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Combining Ability Analysis over F_1-F_5 Generations in Diallel Crosses of Bread Wheat

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Summary. Combining ability studies for grain yield and its primary component traits in diallel crosses involving seven diverse wheat cultivars of bread wheat (*Triticum aestivum* L.) over generations F_1-F_5 are reported. The general and specific combining ability variances were significant in all generations for all the traits except specific combining ability variance for number of spikes per plant in the F_5. The ratio of general to specific combining ability variances was significant for all the traits except grain yield in all the generations. This indicated an equal role of additive and non-additive gene effects in the inheritance of grain yield, and the predominance of the former for its component traits. The presence of significant specific combining ability variances in even the advanced generations may be the result of an additive × additive type of epistasis or evolutionary divergence among progenies in the same parental array. The relative breeding values of the parental varieties, as indicated by their general combining ability effects, did not vary much over the generations. The cheap and reliable procedure observed for making the choice of parents, selecting hybrids and predicting advanced generation (F_5) bulk hybrid performance was the determination of breeding values of the parents on the relative performance of their F_2 progeny bulks.

Key words: Combining ability analysis – *Triticum aestivum* – Diallel crosses

Introduction

It is a common experience that certain combinations combine well producing superior off-spring whereas others involving equally promising parents produce disappointing progeny. It is possible that one reason for this is that combining ability often depends upon complex interaction systems among genes. Diallel crosses have been used extensively to determine the combining ability of the parents but very little information is available on the repeatability of these estimates over various filial generations. In crops such as wheat, the small quantities of crossed seed produced by hand pollination prohibit adequate testing in the F_1 generation and the combining ability studies would, therefore, be easier in the F_2 or F_3 generations if they could be shown to provide similar information. Keeping these points in view, investigations were conducted on the F_1 to F_5 generations of diallel crosses in bread wheat.

Materials and Methods

Seven diverse wheat cultivars were crossed in diallel series, excluding reciprocals. These included three Mexican varieties ('Kalyansona', 'Sonalika' and 'S 413'), three Indian varieties ('C 273', 'K 68' and 'Sharbati Sonora') and the variety 'Argelto' from France. The parents and F_1 to F_5 generations of the crosses were sown during winter 1972 at the research farm of the Punjab Agricultural University, Ludhiana in a randomised block design providing four replications. There were four rows each of the parents, F_2, F_3, F_4 and F_5 and only one row of F_1. The row length was 3 m and the plants in each row were spaced 15 cm apart with a between row distance of 30 cm. Data was collected on 10 randomly selected plants from each row; border plants as well as plants on both sides of the gap, if any, were discarded. Observations recorded on an individual plant basis were subsequently reduced to progeny means for each repeat for statistical analysis. The combining ability analysis was carried out following Model 1 and Method 2 as described by Griffing (1956).

Results and Discussion

The general as well as specific combining ability variances for yield and its component traits, viz. number of spikes per plant, number of grains per spike and grain weight were significant in all generations (F_1-F_5), with the exception of the specific combining ability variance for number

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Table 1. Analysis of variance for combining ability

Character	Generation	Mean squares					
		G.C.A.	(d.f.)	S.C.A.	(d.f.)	Error	(d.f.)
Grain yield	F_1	45.45[a]	6	28.08[a]	21	2.50	54
	F_2	13.23[a]	6	8.88[a]	21	1.50	54
	F_3	12.19[a]	6	8.12[a]	21	0.96	54
	F_4	9.24[a]	6	7.75[a]	21	0.98	54
	F_5	11.75[a]	6	7.96[a]	21	1.25	54
Spikes per plant	F_1	7.70[a]	6	1.21[a]	21	0.45	54
	F_2	8.87[a]	6	1.01[a]	21	0.32	54
	F_3	8.37[a]	6	1.16[a]	21	0.35	54
	F_4	7.65[a]	6	0.61[a]	21	0.22	54
	F_5	9.12[a]	6	0.49[a]	21	0.33	54
Grains per spike	F_1	214.46[a]	6	14.83[a]	21	1.60	54
	F_2	165.95[a]	6	6.46[a]	21	1.51	54
	F_3	111.08[a]	6	25.58[a]	21	1.50	54
	F_4	150.31[a]	6	8.51[a]	21	1.41	54
	F_5	162.10[a]	6	6.78[a]	21	1.39	54
100-Grain weight	F_1	10.26[a]	6	0.16[a]	21	0.01	54
	F_2	0.61[a]	6	0.09[a]	21	0.01	54
	F_3	0.70[a]	6	0.07[a]	21	0.01	54
	F_4	0.69[a]	6	0.06[a]	21	0.01	54
	F_5	0.60[a]	6	0.05[a]	21	0.01	54

[a] significant at 1% level

of spikes per plant in F_5 (Table 1). The ratio of general to specific combining ability variances was significant for all the yield components in all the generations but not for yield itself, indicating the predominance of additive gene effects in the genetic control of component traits and an almost equal importance of additive and non-additive gene effects for grain yield. The greater magnitude of general rather than specific combining ability variances for yield contributing characters has also been reported by Singh et al. (1969) and Knot and Sindhagi (1969).

In a self fertilized crop heterozygosity is expected to decline in the advanced generations and in the absence of selection, the progeny mean is expected to approach the mid-parent value. Ultimately the specific combining ability variance should be non-significant. The results of the present investigation are not in agreement with such expectations. Though the magnitude of the specific combining ability variance declined in the F_2 and later generations for grain yield and other characters, it still remained significant in all generations. The means of some of the advanced progeny bulks were observed to be as good or better than even the higher yielding parent. The epistasis of the additive × additive nature could be the cause of the significant contribution of specific combining ability variances in advanced generations. Another reason could be that the specific combining ability variance in later generations was generated by evolutionary divergence among progeny in the same parental array. Each progeny bulk may have a potentially different interaction system. The different genotypes in bulks would be selected for their own performance as well as for their competing abilities. Natural selection may thus change gene as well as genotype frequencies and, consequently, the mean performance. Tandon et al. (1970) and Jordaan and Laubscher (1968), who studied diallel crosses in wheat from generations F_1-F_3 and F_1-F_5 respectively, also reported significant specific combining ability variances in all generations.

The repeatability of specific combining ability effects (Tables 2 and 3) is much less than that of general combining ability effects. It was particularly more so for the F_1-F_2 generations. Consequently, it may not be possible to extrapolate heterotic effects in the F_1 from those determined in the F_2. The material will have to be studied in the F_1 generation when the objective is to study performance of hybrid varieties. Had the specific combining ability effects been mainly due to dominance and dominance × dominance epistasis in all the crosses the decline in specific effects over various generations would have been proportionate to the decline in heterozygosis and the relative ranking of different crosses would not have varied much over the generations. The absence of this situation indicated the presence of epistasis involving additive effects.

The perusal of specific combining ability estimated from grain yield showed that 'Kalyansona' × 'Argelto', 'K 68' × 'S413' and 'Sonalika' × 'S 413' had exhibited positive and significant specific effects over almost all the filial generations. This may be the result of additive × additive interaction effects. The bulk hybrid 'Kalyansona' × 'Argelto' gave a significantly higher yield in the F_5 generation than the commercially grown variety 'Kalyansona' and outyielded it by an increase of 10.63 per cent. Such crosses showing consistent and high specific effects over various filial generations, probably due to fixable gene effects, could be successfully utilized for the development of high yielding pure breeding lines. The crosses 'Kalyansona' × 'C 273' for number of spikes per plant; 'Kalyansona' × 'Sharbati Sonora' and 'K 68' × 'S 413' for number of grains per spike; and 'Kalyansona' × 'Sonalika', 'K 68' × 'Argelto', 'Sharbati Sonora' × 'S 413', 'Sonalika' × 'Sharbati Sonora', 'C 273' × 'S 413' and 'C 273' × 'Argelto' for 100 grain weight exhibited almost consistently high specific effects over various filial generations. Similarly for yield components, the exploitation of crosses with high specific effects offers a great scope for the isolation of lines with enhanced spike number, grain number and grain weight. The varieties showing a high general combining ability for grain yield were 'Kalyansona', 'Sonalika' and 'Sharbati Sonora' (Table 4). With regard to yield components, the better combining parents were 'Argelto' and 'S 413' for spikes per plant. 'Kalyansona' and 'Sharbati

Table 2. Estimates of specific combining ability effects

Crosses	Grain yield per plant					Number of spikes per plant				
	F_1	F_2	F_3	F_4	F_5	F_1	F_2	F_3	F_4	F_5
Kalyansona X Sonalika	1.81	0.57	0.98	−0.51	−0.31	−1.10	−1.46[a]	−0.14	−0.56	−0.58
Kalyansona X C 273	8.64[a]	−1.17	1.30	−2.11	−2.25	1.89[a]	0.97	1.53[a]	1.33[a]	0.92
Kalyansona X K 68	1.75	2.12	−2.64[a]	−2.80[a]	−2.78[a]	−0.53	0.20	0.05	0.44	−0.05
Kalyansona X Sharbati Sonora	0.35	1.54	−0.87	1.20	2.13	−0.33	0.08	−2.15[a]	−0.28	−0.35
Kalyansona X S 413	1.64	1.70	0.40	1.69	1.52	1.11	0.28	−0.77	−0.85[a]	−0.93
Kalyansona X Argelto	3.70[a]	1.05	3.61[a]	2.58[a]	4.02[a]	1.52	0.38	1.25[a]	−0.13	0.62
Sonalika X C 273	0.02	−0.77	−4.57[a]	−1.93[a]	−2.50[a]	0.26	−0.41[a]	−0.85[a]	−0.85	−0.65
Sonalika X K 68	2.40	−1.01	−0.19	0.07	−0.85	0.39	2.16[a]	0.90	1.81[a]	0.69
Sonalika X Sharbati Sonora	0.87	1.01	1.31	0.10	−0.01	1.49[a]	0.52	1.80[a]	−0.29	0.24
Sonalika X S 413	3.25[a]	2.52[a]	1.62	2.97[a]	2.78[a]	0.09	1.46[a]	−0.26	0.02	0.38
Sonalika X Argelto	−1.49	0.64	1.70	1.79[a]	1.02	−1.33[a]	−0.61	−0.56	0.46	−0.06
C 273 X K 68	−4.99[a]	−3.18[a]	−2.57[a]	−1.64	−1.00	−0.98	−1.06[a]	−1.37[a]	−0.70	−0.89
C 273 X Sharbati Sonora	4.71[a]	2.40[a]	−0.95	−1.26	−1.01	0.23	0.42	0.10	0.30	−0.06
C 273 X S 413	4.47[a]	1.22	2.58[a]	0.69	2.74[a]	0.53	0.20	0.39	0.02	0.27
C 273 X Argelto	2.15	0.74	2.62[a]	0.96	0.87	0.55	0.09	0.28	−0.27	−0.40
K 68 X Sharbati Sonora	5.50[a]	0.65	4.23[a]	−1.37	−0.76	1.42[a]	−1.03[a]	1.16[a]	−0.02	0.32
K 68 X S 413	4.72[a]	2.53[a]	2.49[a]	2.01[a]	0.33	−0.07	−0.76	1.04	−0.77	−0.97
K 68 X Argelto	5.87[a]	3.13[a]	−0.33	0.98	0.03	1.47[a]	1.15[a]	−0.36	−0.99	−1.09[a]
Sharbati Sonora X S 413	−6.44[a]	4.43[a]	3.21[a]	5.44[a]	4.27[a]	−1.24[a]	−1.50[a]	0.22	1.13	0.87
Sharbati Sonora X Argelto	1.18	1.02	0.62	0.93	1.80	−0.43	−0.39	1.27[a]	−0.34	0.04
S 413 X Argelto	−0.61	1.23	0.23	0.85	1.20	−0.49	0.19	0.30	1.30[a]	0.99
S.E. (S_{ij})	±1.42	±1.11	±0.88	±0.89	±0.00	±0.60	±0.53	±0.53	±0.43	±0.52
S.E. (S_{ij}-S_{ik})	±2.11	±1.65	±1.31	±1.32	±1.49	±0.90	±0.76	±0.78	±0.63	±0.77
S.E. (S_{ij}-S_{kl})	±1.97	±1.54	±1.22	±1.23	±1.37	±0.84	±0.71	±0.73	±0.59	±0.72

[a] significant at 5% level

Table 3. Estimates of specific combining ability effects

Crosses	Number of grains per spike					100-grain weight				
	F_1	F_2	F_3	F_4	F_5	F_1	F_2	F_3	F_4	F_5
Kalyansona X Sonalika	6.40[a]	0.31	−6.83[a]	−2.60[a]	−0.76	0.33[a]	0.48[a]	0.33[a]	0.30[a]	0.14[a]
Kalyansona X C 273	1.44	−4.86[a]	−10.10[a]	−4.81[a]	−3.69[a]	−0.30[a]	−0.24[a]	0.36[a]	−0.32[a]	−0.23[a]
Kalyansona X K 68	−6.38[a]	−2.37[a]	−8.56[a]	−5.81[a]	−5.02[a]	0.33[a]	0.13	0.17[a]	−0.15[a]	−0.14
Kalyansona X Sharbati Sonora	3.40[a]	2.47[a]	5.47[a]	4.67[a]	4.01[a]	0.15	0.06	0.21[a]	0.04	0.14
Kalyansona X S 413	1.68	−0.94	0.14	1.24	−0.14	0.06	−0.03	0.08	0.21[a]	0.24[a]
Kalyansona X Argelto	0.97	2.23[a]	5.17[a]	−0.03	2.06	0.03	−0.09	−0.21[a]	0.23[a]	0.25[a]
Sonalika X C 273	−3.06[a]	−1.25	−2.22[a]	−1.09	−1.20	−0.01	−0.34[a]	−0.25[a]	0.03	0.12
Sonalika X K 68	0.91	−0.10	−0.34	−0.50	2.17[a]	−0.07	−0.33[a]	−0.28[a]	−0.26[a]	−0.32[a]
Sonalika X Sharbati Sonora	−1.70	−0.38	−0.23	0.21	−1.77	0.18	0.40[a]	0.06	0.22[a]	0.17[a]
Sonalika X S 413	2.43[a]	1.80	5.66[a]	1.53	1.23	0.09	0.03	−0.14[a]	0.06	0.02
Sonalika X Argelto	0.04	0.59	1.35	0.41	−1.06	0.01	−0.42[a]	0.12	0.05	−0.01
C 273 X K 68	−4.04[a]	−1.93	−1.08	−0.80	−1.55	−0.29[a]	−0.08	0.01	0.01	−0.05
C 273 X Sharbati Sonora	1.05	3.69[a]	5.01[a]	−0.55	−0.70	0.29[a]	0.04	−0.53[a]	−0.31[a]	−0.27[a]
C 273 X S 413	−1.16	−0.63	0.74	0.04	2.08	0.61[a]	0.15	0.22[a]	0.15[a]	0.12
C 273 X Argelto	2.00	−2.88[a]	0.93	2.17[a]	1.41	0.57[a]	0.48[a]	0.14	0.09	0.20[a]
K 68 X Sharbati Sonora	−0.32	−0.70	1.22	−0.34	0.42	0.40[a]	−0.35[a]	0.22[a]	0.01	−0.12
K 68 X S 413	6.64[a]	4.56[a]	6.21[a]	3.03[a]	2.43[a]	0.45[a]	0.43[a]	−0.18[a]	0.26[a]	0.28[a]
K 68 X Argelto	7.21[a]	0.44	−1.45	−0.70	−1.60	0.35[a]	0.27[a]	0.13[a]	0.29[a]	0.24[a]
Sharbati Sonora X S 413	−1.70	−0.40	−1.24	3.03[a]	2.49[a]	0.19	0.26[a]	0.26[a]	0.21[a]	0.26[a]
Sharbati Sonora X Argelto	2.03	1.54	−5.95[a]	1.06	2.47[a]	−0.12	0.06	0.19[a]	0.05	0.05
S 413 X Argelto	−2.43[a]	1.16	0.30	−0.75	0.07	−0.06	0.02	0.07	0.08	−0.04
S.E. (S_{ij})	±1.13	±1.10	±1.10	±1.07	±1.06	±0.10	±0.08	±0.08	±0.07	±0.07
S.E. (S_{ij}-S_{ik})	±1.68	±1.64	±1.63	±1.58	±1.57	±0.14	±0.12	±0.11	±0.11	±0.12
S.E. (S_{ij}-S_{kl})	±1.58	±1.53	±1.53	±1.48	±1.47	±0.15	±0.11	±0.09	±0.10	±0.11

[a] significant at 5% level

Table 4. Estimates of general combining ability

Generation	Parental variety	Grain yield	Number of spikes per plant	Number of grains per spike	100-grain weight
F_1	Kalyansona	2.96	0.04	10.61	−0.35
	Sonalika	−0.02	−0.94	−1.85	0.30
	C 273	1.60	0.22	−4.02	0.26
	K 68	1.23	−0.58	−2.53	0.39
	Sharbati Sonora	−0.47	−0.88	−0.22	0.10
	S 413	−3.90	0.42	−2.06	−0.33
	Argelto	−1.41	1.71	0.08	−0.36
	S.E. (gi)	±0.48	±0.32	±0.60	±0.05
F_2	Kalyansona	1.58	−0.44	8.88	−0.23
	Sonalika	0.65	−0.44	−1.93	0.27
	C 273	−0.70	−0.30	−4.12	0.20
	K 68	0.12	−0.80	−2.63	0.26
	Sharbati Sonora	0.94	−0.85	1.57	0.10
	S 413	−2.06	1.20	−1.10	−0.30
	Argelto	−0.52	1.63	−0.68	−0.29
	S.E. (gi)	±0.58	±0.27	±0.58	±0.04
F_3	Kalyansona	1.37	−0.61	6.67	−0.11
	Sonalika	0.66	−0.62	−2.28	0.28
	C 273	−0.36	−0.33	−3.29	0.19
	K 68	−0.15	−0.60	−3.06	0.27
	Sharbati Sonora	0.60	−0.52	1.63	0.09
	S 413	−2.30	0.71	1.01	−0.42
	Argelto	0.18	1.97	−0.68	−0.29
	S.E. (gi)	±0.46	±0.28	±0.58	±0.03
F_4	Kalyansona	0.98	−0.37	8.04	−0.27
	Sonalika	1.37	−0.43	−2.47	0.40
	C 273	−0.99	−0.12	−3.20	0.11
	K 68	−0.79	−0.81	−3.68	0.26
	Sharbati Sonora	0.27	−0.80	2.25	0.04
	S 413	−1.22	0.89	−0.25	−0.30
	Argelto	0.39	1.63	−0.69	−0.24
	S.E. (gi)	±0.47	±0.22	±0.56	±0.04
F_5	Kalyansona	1.51	−0.32	8.72	−0.26
	Sonalika	0.74	−0.52	−2.60	0.35
	C 273	−0.50	−0.23	−3.13	0.17
	K 68	−1.41	−1.13	−3.46	0.22
	Sharbati Sonora	0.57	−0.53	1.68	0.04
	S 413	−1.47	0.96	−0.52	−0.29
	Argelto	0.56	1.78	−0.68	−0.23
	S.E. (gi)	±0.53	±0.27	±0.56	±0.04

Sonora' for number of grains per spike and 'Sonalika', 'K 68', 'C 273' and 'Sharbati Sonora' for 100 grain weight.

In general, the general combining ability estimates provided better prediction of bulk hybrid performance in the F_5 generation than the per se performance of the parents. Among various filial generations, estimates from the F_2/F_3 generations gave better predictions than those from the F_1. The repeatability of general combining ability estimates over various generations and the availability of rather better estimates from the F_2/F_3 indicate that it may be advisable to study combining ability in wheat in the F_2 rather than in the F_1. This will also enable multi-environment testing as there will not be any limitation of seed quantity usually encountered in the F_1 generation. A cheap and reliable procedure for making a choice of parents, selecting hybrids and predicting advanced generation bulk hybrid performance would, therefore, be the determination of the breeding value of the parents by the relative performance of their F_2 progeny bulks.

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