STUDY OF COMBINING ABILITY AND GENETIC PARAMETERS FOR YIELD AND ITS COMPONENTS IN WHEAT

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Hybridization and selection of superior homozygous lines in the segregating generations have been the main procedure for improving wheat yield. However, in recent years the discovery of cytoplasmic male sterility and restorer genes in wheat has created considerable enthusiasm for the development of hybrid varieties. This approach, according to Cockerham (1961), is useful only if the substantial number of loci exhibit overdominance.

Though significant superior performance of F_1 over the better parent has been reported in several wheat crosses (Briggle 1963; Singh and Kandola 1969) but the evidence for the presence of considerable non-additive genetic variance is somewhat controversial. Whitehouse *et al.* (1958) observed that gene interactions were important for grain yield per plant while Lumpton (1961) reported dominance for high yield. However, Tandon (1961) reported that grain yield in case of five wheat varieties studied by him was controlled by additive gene effects in F_1 generation. Also Kronstad and Foote (1964) and Brown *et al.* (1966) found that most of the variation in yield and other characters of F_1 hybrids in wheat was associated with the high general combining ability rather than with specific combining ability variance.

The true knowledge of the genetic parameters for various characters is useful in making decisions with regard to appropriate breeding system and the estimates of general and specific combining ability may be useful in the choice of parents. Whitehouse *et al.* (1958) and Lumpton (1961) described the application of diallel analysis suggested by Hayman (1954) and Jinks (1954) for this purpose, but not much work has been done on these lines, particularly when the estimates made on a set of material may not have general application. Therefore, the present investigation was undertaken to estimate various genetic parameters and general and specific combining ability in a seven $\times$ seven diallel cross involving some of the most promising wheat varieties in India from the United States and Mexican origin.

MATERIALS AND METHODS

A diallel set was made by crossing (one way, no reciprocals) seven well adapted wheat varieties; two from U.S.A. and five from Mexico during 1966-67 season at the

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Punjab Agricultural University, Ludhiana. The seven parents and their 21 F_1 s were sown in a randomised block design with four replications. Each plot consisted of a single row of 120 cm length, having 12 plants in each row at 10 cm apart. The rows were spaced at 22.5 cm apart. To ensure perfect stand, two seeds at each hill, where sufficient F_1 seed was available, were planted and the extra seeding was pulled out as soon as one plant was well established. Non-experimental rows were planted all around the experimental plots to remove the border effect. Since the varieties under study included tall as well as dwarf plant types, the crop was grown at 80 lbs N/acre so that the tall parent and their crosses do not lodge and have disadvantage. Five plants were selected at random from each plot and observations were recorded on spikes per plant, number of spikelets per spike, 100-kernel weight and grain yield. The analysis was made on mean of five plants. The analysis of variance for combining ability and estimation of various effects was done following the technique of Griffing (1956) for system 2, Model I, assuming that the inference is to be drawn only on the population studied, and the genetic parameters D , H_1 , H_2 , F , $\sqrt{H_1/D}$, U , V were estimated as described by Hayman (1954). Also the data for various characters were subjected to graphic analysis for determining gene action (Jinks 1954).

RESULTS

The mean values of the seven parents and their 21 F_1 hybrids for all the four characters are given in Table 1. The variances due to general combining ability of the parents, specific combining ability of their crosses and error variances for different characters are presented in Table 2. The analysis of variance for general and specific combining ability indicated highly significant differences for all characters except grain yield where specific combining ability was highly significant but general combining ability was significant at 5 per cent only. When tested against the specific combining ability variance, the general combining ability variance was not significant for spike number and grain yield. This indicates that the specific combining ability effects were as important as the general combining ability effects for these characters.

The estimated general combining ability of the parents and the specific combining ability of the crosses are given in Table 3 and 4, respectively. The general combining ability estimates show that the parents S 210, for spike number, U. S. A. 255 and Kalyan 227 for spikelet number, U.S.A. 190 and U.S.A. 255 for 100-kernel weight and Kalyan 277 and U.S.A. 255 for yield had the highest general combining ability and the crosses between, Kalyan 277 $\times$ S 308 for spike number, U.S.A. 190 $\times$ S 308 and U.S.A. 255 $\times$ S 310 for spikelet number, U.S.A. 190 $\times$ PV-18 for 100-kernel weight and U.S.A. 255 $\times$ Kalyan 277 and Kalyan 277 $\times$ S 308 for yield had the highest values for specific combining ability.

GRAPHICAL ANALYSIS

The graphical presentation for different characters is given in Figures 1 to 4.

Spike number

In V_r - W_r graph, the slope of regression line fell significantly below unity ($b = .25$)

Table 1. Mean values of seven parents and their F₁ hybrids for spike number, spikelet number, 100-kernel weight and grain yield in wheat

Pedigree	Spike number	Spikelet number	100-kernel weight	Grain yield
USA 190	11.3	19.3	4.76	21.75
USA 255	9.5	21.2	4.77	24.87
Kalyan 227	9.5	21.9	4.26	26.78
S 210	12.3	20.4	4.45	22.00
S 310	10.0	20.3	4.29	19.82
PV 18	9.8	20.9	4.11	25.78
S 308	11.1	18.7	4.72	22.89
USA 190 × USA 255	11.6	21.1	5.08	31.10
× Kalyan 227	11.5	21.9	5.01	35.85
× S 210	12.3	20.0	5.14	30.51
× S 310	12.4	21.1	5.08	29.25
× PV 18	12.1	21.2	5.02	31.90
× S 308	10.3	20.9	5.32	28.73
USA 255 × Kalyan 227	10.8	22.2	4.82	39.18
× S 210	12.7	21.7	4.93	30.81
× S 310	11.5	22.1	5.13	30.48
× PV 18	11.7	20.8	4.79	34.02
× S 308	10.9	21.0	5.09	28.60
Kalyan 227 × S 210	12.7	21.8	4.69	34.87
× S 310	11.4	20.9	4.72	29.37
× PV 18	11.8	21.3	3.95	27.90
× S 308	14.5	20.9	4.52	36.10
S 210 × S 310	11.4	21.5	4.99	26.38
× PV 18	13.7	22.1	4.59	34.60
× S 308	11.8	19.6	4.81	27.56
S 310 × PV 18	11.9	21.3	4.49	28.24
× S 308	10.3	20.4	4.81	26.95
PV 18 × S 308	12.4	20.4	4.77	29.06
S.E. ±	1.04	0.39	0.15	3.60
L.S.D. 5%	2.07	0.78	0.30	7.16

Table 2. Analysis of variance for combining ability

Source of variation	d.f.	Mean squares for different characters			
		Number of spikes	Number of spikelets/spike	100-kernel weight	Grain Yield
g.c.a.	6	1.78**	1.84**	0.2817**	24.71*
s.c.a.	21	1.27**	0.42**	0.0605**	20.70**
Error	81	0.55	0.08	0.0019	8.46

* Significant at P=.05

** Significant at P=.01

Table 3. General combining ability effects of parents

Parents	Estimated g.c.a. effect of parents			
	Number of spikes	Number of spikelets/spike	100-kernel weight	Grain yield
1. USA 190	0.06	-0.32	0.24	-0.32
2. USA 255	-0.46	0.40	0.15	1.22
3. Kalyan 227	-0.07	0.57	-0.20	2.65
4. S 210	0.77	-0.02	0.00	-0.47
5. S 310	-0.38	0.02	-0.03	-2.52
6. PV 18	0.10	0.13	-0.24	0.48
7. S 308	0.01	-0.79	0.08	-1.13
S.E. $\pm$ (gi)	0.48	0.18	0.07	1.91

Table 4. Specific combining ability effects of different cross combinations

Crosses		Spike number	Spikelet number	100-kernel weight	Grain yield
USA 190	$\times$ USA 255	0.47	0.05	0.05	1.00
	$\times$ Kalyan 227	-0.02	-0.11	0.22	4.31
	$\times$ S 210	-0.05	-0.62	0.15	2.10
	$\times$ S 310	1.20	-0.57	0.20	2.88
	$\times$ PV 18	0.41	0.42	0.28	2.54
	$\times$ S 308	-1.30	1.01	0.25	0.98
USA 255	$\times$ Kalyan 227	-0.22	0.27	0.12	6.19
	$\times$ S 210	0.86	0.36	0.03	0.94
	$\times$ S 310	0.80	0.71	0.25	2.66
	$\times$ PV 18	0.52	-0.70	0.13	3.20
	$\times$ S 308	-0.19	0.42	0.11	-0.60
Kalyan 227	$\times$ S 210	0.47	0.29	0.14	3.57
	$\times$ S 310	0.31	-0.66	0.19	0.12
	$\times$ PV 18	0.24	-0.37	-0.36	4.35
	$\times$ S 308	3.02	0.16	-0.11	5.46
S 210	$\times$ S 310	-0.52	0.51	0.26	0.25
	$\times$ PV 18	1.38	0.22	0.08	5.13
	$\times$ S 308	-0.51	-0.56	-0.02	0.05
S 310	$\times$ PV 18	0.65	-0.16	0.01	1.16
	$\times$ S 308	0.86	0.20	0.00	1.48
PV 18	$\times$ S 308	0.76	0.09	0.18	0.60
S.E. $\pm$ (Sij)		0.69	0.16	0.20	2.69
L.S.D. at 5%		1.37	0.52	0.20	7.10

indicating the presence of genetic interactions. As the regression line intersects the Wr-axis below the point of origin, it indicates the presence of overdominance for the character. The array points are lying away from the regression line suggesting the presence of environmental interaction. The parents USA 190 and S 210 were nearest to the point of origin and thus have the highest number of dominant genes, while Kalyan 227 was at the farthest from the point of origin which shows that Kalyan 227 have the lowest number of dominant genes. In Wr-W' graph, the regression line significantly

Fig. 1. a. Vr .- Wr graph for number of spikes per plant for seven wheat varieties.

Fig. 1. b. Wr .- W' graph for number of spikes per plant for seven wheat varieties.

Fig. 2. a. Vr .- Wr graph for spikelets per spike for seven wheat varieties.

Fig. 2. b. Wr .- W' graph for spikelets per spike for seven wheat varieties.

Fig. 3. a. Vr .- Wr graph for 100-kernel weight for seven wheat varieties.

Fig. 3. b. Wr .- W' graph for 100-kernel weight for seven wheat varieties.

Fig. 4. a. Vr-Wr graph for grain yield for seven wheat varieties.

Fig. 4. b. Wr-W' graph for grain yield for seven wheat varieties.

deviated from the unit slope and thus indicating the presence of gene interactions. The scatter of parental points along the regression line in Wr-W' graph showed homozygosity to be present in the parents with regard to this character. The parents U.S.A. 190, S 310 and S 308 falling in the second quadrant confirmed the presence of overdominance for this character.

Spikelets per spike

In the Vr-Wr graph for this character, the regression line has a slope of approximately unity ($b = .94$). The presence of parental point along the regression line confirms the absence of environmental interaction. The regression line shifted slightly to the right indicating the presence of overdominance. The parent PV 18 being nearest to the point of origin has maximum number of dominant genes for the increased number of spikelets per spike. The parents U.S.A. 255, Kalyan 227 and S 310 appeared to have more number of dominant genes than the parents U.S.A. 190, S 308 and S 210 but less than PV 18. The parent S 210 being farthest from the point of origin indicates the presence of minimum number of dominant genes. The parents U.S.A. 190 and S 310 appeared to have equal number of dominant and recessive genes. In the Wr-W' graph the regression line significantly deviated from the expected regression line which confirms the presence of genic interactions. The presence of genetic diversity as indicated in Vr-Wr graph was confirmed by this graph. In both the graphs the parents U.S.A. 255, Kalyan 227, S 310 and PV 18 formed a cluster along the regression line while the parents U.S.A. 190, S 210 and S 308 occupied their position well away from them showing differences between the parents with regard to this character.

100-kernel weight

In Vr-Wr graph the slope of the regression line, $b = 0.75$, deviated significantly from the unit slope indicating the presence of genic interactions. As the regression line intersects the Wr-axis below the point of origin, it suggests the presence of overdominance. This point was confirmed from the fact that all the array points fell below the expected regression line. All the array points occupied their position along the regression line, which indicate the absence of environmental interactions. The parents U.S.A. 190 and U.S.A. 255 being closest to the point of origin have higher number of dominant genes for increased 100-kernel weight, while PV 18 and Kalyan 227 being farthest from

the point of origin carry maximum number of recessive genes for this character. Remaining parents seem to have varying number of genes. In the W_r-W' graph the regression line deviated significantly from the expected regression line, thus confirming the presence of genic interactions. The presence of majority of parental points above the regression line confirms the presence of complementary type of epistasis. The presence of array points along the regression line confirmed the absence of environmental interactions as indicated by V_r-W_r graph. Wide genetic diversity was also exhibited by W_r-W' graphs as the parental points occupy their position well away from each other.

Grain yield

In the V_r-W_r graph, the slope of regression line is $b=0.28$ which deviated significantly from unit slope indicating the presence of genic interaction, poor heritability and complex nature of the character. All the array points occupied their positions well away from the point of origin, which indicates that none of the parents is having sufficient number of dominant genes for this character but the scattered array points suggests differences between parents with regard to yield. The W_r-W' graph helped in identifying similar conclusion, as was drawn from V_r-W_r graph viz., genic interaction, overdominance, genetic diversity and complimentary type of epistasis.

ESTIMATION OF GENIC COMPONENT OF VARIATION

The component of variation for different characters are given in Table 5. The values for D , which is the measure of additive component, for spike number and spike-

Table 5. Variance components for different characters

	D	F	H_1	H_2	UV	Degree of dominance $\sqrt{H_1/D}$
Number of spikes per plant	6.43	12.08	10.28	4.16	0.101	1.60
Spikelets per spike	7.17	12.56	45.00	38.36	0.213	2.51
100-kernel weight	0.07	-0.06	0.18	0.16	0.220	1.60
Grain yield	0.14	-9.48	46.12	44.2	0.2388	15.13

lets per spike were higher than the 100-kernel weight and grain yield suggesting that additive portion of variation was higher for spike number and spikelets per spike. The F values for spikelet number and spike number were positive while for seed size (100-kernel weight) and grain yield were negative suggesting that spikelet number and spike number had more dominant genes while other two characters had more recessive genes. The measure of H_1 and H_2 for spikelet number and grain yield was much higher whereas for seed size it was very low and for spike number it was moderate. The measure of degree of dominance, $\sqrt{H_1/D}$, was quite high for grain yield while for other characters it was fairly low. The values of UV were slightly lower than the maximum possible value (0.25) expected under an equality of positive and negative values whereas for spike number the value was much lower.

DISCUSSION

The general combining ability for various characters showed that the magnitude of general combining ability effects was much higher in case of spikelets per spike and 100-kernel weight, though statistically both general and specific combining ability variances were significant. However, in case of spike number and grain yield general and specific combining ability effects were of almost same order. These findings are at variance with the earlier reports of Kronstad and Foote (1964), Brown *et al.* (1966) who observed the non-existence of specific combining ability variance in wheat.

The gene action expressed by the Vr-Wr and Wr-W' graphs for these characters in general showed non-additive type of action, and gave an indication of complimentary duplicate epistasis and high environmental interactions for the characters spike number and grain yield, which is clearly reflected in the general and specific combining ability estimates. Importance of non-allelic interaction for spike number and grain yield has also been observed by Lumpton (1961) and for grain weight by Patterson and Bitzer (1966). The character 100-grain weight has been found to be controlled mainly by additive gene action by the earlier workers (Kronstad and Foote 1964; Brown *et al.* 1966; Lumpton 1961). However, indications of overdominance and genic interactions in the present study may be due to the fact that though there were significant differences in seed size of the parental varieties, but the gap was quite narrow, hence the parents may not have the same dominant genes which may be the cause for the observed overdominance. Johnson (1966) also observed considerable degree of overdominance for this character.

Though the predictions from Vr-Wr and Wr-W' graphs are in agreement with the combining ability estimates, but as has already been stated the magnitude of specific combining ability in case of yield is the only sizeable estimate which reflects importance of non-additive type of gene action, Matzinger (1963) reviewed the literature on quantitative inheritance studies in self pollinating species and stated that 'large amount of dominance may have been due to the bias in the estimates, which is inherent in almost all the designs.' Also the environmental conditions have been found to accentuate specific combining ability estimates to a fair degree. The grain yield is known to be highly effected by the environmental conditions for which there is an indication in Vr-Wr graph for the character, and therefore, may have affected this estimate to a greater degree than the specific combining ability estimate for other components of yield. This may be particularly relevant in the light of the fact that the trial in the present study was conducted at 80 lbs of N level which was not conducive for full expression of potential of two gene dwarf parents and therefore, the hybrids between them and the other parents would have expressed better, as hybrids are generally known to do well even in suboptimal conditions (Griffing and Langridge 1963; Finley 1960a, b)

With regard to the importance of different parents in a breeding programme for improving yield or any of its components, the results of the study show that the parents Kalyan 227 and U.S.A. 255 were the best since they had the highest general combining ability value for yield and spikelet number while U.S.A. 255 was also having the highest

general combining ability value for 100-kernel weight. Also these two parents were having the highest specific combining ability for yield and the parent U.S.A. 255 was one of the parents involved in high specific combinations for spike number, spikelet number and the 100-kernel weight. The parents PV 18 and U.S.A. 190 were the next best general combiners for most of the characters and the parents S 308, S 310 and S 210 as one of the parents among the best specific combinations for yield and its components.

In general the predictions regarding the parents made from general and specific combining ability are in line with the gene action indicated by the V_r - W , W_r - W' graphs for different characters. The parents Kalyan 227, U.S.A. 255 and PV 18 which had high general combining ability also had more number of dominant genes for spikelet number and U.S.A. 190 and U.S.A. 255 for 100-kernel weight.

The graphical analysis indicates that in case of yield the gene interactions are quite important, this is evident from the crosses Kalyan 227 $\times$ S 308 and Kalyan 227 $\times$ U.S.A. 255 which showed the maximum heterosis and the specific combining ability.

It may be pointed out here that the value of the parents *per se* for yield and its components was in fairly close agreement with the one obtained by general combining ability estimates and therefore, the selection of the parents based on parental value, which has been the common practice is reasonably good.

Implications on breeding approach in wheat

The estimates of high general combining ability suggest the importance of additive genetic variance for all other characters except yield, where general as well as specific combining ability variances are of similar magnitude. Though on evolutionary grounds (Fisher 1930; Metzinger 1963) specific combining ability based on non-additive gene action is likely to be small in wheat but the reports of fairly high expression of heterosis in certain crosses of wheat points out towards its presence particularly in specific combinations, which is evident from the present study also. This suggests for a breeding approach by which the advantage of both type of variances viz. additive and non-additive is taken.

Ordinarily the exploitation of additive genetic variance is easy since this can be mobilized by simple methods of progeny selection. However, when large number of genes are involved, it becomes difficult to accumulate all of them in homozygous pure lines due to linkage limitations. Under these circumstances very intricate, time consuming methods of recurrent selection as suggested by Andrus (1963) or obligate cross fertilizing system through the use of cytoplasmic male sterility (Athwal and Bourlaug 1968) may be used. Once a plateau has been reached through these approaches, the further increase may be possible by the exploitation of non-additive genetic variance, which is done best by developing hybrid varieties. These may prove highly useful, short time solution for yield improvement or circumventing specific situations like overcoming a particular disease by use of dominant genes. Since the work in other self pollinated species like tobacco (Smith 1952) and tomato (Powers 1952; Williams 1959) has shown that in these crops, which show high degree of heterosis, it is possible to develop pure line varieties, which perform better or as good as the hybrid varieties. This

may be true in wheat also, because even in case of a cross pollinated crop like maize increasing importance of additive genetic variance is being realized.

It has been generally observed in many plant species including wheat (Singh and Kandola 1969) that crosses between genetically diverse parents exhibit more heterosis than crosses between more closely related lines. This indicates that selection for favourable genes with additive effects in separate and diverse populations as a first step would be desirable and maximum useful heterosis might be obtained in the specific combination later on.

SUMMARY

A set of seven wheat varieties from two different ecogeographical origins were studied in a diallel cross to find out the combining ability and the genetic parameters for yield and its components. The general and specific combining ability estimates for spike number per plant, spikelets per spike and seed size indicated predominance of additive gene effects, while for yield the variance for general and specific combining ability were of same order, suggesting importance of additive as well as non-additive effects. *Per se* performance of the varieties was in close agreement with the general combining ability estimate.

The Vr-Wr and Wr-W' graphs showed overdominance for spikes per plant, spikelets per spike, 100-kernel weight and grain yield. In general the predictions regarding the parents made from general and specific combining abilities are in line with gene action indicated by the Vr-Wr and Wr-W' graphs for different characters.

Implications of the genetic parameters on breeding approach in wheat have been discussed.

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