parents was also corroborated by the direction (sign) and degree of F component which was positive and more than zero for all traits under study, indicated dominant alleles are more frequent than recessive alleles under both normal and heat-stress environment (Table 4). When this value is equal to 0.25 then the genes are equally distributed among the parents (Singh and Chaudhary 1985).

The mean degree of dominance $(H_1/D)^{1/2}$ was more than one (with the range of 1.30 to 2.89) for all the traits under study in normal and heat-stress environments, indicating preponderance of over-dominance gene action. The relative proportion of dominant and recessive alleles was more than one (with the range of 1.21 to 4.39) for all the traits in both the environment, indicating the excess of dominant alleles and minority of recessive alleles for all traits under study. The value of h^2 was significant in both environment, showing the presence of overall dominant gene effect under study, excepting for the trait days to maturity and number of tillers per plant. The environment component (E) was significant for six traits and non-significant for other traits. However, its value was much lower than that of D or H_1 component for all studying traits. The traits showing significant of environmental components (E) were: days to 50% flowering, grain filling duration, days to maturity, number of tillers per plant, grain yield per plant, and thousand grains weight. It may be concluded that these traits are under the influence of environmental factors (Table 4). Sharma and Sain (2002) also reported that non-additive types of gene effects are important for number of tillers per plant. Farooq *et al.* (2010) and Hussain *et al.*

Table 4 Estimates of genetic component for yield and protein content in a 10×10 half diallel set of bread wheat under normal/heat-stress environment

Traits	Environments	Genetic component of variation									
		Additive variance (D)	Dominance variance (H_1)	Proportion of +/- genes (H_2)	Mean covariance of additive and dominance effects (F)	Overall dominance Effect (h^2)	Environmental variance (E)	Mean degree of dominance	Proportion of dominant genes with +/- effects	Proportion of dominant and recessive genes	Heritability in narrow-sense (%)
Days to 50% flowering	NE	95.98*± 12.44	161.76*± 26.49	128.08*± 22.51	91.76*± 28.71	14.11*± 15.07	0.20*± 0.15	1.30	0.20	2.17	57
	HE	25.97*± 1.61	60.96*± 3.45	52.64*± 2.91	34.96*± 3.71	6.90*± 1.95	0.19*± 0.17	1.53	0.21	2.56	49
Number of tillers/plant	NE	6.77*± 1.69	21.60*± 3.60	18.04*± 3.06	6.63*± 3.90	-0.08 ^{ns}± 2.05	0.24*± 0.19	1.79	0.21	1.76	29
	HE	11.71*± 2.45	45.94*± 5.21	31.10*± 4.43	12.31*± 5.46	2.61 ^{ns}± 2.96	0.20*± 0.16	1.97	0.17	3.63	25
Plant height (cm)	NE	55.73*± 11.47	102.60*± 24.42	70.03*± 20.76	85.50*± 26.47	86.87*± 13.89	0.31 ^{ns}± 3.46	1.63	0.17	2.02	54
	HE	84.92*± 11.37	167.93*± 24.21	110.50*± 20.57	65.46*± 26.24	103.33*± 13.77	0.21 ^{ns}± 3.43	1.55	0.20	2.32	45
Spike length (cm)	NE	1.86*± 0.45	5.66*± 0.96	4.19*± 0.82	2.38*± 1.04	0.84*± 0.55	0.01 ^{ns}± 0.14	1.75	0.19	2.16	35
	HE	1.37*± 0.22	4.11*± 0.47	2.74*± 0.40	1.89*± 0.51	0.27*± 0.10	0.01^{ns}± 0.07	1.73	0.17	2.32	43
Grain filling duration	NE	13.53*± 8.30	112.59*± 17.66	88.93*± 15.01	15.65*± 19.14	10.73± 10.05	0.45*± 0.30*	2.89	0.20	1.50	12
	HE	4.50*± 3.27	35.79*± 6.96	26.05*± 5.91	5.82^{ns}± 7.54	41.99*± 3.96	0.35*± 0.25	2.82	0.18	1.60	12
Days to maturity	NE	95.33*± 15.93	200.82*± 33.90	124.50*± 28.81	159.55*± 36.75	0.27^{ns}± 19.29	0.24*± 0.21	1.45	0.15	3.72	69
	HE	45.03*± 3.24	57.60*± 6.89	28.02*± 5.86	72.84*± 7.47	15.24*± 3.92	0.21*± 0.17	1.50	0.17	4.39	71
Number of grain/spike	NE	37.48*± 20.56	238.41*± 43.77	203.85*± 37.20	36.48*± 47.45	19.22*± 24.90	0.32^{ns}± 6.20	2.52	0.21	1.48	15
	HE	10.46*± 6.74	79.29*± 14.34	65.29*± 12.19	19.31*± 15.54	8.47*± 8.16	0.43^{ns}± 2.03	2.75	0.21	2.01	14
Grain yield/ plant (g)	NE	7.66*± 3.06	36.92*± 6.51	33.36*± 5.53	5.19^{ns}± 7.06	21.21*± 3.70	0.09*± 0.07	2.20	0.23	1.37	19
	HE	6.09*± 2.56	36.30*± 5.46	29.89*± 4.64	10.86*± 5.92	6.31*± 3.10	0.07*± 0.05	2.44	0.21	2.15	17
1000-grain weight (g)	NE	24.78*± 10.21	89.89*± 21.73	83.45*± 18.47	9.16*± 23.56	14.52*± 12.36	0.08*± 0.05	1.90	0.23	1.21	21
	HE	22.31*± 13.02	116.26*± 27.72	88.79*± 23.56	29.73*± 30.04	3.71*± 15.77	0.09*± 0.02	2.28	0.19	1.82	17
Protein content (%)	NE	0.53*± 0.20	2.58*± 0.42	1.94*± 0.36	0.60*± 0.46	0.32*± 0.24	0.01^{ns}± 0.06	2.21	0.19	1.69	20
	HE	0.43*± 0.08	1.27*± 0.17	1.00*± 0.15	0.45*± 0.19	0.30*± 0.10	0.01^{ns}± 0.02	1.72	0.20	1.87	30

NE/HE, Normal/Heat-stress environment. *, ** Significant at 5% and 1% probability level respectively. NS, non-significant

(2008) reported that additive gene action played a predominant role in the inheritance of plant height and peduncle length. The gene action for grain yield in bread wheat under drought conditions has been reported by Mirzamasoumzadeh *et al.* (2011).

The narrow-sense heritability was higher for days to 50% flowering (57% and 49%); days to maturity (69% and 71%); plant height (54% and 45%) and spike length (35% and 43%) under normal and heat-stress environment respectively (Table 4). The selection for these traits will be rewarding in further generations for crop improvement programme. Singh *et al.* (2003) reported high estimates of broad and narrow sense heritability for days to heading. Narrow sense heritability estimates for all the characters (plant height, spike length, peduncle length) were higher, varying from 76 percentages to 95 percentages as reported

(Yao *et al.* 2011).

Under normal environment the performance of parents in respect to general combining ability effect is as that out of ten parents three parents HD 2285 for grain filling duration and thousand grain weight; PBW 373 for days to maturity and plant height; and UP 2425 for number of tillers and grain yield showing good favorable GCA effect. Similarly under heat-stress environment also three parents-HD 2285 exhibiting highest GCA effect for days to 50% flowering, grain filling duration and thousand grain weight; HD 2733 for plant height and protein content and PBW 373 for number of tillers and grain yield. There was one parent HD 2285 showing good favorable GCA effect under both normal and heat-stress environment in respect to, days to 50% flowering, grain filling duration and thousand grain weight. These four parents HD 2285, PBW 373, UP 2425, HD 2733 are good general combiner in normal as well as heat-stress environment. It is clear from above study that some parents are good as general combiner for more than one trait. Therefore these parents can be used for crossing programme under normal as well as heat-stress environment (Table 5).

High GCA effects are mostly due to additive gene effects or additive × additive interaction effects (Griffing 1956). In view of this, breeders may utilize the good general combiners in specific breeding programme for improvement of grain yield in wheat. It appears that the GCA rank for grain yield is related to the GCA for the useful yield components. It is therefore recommended that the breeder should breed for superior combining ability for the component traits with an ultimate objective to improve the overall GCA for grain yield in bread wheat. In order to synthesize a dynamic population with most of the favorable genes accumulated, it will be pertinent to make use of these parents, which are good general combiner for several characters, in multiple crossing programmes. Apart from conventional breeding methods relying upon additive or additive × additive types of gene action, population improvement appears to be a promise alternative.

Estimates of specific combining ability effects, under normal environment revealed that the cross combinations HD 2733/PBW 226 exhibiting highest negative SCA effect for days to 50% flowering with highest positive effect for grain filling duration; HD 2733/HUW 468 exhibiting highest negative effect for days to maturity with positive SCA effect for number of tillers and thousand grain weight; HD 2733/PBW 343 exhibiting highest negative SCA effect for plant height with positive effect for spike length. The other cross combinations exhibiting highest SCA effect only for single trait- HUW 468/HD 2285 as for number of grains per spike; HD 2733/WH 542 for grain yield; and HD 2687/PBW 226 exhibiting highest SCA effect for protein content. Similarly under heat-stress environment the cross combination PBW 373/HD 2285 exhibiting highest SCA effect for days to 50 percent flowering and grain filling duration. While other cross combinations showing favorable SCA effect only for one trait: HD 2733/PBW 373 negative

Table 5 Estimates of general combining ability effects for yield and protein content in a 10×10 half diallel set of bread wheat under normal/heat–stress environment

Parents	Days to 50% flowering		Grain filling duration		Days to maturity		Plant height (cm)		Number of tillers/plant		Spike length (cm)		Number of grains/spike		Grain yield/ plant (g)		1000–grain weight (g)		Protein content (%)	
	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE
HD 2733	1.61**	1.94**	–1.39**	–2.22**	0.01	–0.29	–2.47**	–7.54**	–0.49*	–0.39	–0.23**	–0.44**	0.50	–1.87**	–0.09	–0.79**	1.36**	–1.32**	–0.03	0.34**
PBW 373	–0.97**	2.39**	–1.74**	–0.84**	–2.47**	1.56**	–2.58**	3.44**	–0.67**	1.20**	–0.27**	0.21**	–0.13	0.79*	–0.55**	0.92**	0.75**	1.61**	–0.21	–0.43**
HD 2687	4.19**	1.25**	–1.60**	–1.16**	2.49**	0.07	–1.51**	–2.85**	0.64*	–0.51*	–0.21**	–0.07	–2.24**	1.03**	–0.20	–0.89**	–1.35**	–2.69**	0.02	0.25**
PBW 343	4.79**	0.34	–1.27**	–0.62*	3.59**	–0.26	–0.01	–2.32**	0.46*	–0.25	0.19**	–0.12*	–2.46**	1.36**	0.08	–0.24	–0.10	–1.21**	–0.06	–0.02
UP 2382	–0.42*	2.08**	0.18	0.06	–0.04	2.13**	1.33**	1.63**	–0.26	–0.07	0.44**	0.57**	3.11**	–1.18**	–1.10**	–0.20	–0.94**	–0.19	0.65**	0.23**
WH 542	3.07**	0.55*	–2.20**	–0.36	0.30	0.18	–0.80**	–1.74**	0.87**	0.43*	0.56**	–0.10*	4.28**	0.53	1.12**	0.71**	–4.23**	–2.80**	–0.17	–0.07
PBW 226	–4.47**	–1.46**	2.54**	1.31**	–1.72**	–0.12	–0.88**	1.57**	–0.97**	0.67**	–0.74**	–0.12*	–1.97**	–0.24	–1.76**	0.19	–2.70**	1.59**	0.13**	–0.20**
UP 2425	–2.17**	–2.20**	2.87**	0.75*	0.96**	–1.48**	1.17**	1.04**	2.03**	–0.66**	–0.05	–0.26**	0.15	–0.18	2.67**	–0.44**	2.15**	0.30*	–0.46**	0.11*
HUW 468	–1.75**	–2.11**	–0.44	1.42**	–2.15**	–0.66**	6.45**	4.97**	–0.76**	–0.08	0.74**	0.34**	3.07**	–0.42	–0.15	0.55**	1.84**	1.15**	0.47**	0.05
HD 2285	–3.89**	–2.78**	3.06**	1.67**	0.98**	–1.12**	–0.70*	1.79**	–0.85**	–0.34	–0.44**	–0.01	–4.19**	–0.65*	–0.02	0.20	3.22**	3.56**	0.34**	–0.25**
SE (g_i) ±	0.12	0.12	0.18	0.16	0.13	0.13	0.15	0.13	0.13	0.12	0.03	0.03	0.15	0.18	0.08	0.07	0.08	0.08	0.03	0.03
SE(g_i–g_j)	0.18	0.18	0.27	0.24	0.20	0.19	0.23	0.19	0.20	0.18	0.04	0.04	0.23	0.27	0.12	0.11	0.12	0.12	0.04	0.04
CD at 5%	0.41	0.41	0.61	0.54	0.45	0.43	0.52	0.43	0.45	0.41	0.09	0.09	0.52	0.61	0.27	0.25	0.27	0.27	0.09	0.09
CD at 1%	0.59	0.59	0.88	0.78	0.65	0.62	0.75	0.62	0.65	0.59	0.13	0.13	0.75	0.88	0.39	0.36	0.39	0.39	0.13	0.19

NE/HE, Normal/Heat–stress environment. *, **, Significant at 5% and 1% probability level respectively

Table 6 Estimates of specific combining ability effects for yield and protein content in 10×10 half diallel set of bread wheat under normal/heat-stress environment

Cross combinations	Days to 50% flowering		Grain filling duration		Days to maturity		Plant height (cm)		Number of tillers/plant		Spike length (cm)		Number of grains/spike		Grain yield/ plant (g)		1000-grain weight (g)		Protein content (%)	
	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE	NE	HE
HD 2733/ PBW 373	4.82 **	–0.86	–0.60	–4.90**	4.41**	–5.78**	0.55	–0.52	1.08	3.95**	0.95**	–0.40**	2.29**	–1.40	–1.86**	2.25**	–2.03**	–0.53	–0.03	0.25
HD 2733/ PBW 343	–1.85**	0.51	–1.40	–0.29	–2.32**	0.20	–8.69**	1.91**	–2.88**	–0.51	1.72**	0.42**	0.61	–1.64	–3.30**	4.04**	–3.68**	4.00**	–0.12	–0.24
HD 2733/ WH 542	–0.06	1.64**	1.03	–0.89	1.98**	0.76	1.27	–0.34	2.87**	0.38	1.31**	1.03**	10.21**	7.86**	8.55**	0.17	2.59**	0.99**	–1.00**	–0.11
HD 2733/ PBW 226	–10.68**	–0.68	9.96**	3.11**	–0.51	2.40**	–6.81**	6.52**	–3.28**	–2.52**	–0.41**	–0.15	–8.27**	–0.04	–3.06**	–1.16**	–0.06	–2.43**	–1.30**	–0.85**
HD 2733/ HUW 468	–9.41**	–0.36	–6.24**	2.83**	–16.91**	2.44**	0.86	–13.72**	4.84**	1.39*	1.14**	–0.16	5.75**	–1.19	5.52**	–0.72	9.87**	–9.91**	1.38**	0.58**
PBW 373/ HD 2687	1.23*	–0.50	–0.06	–0.12	1.25	–0.64	–4.91**	–14.39**	1.79**	2.91**	0.14	0.14	3.36**	–2.14**	1.75**	3.65**	3.45**	–0.45	–1.14**	0.55**
PBW 373/ PBW 226	–8.10**	–3.96**	–4.69**	4.07**	–12.87**	0.05	–1.20	–5.30**	–1.94**	–3.27**	–0.34*	–0.88**	0.37	–6.71**	–1.32**	–2.86**	6.10**	2.28**	–0.02	0.12
PBW 373/ UP 2425	6.26**	0.28	–3.19**	0.46	2.78**	0.75	–8.26**	–3.11**	2.06**	–2.17**	0.15	0.27*	–6.70**	–0.60	2.36**	–0.23	1.55**	4.35**	0.40**	0.76**
PBW 373/ HD 2285	–0.85	–4.64**	3.94**	5.04**	–3.23**	0.39	2.79**	1.98**	–0.56	–1.59**	0.41**	–0.03	–2.75**	–3.29**	–0.22	–1.22**	1.04*	0.49	–0.74**	0.10
HD 2687/ PBW 343	1.30*	1.04	–6.36**	1.49	–5.14**	2.51**	–0.48	2.71**	–3.67**	–0.51	0.51**	1.46**	7.85**	4.63**	–3.33**	–4.77**	–2.78**	–0.89*	0.64**	0.67**
HD 2687/ PBW 226	13.23**	–1.65**	–1.33	1.72*	12.00**	0.04	–3.10**	–4.84**	1.42*	0.10	–0.28*	0.21	0.80	9.72**	2.87**	2.05**	4.84**	–0.48	1.43**	0.97**
HD 2687/ HUW 468	–5.82**	–2.83**	5.64**	3.28**	0.10	0.41	–4.10**	0.09	0.38	4.02**	–1.99**	–1.00**	–8.18**	–3.43**	1.76**	3.81**	3.70**	–2.97**	–0.82**	–0.03
PBW 343/ HUW 468	–8.59**	–3.13**	6.69**	3.10**	–1.94**	–0.05	3.69**	–5.59**	–0.60	1.24*	0.01	–0.01	0.17	–3.67**	1.40**	3.70**	4.57**	7.18**	–0.80**	–0.04
PBW 343/ HUW 468	1.83**	–0.35	–4.00**	0.90	–2.27**	0.57	–5.66**	–2.84**	1.27	2.34**	0.35*	0.51**	4.79**	8.67**	4.27**	1.74**	5.59**	–5.08**	0.11	0.04
UP 2382/ HUW 468	6.04**	0.08	–4.78**	–1.11	1.02	–0.99	2.51**	–9.29**	2.83**	2.87**	1.40**	–0.04	9.72**	–1.79**	4.51**	4.74**	–1.32**	1.34**	0.72**	–0.01
WH 542/ HUW 468	–3.45**	–0.06	1.60	–4.36**	–1.32	–4.38**	–7.37**	–0.59	–3.98**	1.66**	1.14**	0.64**	12.72**	–0.17	–4.39**	3.58**	–6.17**	4.17**	0.40**	1.08**
PBW 226/ HUW 468	2.68**	0.21	–1.17	–0.86	1.48*	–0.23	–0.06	7.50**	–0.01	–0.49	–0.29*	0.08	–7.83**	6.67**	–0.42	–0.43	–5.31**	9.73**	1.31**	–0.56**
HUW 468/ HD 2285	0.43	1.53*	3.97**	0.44	4.74**	1.94**	3.93**	–3.39**	–3.46**	–2.15**	1.39**	–0.09	16.78**	–4.25**	–2.26**	–1.66**	2.28**	–1.94**	–0.48**	0.37**
SE (s_{ij}) ±	0.41	0.39	0.61	0.55	0.45	0.43	0.52	0.42	0.45	0.41	0.09	0.09	0.52	0.60	0.28	0.24	0.26	0.28	0.10	0.09
SE (s_{ij}-s_{ik})	0.61	0.58	0.90	0.80	0.66	0.63	0.75	0.62	0.66	0.59	0.14	0.13	0.76	0.89	0.41	0.36	0.39	0.41	0.15	0.13
CD (P=0.05)	1.23	1.17	1.81	1.62	1.33	1.27	1.52	1.25	1.33	1.19	0.28	0.26	1.54	1.80	0.83	0.73	0.79	0.83	0.30	0.26
CD (P=0.01)	1.64	1.56	2.42	2.15	1.78	1.69	2.01	1.67	1.78	1.59	0.38	0.35	2.04	2.39	1.10	0.97	1.05	1.10	0.40	0.35

NE/HE, Normal/Heat-stress environment. *, ** Significant at 5% and 1% probability level respectively effect for days to maturity; PBW 373/HD 2687 negative effect for plant height; HD 2687/HUW 468 positive SCA effect for number of tillers; HD 2687/PBW 343 for spike length; PBW 343/UP 2425 for number of grains per spike; UP 2382/UP 2425 for grain yield; PBW 226/HUW 468 for thousand grain weight; and WH 542/UP 2425 exhibited highest positive SCA effect for protein content (Table 6).

There were five cross combinations out of 45 showing contrasting favorable SCA effect for more than one traits under both the environments: PBW 373/PBW 226 for days to 50% flowering with thousand grain weight; PBW 373/UP 2425 for thousand grain weight with protein content; HD 2687/PBW 226 for plant height and protein content; PBW 343/UP 2382 for days to 50% flowering, grain yield and thousand grain weight; and PBW 343/PBW 226 for plant height, grain yield and protein content (Table 6).

Diallel selective mating system is good technique, which delays quick fixation of gene complexes, and permits break down of linkage, general fostering of recombination and concentration of favorable gene complexes into central gene pool by a series of multiple crosses. The SCA represents the dominance and epistatic interaction, which can be related with heterosis. However, in self-pollinated crops like wheat, the additive × additive type epistasis is fixable in later generations. Breeder's interest therefore best in obtaining transgressive segregants through crosses and producing more potent homozygous lines. Jinks and Jones (1958) emphasized that the superiority of hybrids might not indicate their ability to yield transgressive segregants rather SCA would provide satisfactory criteria.

Those traits exhibited dominance or non-additive type gene effect, methods which will exploit non-additive gene actions, such as restricted recurrent selection by way of intermating the most desirable segregates followed by selection or multiple crosses or biparental mating in early segregating generations could be held promising for genetic improvement. Heterosis breeding is also an effective breeding strategy for exploiting non-additive gene effects. The traits which show predominance of non-additive gene effects indicates that the improvement of such trait would be difficult, as simple pedigree breeding will not be able to fix the superior lines in the early generations. In such situation, maintaining considerable heterozygosity through mating of selected plants in early segregating generations could attain maximum gain. Therefore, few cycles of recurrent selection followed by pedigree breeding will be effective and useful for the improvement of yield in such cases in the present material.

The present study demonstrates that both additive (fixable) and non-additive (non-fixable) components of genetic variances were involved in governing the inheritance of almost all the quantitative and quality traits. Therefore, bi-parental mating and/or diallel selective mating which may allow intermating of the selects in different cycles and exploit both additive and non-additive gene effects could be useful in the genetic improvement of the characters of bread wheat. The traits which show high narrow-sense heritability over the both environments indicating greater role of additive genetic components therefore, selection for these traits in early generation would be effective for the improvement of grain yield and yield components. Inclusion of F_1 hybrids showing high SCA and having parents with good GCA into multiple crosses could also be a worthwhile approach for tangible improvement of grain yield in spring wheat.

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