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HETEROSIS, INBREEDING DEPRESSION AND COMBINING ABILITY IN *TRITICUM AESTIVUM* L.

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The objective of the present study was to investigate the magnitude of heterosis, inbreeding depression and combining ability in F_2 population for seven quantitative traits in a 6 x 6 complete diallel cross involving six cultivars of spring wheat. F_2 population suffered from considerable amount of inbreeding depression for all the traits suggesting that upward values in observed depression were attributable to factors like epistasis, linkage disequilibrium and abnormal segregation at meiosis due to higher ploidy level. Grain yield per plant displayed maximum observed and predicted inbreeding depression ranging from 25.25 to 88.71% and 10.16 to 19.85% respectively. Fair degree of mid parent heterosis in majority of the F_2 hybrids cannoted that these hybrids could be exploited for commercial hybrid wheat development. General combining ability (GCA) indicated a large proportion of the total genetic variation for six out of seven effects. Specific combining ability (SCA) effects were significant for four of the seven traits indicating the presence of epistasis and dominant gene effects in these traits. Magnitude for GCA variance was more pronounced than SCA variance for all the traits. Therefore selection has been advocated on the basis of GCA's of hybrids and breeding method should be designed to exploit both additive and non-additive gene actions.

Key words: combining ability, heterosis, inbreeding depression, *Triticum aestivum* L.

INTRODUCTION

Considerable research work has already been carried out on the heterotic expression of polygenic traits in allogamous (Baloch *et al.,* 1991 and Larik and Hussain, 1990) as well as in autogamous crops (Larik *et al.,* 1992, 1995). Heterosis has important implications for both in F_1 and for obtaining transgressive segregants in F_2 generation. In succeeding selfing generation, homozygosity increases, vigour and productiveness reduces by 50% due to inbreeding depression (Falconer, 1989). If F_2 hybrids still express sufficient amount of heterosis over parents, the high cost due to low quantity of seed in F_1 will be paid off by more seed produced from F_2 hybrids. Improvement in both quantitative and qualitative traits can only be established when the nature of genetic effects such as additive or non-additive is thoroughly studied. Combining ability analysis in this respect is necessary which exploits relevant type of gene action for a breeding programme. This study thus intends to provide information regarding (i) the amount of heterosis expressed by F_2 hybrids, (ii) the rate of inbreeding depression, and (iii) the type of gene action involved so that breeding methodology could be directed accordingly.

MATERIALS AND METHODS

F_2 hybrids along with six parents were grown during 1992-93 in a randomized complete block design with three replications in the experimental field of Agriculture Research Substation, Kot Diji, Khairpur, Sindh. Standard distances between row to row (30 cm) and plant to plant (15 cm) were kept so as to let the plants express themselves into the environment with full potential. Parentage of the varieties used in the study have already been reported (Larik *et al.,* 1995). Data on seven quantitative traits were collected from 25 sample plants selected randomly from each parent and their F_2 hybrids. The analysis of variance method according to Steel and Torrie (1980) was adopted to figure out the difference among the genotypes for various traits. Heterosis values were calculated by using the formula as reported earlier by Larik *et al.* (1995). Inbreeding depression was calculated using the formula adopted by Paul *et al. (1987).*

Inbreeding depression = 100 $(F_1-F_2)/F_2$. The expected inbreeding depression of F_2 hybrids was also calculated using the formula developed by Falconer (1989). Expected inbreeding depression in

Table 1. Heterosis values (%) over mid parent (MP) and better parent (BP) in F_2 for seven quantitative traits in bread wheat *(Tritium aestivum* L.)

Cross	Tillers per plant		Seeds pre spike		Seed index (g)		Single plant yield	
Direct	MP	BP	MP	BP	MP	BP	MP	BP
P_1P_2	-3,03	-5.88	+16.66	+5.00	+0,97	+0.32	+6.21	+1,99
PIP,	-3.57	-9,37	+4.00	-2.50	-0.65	-0.97	+6.71	+2.73
P_1P_4	-3.03	-5.88	+26.31	+20.00	+7.64	-5.00	+6,42	+2.89
PIPS	+1,93	-1,25	+2.56	0.00	+20.91	-20,52	+6.35	+1,74
P_jP_6	+2.00	-4.37	+2.85	-10.00	+0.00	-13.75	+4.34	+1,49
P_2P,	+5.51	-10.00	+2.98	-1,42	+41,47	+18.12	+2,42	+1,15
P_2P_4	-5.29	-5.29	+11.76	+5.55	+5.51	+5.17	+1,73	+1,06
P_2P_s	-0.62	-6,47	+2.85	-5.25	+2.25	-9.50	+3.29	+1,62
P_2P_6	+1,93	-7.05	+1,61	-4.68	+5.51	+5.17	+2.93	+1.57
P,P_4	-3,44	-17.64	+2.81	+1,38	+2.25	-9.50	+2.67	+2.12
P,P_s	-7,40	-16.66	-1.36	-5.26	+17.50	-1,94	+4.65	+2.68
P,P_6	+8.07	+0.35	+1.53	-5.71	+4.23	+3.89	+4.25	+3.15
P_4P_s	-7,50	-12.94	+1,35	-1,30	+15.51	-12.50	+8.99	+6.38
P_4P_6	+2.58	-6,43	+3.03	-5.53	+3.39	-8.75	+1,32	+0.87
P_sP_6	+3,44	0.00	+5.88	-5.26	+20.62	+0.97	+4,33	+1,31
Reciprocals								
P_2P_1	-2.24	-7.05	+5.50	-5.00	+5.86	+5.17	+5,44	+1.24
P,P_j	+3.57	-9.32	+1,33	-5.00	-2.28	-2.59	+5.69	+1,71
P_4'P_j	-12.12	-14.70	+2.63	-2.50	+1,10	-10.00	-1,28	-4,47
PSP_1	-1,93	-5.00	-2.56	-5.00	+5,40	-11,76	+7.10	+1,71
P_6P_1	+1.33	-5.00	+8.57	-5.00	+4.57	+4.23	-2.55	-5.22
P,P_2	+3,44	-11,76	+0.00	-4.28	+0.64	+4,32	+2,44	+2.15
P_4P_2	-4.70	-4.70	+2.94	-2,47	+3.18	-8.75	+1,34	+0,53
P_sP_2	+2,58	-6,47	+2.85	-5.26	+21,90	+6.79	+1,09	+0,54
P_6P_2	+3.10	-7.64	+37.09	+32.81	+2.27	+1,94	+0.85	-0,52
P_4P,	+2.06	-12.94	-1,40	-2.77	+1,69	-10.00	+1,66	+1,06
PsP,	0.00	-10.00	-4.10	-7.89	+16.73	-2.59	+0.82	-1,07
P_6P,	+3.84	-3.57	+1,53	-5.71	+7,49	+7.14	+5.05	+3.94
P_sP_4	-3.12	-8.80	-2.70	-7.26	+7.26	-18.75	+1.90	+0,53
P_6P_4	+3.22	-5.88	+4.54	-4.16	+4.81	+7,50	+0.79	+0.26
P_6P_s	0.00	-3.33	+5.88	-5.26	+20.62	+0.97	+4.60	+1.57

F_2 = % (PI + P_2 + F_1) where Pp P_2' and Fp respectively are parent one, parent two and F_1 hybrid performance. The method of analysis of variance for combining ability with model-2 of Griffing (1956) was used.

RESULTS AND DISCUSSION

Heterosis: In F, generation, generally most of the hybrids displayed positive heterosis over MP and negative heterosis over BP for all the traits except spike length, seed index and yield per plant (Table 1). Of 30 crosses, 28 and 26 exhibited positive MP and BP heterosis for yield per plant respectively. Among the crosses P_4 x P, displayed 8.99% MP and 6.38% BP heterosis. However, the magnitude of heterosis was much more smaller than that observed in the F_1 generation (Larik *et al., 1995).* There was no cross exceeding 8.99% heterosis for yield per plant. In comparison to F_1 generation, heterozygosity in the F_2 generation was much more reduced due to allelic segregation and this led to drastic decrease in heterosis in F_2 generation. The results from F_2 hybrids suggested that these hybrids still expressed heterosis which is reasonable because according to Falconer (1989) if the character is controlled by dominant genes, a change towards recessive allele is only 50% in F_2.

In F_2 generation, the ranges of heterosis were -17.64 to 8.07% for tillers per plant, -7.77% to 14.2% for spike, length, -17.85% to 16.66% for spikelets per spike, -10% to 37.09% for seeds per spike, -31.03% to 28.20% for yield per spike, -18.75% to 41.47% for

Table 2. Mean squares of wheat genotypes (varietieslF 2) for different quantitative characters

Character studied	D.F.	Mean squares	F-value	Significance
Tillers per plant	35	3.69	3.65	***
Spike length	35	0.46	0.66	NS
Spikelets per spike	35	5.00	5.05	***
Seeds per spike	35	22.25	19.18	***
Yield per spike	35	0.317	317.00	***
Seed index	35	0.383	25.53	***
Single plant yield	35	0.70	2.18	***

, * = Significant at I% and 0.01 % probability; NS= Non-significant.

Table 3. Analysis of variance (mean squares) for combining ability in F_2 generation

Source of variation	D.F.	Tillers per plant	Spike length	Spikelets per spike	seeds per spike	Yield per spike	Seed index	Single plant yield
GCA	5	3.91 ••	0.17^{NS}	5.31"*	28.92'-	0.29"	0.28"	1.73-'
SCA	9	0.63^{NS}	0.19^{NS}	0.45^{NS}	1.95**	0.27"*	0.06"*	0.26"*
Reciprocal	15	0.62'	0.37^{NS}	0.48^{NS}	1.52"*	0.02"*	0.02"*	0.22'
Error	70	0.33	0.23	0.33	0.38	0.001	0.002	0.70
GCA:SCA ratio		1:6.30	1:0.89	1:11.80	I: 14.83	1:1.07	1:4.66	1:6.65

*, ** = Significant at 5% and 1% level of probability; NS = Non-significant.

seed index and -5.22% to 8.99% for yield per plant (Table 1). Heterosis of these yield components has an important relationship with heterosis of grain yield. The crosses expressing significant and positive heterosis for yield per plant had significant and positive heterosis for some yield components. In F_2 generation, there were 28 crosses showing significant positive heterosis for yield per plant. They also displayed significant and positive heterosis for one or more yield components. Such positive relationship between heterosis for yield per plant and heterosis for yield components was also reported earlier by Larik *et al.* (19988, 1992, 1995). They suggested that heterosis for primary yield components such as tillers per plant, seeds per spike and seed index influenced the heterosis for yield per plant.

When the heterosis of these crosses was compared with their SCA effects, it was observed that both were positively related. The crosses PI x P_2, P_4 X Ps, P, x 4 and P, x P_6 had significant SCA effects and heterosis for yield per plant (Table 1). Significant estimates of both heterosis and SCA effects suggest predominance of non-additive gene action for yield per plant in these crosses. Selection through conventional breeding methods would not be effective in these crosses. Alternatively development of a hybrid variety might be a good choice.

Combining Ability: The analyses of variance for general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (RE) are presented in Table 3. In F_2 generation, GCA variance and RE are highly significant (P<O.Ol) for seeds per spike, yield per spike and seed index, whereas SCA and RE were only significant (P< 0.05) for plant yield. General combining ability variance contains additive and additive x additive epistasis, while SCA variance contains dominance and additive x dominance, dominance x dominance epistasis (Griffing 1956, Baker 1978). Thus the significant estimates of GCA and SCA variances suggest that both additive and non-additive gene actions were involved in controlling these characters in the present material. Significant mean squares for these traits also confirmed the presence of additive and non-additive gene actions (Table 2). The variances for GCA were larger than those of SCA for all the traits except spike length which suggest that the major portion of genetic variability in the base population was additive in nature and the yield components were predominantly controlled by additive gene action. Expression of predominance of additive gene action for Seeds per spike was due to fixation of alleles by. segregation. Genetic variance in F_2 generation generally conformed to those in F, generation (Larik *et al.,* 1995). Mean

Table 4. Estimation of GCA and SCA effects in F_2 generation for various quantitative traits in bread wheat

Parents/cross	Tillers/ plant	Spike length	Spikelets per spike	Seeds/ spike	Yield! spike	Seed index	Single plant yield
PI Vees	+0.36	-0.02	+1.25	+3.22	-0.23	-0.07	+0.93
PzBuc's	+0.95	-0.15	+0.30	-0.77	-0.18	-0.07	-0.31
Pj Mous	+11.02	-0.16	-0.42	-1.08	+0.02	-0.13	-0.06
P_4 ZA-77	+0.11	+0.09	+0.75	+0.41	-0.02	+0.35	-0.02
P_5 TJ-83	-0.55	+0.20	-0.40	+0.54	+0.21	+0.17	-0.23
P_6 Blue Silver	+0.13	+0.05	-0.87	-2.23	+0.21	+0.04	-0.11
SE	0.28	0.23	0.28	0.30	0.01	0.02	0.15
Direct							
P1xPZ	-0.41	+0.21	+0.17	+1.32	+0.06	-0.05	+0.33
p\x$P_3$	-0.17	-0.53	-0.38	-1.36	+0.17	-0.07	+0.21
P,xP4	+0.17	+0.11	-0.73	-0.36	+0.05	+0.13	-0.23
P_1xP_S	-0.70	+0.22	+0.17	-0.99	-0.12	-0.20	+0.24
P_IXP_6	-0.24	+0.00	+0.74	-0.11	-0.19	+0.19	+0.57
PZxP_3	+0.23	+0.10	-0.11	-0.36	-0.03	-0.08	-0.09
PZxP4	+0.09	-00]| 6	+0.07	+0.04	-0.13	-0.05	+0.01
PzxPs	+0.41	-0.37	+0.27	+0.01	-0.06	+0.35	-0.32
PZxP_6	-0.33	+0.23	-0.41	-1.61	+0.12	+0.01	-0.42
P_3XP4	+0.32	+0.10	+0.39	+0.20	-0.18	+0.04	+0.38
P_3xP_S	-0.41	+0.45	+0.09	-0.11	+0.12	+0.01	-0.42
P_3XP_6	-0.33	+0.11	-0.03	+0.20	-0.12	+0.04	+0.38
P4xP_S	-0.90	-0.12	+0.02	-0.43	+0.05	-0.11	+0.34
P_4XP_6	+0.71	+0.08	+0.24	-0.05	+0.18	-0.02	-0.04
P_SxP_6	-0.53	-0.18	-0.56	+1.57	-0.02	-0.07	+0.15
S.E.	0.40	0.33	0.40	0.43	0.02	0.03	0.22
Reciprocal							
PZxP_1	+0.10	+0.20	-0.55	+2.00	-0.10	-0.075	+0.075
P_3xP\	+0.00	+1.45	+0.70	+0.50	+0.30	+0.025	+0.100
P4XP1	+0.05	-0.05	+0.10	+0.50	+0.15	+1.00	+0.750
P_5XP_1	+0.30	+0.07	+0.25	+ 1.00	+0.02	+0.15	+0.050
P_6xP\	+0.05	-0.10	+0.35	-1.00	+0.15	+0.25	+0.675
P_3xPZ	+0.15	-0.25	-0.70	+0.50	+0.02	-0.02	+0.000
P4XP_2	-0.05	-0.05	+0.55	+1.50	+0.12	-0.100	+0.05
PsxPz	-0.10	-0.15	+0.70	0.00	+0.06	+0.175	+0.20
P_6xPZ	+0.05	0.00	+0.05	-1.00	-0.03	+0.05	+0.20
P4XP_3	-0.40	+0.10	+0.25	+0.75	-0.07	+0.01	+0.10
P_SxP_3	-0.50	+0.75	-0.10	+0.50	+0.02	-0.05	-0.07
P_6XP_3	+0.27	-0.15	+0.10	0.00	+0.02	-0.05	+0.65
P_SxP4	-1.85	+0.05	+0.50	+0.75	0.00	+0.12	+0.65
P_6XP4	-0.05	+0.10	+0.95	-0.25	+0.07	-0.02	+0.05
P_6xP_S	+0.25	+0.05	-0.40	0.00	-0.02	0.00	+0.02
S.E.	0.49	0.47	0.49	0.53	0.02	0.03	0.27

squares due to reciprocal effects were not significant for spike length and spikelets per spike, indicating the absence of reciprocal differences among the hybrids studied. The preponderance of additive genetic variation for seven traits in F_1 generation indicated that the parents involved in these crosses may be selected on the basis of their GCA. The importance of additive and non-additive gene action for the quantitative traits in hexaploid wheat was also reported by Sharma and Singh (1986) and Larik *et al.,* (1988). Paroda and Joshi (1970) working on spring wheat obtained significant GCA and SCA variances for grain yield and its primary components in F_2 generation.

Table S. Inbreeding depression (%) in F_2 of thirty direct and reciprocal crosses for different quantitative traits in Hexaploid bread wheat

Cross	Tillers/plant		Seeds/spike		Seed index		Single plant yield	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Direct								
P_1XP_2	0.00	+11,5	+42.85	+33.75	+58.06	+3.16	+71,70	+12.83
P,xP_3	+10.30	+11,00	+17.94	+31,00	+32.78	+2.93	+35.59	+17.02
P,xP_4	+12.50	+12.00	+20.00	+32.0	+13.15	+3.04	+52.17	+18.85
P1xPS	+7.59	+11,75	+17,50	+32.0	+43.0	+3.01	+53.54	+19,10
P_1XP_6	-1,96	+10.75	+33.33	+30.73	+10.81	+2.91	+29.90	+16.65
P_2XP_3	+11,11	+11,75	+27.53	+28.25	+37.26	+3.01	+46.01	+16,46
P_2XP_4	+11,80	+12.0	+26.31	+29.75	+21,15	+3.05	+69.73	+18,47
P_2xPS	+14.64	+12.0	27.77	+29.0	+14,52	+2.95	+69.68	+18.71
P_2XP_6	+7.59	+11:75	+57,37	+28.5	+27.69	+2.97	+55.18	+16.72
P_3XP_4	+14.28	+11,50	+9,58	+28.5	+13.25	+2.76	+25,52	+16.27
P_3XP_5	+20.00	+11,25	+33.33	+30.75	+35.76	+2.19	+38.74	+17.35
P_3XP_6	+28.11	+11.50	+45,45	+29.25	+31,25	+2.96	+28.06	+15.50
P_4xPS	+28.37	+12.75	+70.77	+35.25	+27.71	+3.05	+64,50	+19.85
P_4XP_6	+13.07	+12.0	+41,17	+29.75	+15.06	+3.01	+71,54	+18.18
~~'i~~ft	±~Q~Qg	± ~~:Q	2"}} :??..	± ~g . QQ	±~? :~Q	±~:~?	2" ? Q:~Q	±L~~ ~2~
Reciprocal								
P_2XP_1	-5.06	+11,25	+47.36	+32.75	+27.69	+2.98	+50.85	+17.71
• P_3XP_1	+3,44	+10.75	+10.52	+30.00	+36.66	+2.95	+17.84	+16.05
P_4xP,	+10,34	+11,75	+7.59	+30,50	+13.61	+2.99	+39,58	+17,54
PSxP_1	+18,42	+12.00	+26.31	+32.25	+57,40	+2.92	+31.20	+17.92
P_6xP_1	+18.42	+11.50	+26,31	+30.75	+31,56	+2.94	+72.59	+17.97
P_2XP_2	+20.00	+12.00	+13,43	+26.75	+33.87	+3.00	+36.31	+15.98
P_3XP_2	+32,45	+13.00	+31,42	+29.25	+12.32	+3.03	+84.12	+18.96
P_4XP_2	+0.62	+12.00	+33.33	+30.00	+27.87	+2.96	+56.25	+17.92
PSxP_2	+14.64	+12.00	+20.26	+27.00	+33,33	+2.98	+52.11	+15.95
P4XP_3	+1.35	+11.25	+37.14	+30,50	-19,44	+3.06	+41.57	+16.97
PSxP_3	+11,11	+11,25	+31,42	+30.25	+33.23	+2.89	+61,95	+18.17
P_6XP_3	25.95	+11.25	+42,42	+29.00	+30.00	+2.99	+58.98	+17.07
PSxP_4	+22.58	+12.75	+33.36	+31,25	+39.07	+3.06	+86.63	+19,45
P_6XP_4	+18.75	+12.25	+44.95	+30.25	+10.81	+2.98	+88.71	+10.16
P_6xPS	+31,03	+12.25	+33.33	+30.00	+29.03	+2.85	+80,56	+18.96

Obs.: Observed; Exp. = expected.

GCA Effects of the Parents: Estimates of GCA effects of the parents in F_2 generation are shown in Table 4. Vees appeared to be a good general combiner for single plant yield, seeds per spike, spikelets per spike and tillers per plant. It was also observed that significant GCA effects of the parent Vees for single plant yield were associated with the significant GCA effects for some of the yield components (Table 4). Such positive association of GCA effects for yield components with GCA effects for single plant yield of spring wheat was also reported by Liu *et al.* (1989). This suggests that assessment of GCA effects for yield components has considerable importance in selecting parents for yield improvement. The parent Vees had also good agronomic performance for the trait in which it expressed significant GCA effect.

SCA Effects of the Crosses: The crosses PI x P_2, PI x Ps,P_3 x P_6, P_4x Ps, P_4 x PI' P_6 x PI' Ps x 3 and P_6 x P_4 showed significant positive estimates of SCA effects for single plant yield (Table 4). Some of these crosses had also significant and positive SCA effects in some of the yield components such as tillers per plant, seeds per spike, yield per spike and seed index. Among yield components, seed index displayed significant SCA effects in maximum number of crosses (11 out of 30 crosses) followed by yield per spike. The arrays ofVees, ZA-77 and TJ-83 had comparatively more number of significant SCA

estimates than others, when all characters were considered together.
The crosses with significant SCA effects indicate presence of non-additive (dominance and epistasis) gene action in them. The combining ability studies indicate the existence of both additive and non-additive gene actions in the present material. Additive gene action was more prominent for yield components, while non-additive gene action was strong for single plant yield. Therefore, breeding method should be designed to exploit both additive and non-additive gene actions. The crosses which have shown significant SCA effects for single plant yield may be used in the development of hybrid variety. Another possibility of these crosses is that the non-additive genes of the crosses would give wider transgressive segregation. Careful selection of the potential transgressive segregants through family selection would be worth while for yield improvement.

Inbreeding Depression: The results presented in Table 5 demonstrate that generally the observed inbreeding in F_2 hybrids was quite higher than the expected inbreeding for all the traits studied which confirmed the involvement of dominant and over-dominant gene action since grain yield per plant displayed maximum inbreeding depression. The observed depression varied from 25.25 to 88.71% and. expected depression ranged from 10.16 to 19.85% for this trait. The discrepancy between the observed and the expected inbreeding depression could be explained by three factors such as linkage disequilibrium, epistasis interactions and abnormal segregation at meiosis. Gardner *et al. (1953)* reported that linkage biases may be serious in the expression of dominance variance in F_2 population where linkage effects are expected to be maximum. Comstock and Robinson (1948) suggested that if only disgenic epistasis was present the estimates of dominance will be biased upward, ultimately the observed heterosis will also go up than is predicted. Inbreeding depression in polyploids has been found to exceed than what is predicted by the coefficient of inbreeding, Aycock and Wilsie (1968) reported that in alfalfa, an autotetraploid, the yield decreased twice as much than what was predicted. This response according to them may be attributed to a decrease in favourable interactions among multiple alleles due to inbreeding and abnormal segregation at meiosis. Depression in F_2's performance reported in this study is in accordance with that of Falconer (1989).

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