

Comparative Evaluation of Combining Ability and Graphical Analyses of Diallel Cross

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Combining ability and graphical analyses in F_1 to F_5 generations of diallel cross of seven genetically diverse parents of wheat (*Triticum aestivum* L.) were carried out. Grain yield/plant, number of spikes/plant, number of grains/spike and 100-grain weight were studied. Both the analyses in F_1 generation indicated a greater importance of non-additive than additive genetic variation for grain yield and almost equal importance of additive and non-additive components for spikes/plant. Combining ability analysis of grains per spike and 100-grain weight revealed a greater role of additive variation but graphical analysis indicated complete dominance to over-dominance. Additive \times additive epistasis seemed to be predominant component of specific combining ability variance. The results over various generations were not as expected on simple additive-dominance model—results from the F_2 generation were in better agreement with those from the F_3 , F_4 and F_5 when compared to results from the F_1 . The combining ability analysis appeared better than the graphical analysis with respect to consistency of results over generations and as a predictor of prepotency of parents.

Key Words: *Triticum aestivum* L., Diallel analysis, Epistasis, Successive generations, Parental selection

Introduction

Plant breeders, in their endeavour to develop better genotypes, are concerned with the estimation of various genetic parameters. These estimates guide in choosing parents and provide information about appropriate methods and expected genetic gains. Diallel analysis has been widely used to investigate the inheritance of quantitative characters. Combining ability estimation (Griffing 1956a), graphical

and variance component estimation (Hayman 1954, Jinks 1954) are the most frequently used approaches. In the present investigation, combining ability and graphical analyses methods are compared using F_1 to F_5 generations of a seven parent diallel cross in bread wheat (*Triticum aestivum* L.) in order to determine the nature and magnitude of gene action and prepotency of parents.

Materials and Methods

Materials included seven genetically diverge parents (Kalyansona, Sonalika, Sharbati Sonora, and S 314 of Mexican origin; C 273 and K 68 of Indian origin and Argelto from France) and the F₁ to F₅ generations of all possible crosses among them excluding reciprocals. The materials were grown in a randomised complete block design with four replications at the Punjab Agricultural University, Ludhiana. Each F₁ plant was grown in one-row plot whereas the parents and F₂ to F₅ generations of the diallel were grown in four-row plots. Rows were 3m long and spaced 30cm apart with the plants spaced 15cm apart. The data were recorded on 10 competitive plants in each row for grain yield/plant (g), number of spikes/plant, number of grains/spike and 100-grain weight (g). Plot means were subjected to

graphical analysis following Hayman (1954) and Jinks (1954) and combining ability analysis using Method 2 of Griffing (1956a) assuming the Model I, fixed effects model, of Eisenhart (1947).

Results and Discussion*Combining Ability Analysis*

The estimates of fixed components of variance relating to general combining ability (GCA) and specific combining ability (SCA) are given in (table 1). For grain yield the magnitude of SCA component was considerably greater than that of GCA component in all the filial generations. For the component traits, on the other hand, GCA component was greater than the SCA component in all the cases except grains/spike and grain weight in F₃ and F₂ generations, respectively.

Table 1 Estimates of fixed components of general (ϕ_g^2) and specific (ϕ_e^2) combining ability variances

Character	Generation	ϕ_g^2	ϕ_e^2	σ^2
Grain yield/plant	F1	4.73**	25.58**	2.50
	F2	1.31**	7.35**	1.53
	F3	1.25**	7.16**	0.96
	F4	0.92**	6.77**	0.98
	F5	1.17**	6.71**	1.25
Spikes/plant	F1			
	F2	0.81**	0.70**	0.45
	F3	0.95**	0.68**	0.32
	F4	0.89**	0.81**	0.35
	F5	0.83**	0.38**	0.22
Grains/spike	F1			
	F2	0.98**	0.16	0.33
	F3	23.65**	13.24**	1.60
	F4	18.27**	4.96**	1.51
	F5	12.18**	24.08**	1.50
100-grain weight	F1			
	F2	16.53**	7.10**	1.41
	F3	17.86**	5.40**	1.39
	F4	1.13**	0.15**	0.01
	F5	0.07**	0.09**	0.01
	F3	0.08**	0.06**	0.01
	F4	0.08**	0.05**	0.01
	F5	0.07**	0.04**	0.01

**Significant at 1% level.

The estimates of GCA effects are given in table 2. Kalyansona was a good general combiner for grain yield, whereas Sonalika and Sharbati Sonora had average to good GCA. With regard to spike number, S 413 and Argelto had positive GCA effects in all the generations. Kalyansona and Sharbati Sonora for grains per spike and Sonalika, C 273 and K 68 for grain weight showed in general better GCA. Poor combining ability

was shown by C 273 and S 413 for grain yield; Kalyansona, Sonalika, K 68, and Sharbati Sonora for spike number; Sonalika, C 273, K 68 and S 413 for grains/spike; and Kalyansona, S 413 and Argelto for grain weight.

Rank correlations among GCA effects obtained from the analysis of different generations are presented in table 3. The correlation coefficients were positive and significant

Table 2 Estimates of general combining ability effects

Character	GCA effects				
	F ₁	F ₂	F ₃	F ₄	F ₅
GRAIN YIELD PER PLANT					
Kalyansona	2.96	1.58	1.37	0.98	1.51
Sonalika	-0.02	0.65	0.66	1.37	0.74
C 273	1.60	-0.70	-0.36	-0.99	-0.50
K 68	1.23	0.12	-0.15	-0.79	-1.41
Sharbati Sonora	-0.47	0.94	0.60	0.27	0.57
S 413	-3.90	-2.06	-2.30	-1.22	-1.47
Argelto	-1.41	-0.52	0.18	0.39	0.56
S.E. (gi)	±0.48	±0.58	±0.48	±0.47	±0.53
SPIKES PER PLANT					
Kalyansona	0.04	-0.44	-0.61	-0.37	-0.32
Sonalika	-0.94	-0.44	-0.62	-0.43	-0.52
C 273	0.22	-0.30	-0.33	-0.12	-0.23
K 68	-0.58	-0.80	-0.60	-0.81	-1.13
Sharbati Sonora	-0.88	-0.85	-0.52	-0.80	-0.53
S 413	0.42	1.20	0.71	0.89	0.96
Argelto	1.71	1.63	1.97	1.63	1.78
S.E. (gi)	±0.32	±0.27	±0.28	±0.22	±0.27
GRAINS PER SPIKE					
Kalyansona	10.61	0.88	6.67	8.04	8.72
Sonalika	-1.85	-1.93	-2.28	-2.47	-2.60
C 273	-4.02	-4.12	-3.29	-3.20	-3.13
K 68	-2.53	-2.63	-3.06	-3.68	-3.46
Sharbati Sonora	-0.22	1.57	1.63	2.25	1.68
S 413	-2.06	-1.10	1.01	-0.25	-0.52
Argelto	0.08	-0.68	-0.68	-0.69	-0.68
S.E. (gi)	±0.60	±0.58	±0.58	±0.56	±0.56
100-GRAIN WEIGHT					
Kalyansona	-0.35	-0.23	-0.11	-0.27	-0.26
Sonalika	0.30	0.27	0.28	0.40	0.35
C 273	0.26	0.20	0.19	0.11	0.17
K 68	0.39	0.26	0.27	0.26	0.22
Sharbati Sonora	0.10	0.10	0.09	0.04	0.04
S 413	-0.33	-0.30	-0.42	-0.30	-0.29
Argelto	-0.36	-0.29	-0.29	-0.24	-0.23
S.E. (gi)	±0.05	±0.04	±0.03	±0.04	±0.04

Table 3 Rank correlations among different generations with respect to GCA effects and Wr + Vr estimates

		Grain yield/plant				Spikes/plant			
		F ₂	F ₃	F ₄	F ₅	F ₂	F ₃	F ₄	F ₅
F ₁	GCA	.500	.428	.286	.643	.893**	.750*	.857*	.857*
	Wr+Vr	.893**	.571	.857*	.714	.214	.357	-.607	.000
F ₂	GCA		.928**	.768*	.857*		.938**	.964**	.964**
	Wr+Vr		.357	.750	.714		.500	-.750	-.714
F ₃	GCA			.928**	.928**			.928**	.964**
	Wr+Vr			.750	.714			-.393	-.143
F ₄	GCA				.857*				1.000**
	Wr+Vr				.893**				.750

*, **Significant at 5 and 1% respectively

with the exception of those involving F₁ generation for grain yield. It may be added that it was only for grain yield that SCA component was markedly greater than the GCA component. The correlation coefficients of F₂ versus F₃ to F₅ generations were generally higher than F₁ versus F₃ to F₅ generations for all the traits. However, these correlation coefficients are based on 5 degrees of freedom only.

Arunachalam (1976) cautioned against the use of F₂ and other segregating generations for various analyses. According to him the results obtained from the segregating generations may be biased due to differential segregation, unconscious selection or natural selection. In addition, a large sample is required in segregating generations. However, reports on combining ability analysis of F₂ or advanced generations are being published (Jordaan & Laubscher 1968, Gupta & Ahmed 1979).

In the F₁ generation of crosses among pure bred parents, the inbreeding coefficient of parents will be one and that of the progenies zero (Stuber 1970). Considering random effects model, the relationship of the variance components of general (σ_g^2) and specific (σ_s^2) combining abilities with additive-genetic (σ_A^2) and dominance (σ_D^2) and interaction

($\sigma_{AA}^2, \sigma_{AD}^2, \sigma_{DD}^2, \dots$) as defined by the subscript A and D) variances are:

$$2 \sigma_g^2 = \sigma_A^2 + \frac{1}{2} \sigma_{AA}^2 \dots \dots \dots$$

$$\sigma_s^2 = \sigma_D^2 + \frac{1}{2} \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 \dots$$

The relationship involving σ_s^2 will change with a change in the inbreeding coefficient of the progenies as the segregating generations are advanced, resulting in a decreased contribution of $\sigma_D^2, \sigma_{AD}^2$ and σ_{DD}^2 . However, contribution of σ_{AA}^2 towards σ_s^2 is not affected. In the F₁ $\sigma_s^2 = \sigma_D^2$, in F₂ $\sigma_s^2 = 1/4 \sigma_D^2$, in F₃ $\sigma_s^2 = 1/16 \sigma_D^2$ and so on if the epistasis is assumed to be absent.

The expected trend of a consistent GCA component and a decreasing SCA component over generations was not realised in the present study. Both GCA and SCA components decreased from F₁ to F₂ for grain yield, grains/spike and grain weight (table 1) and in case of grain weight the fall in the GCA component was very drastic. From F₂ to F₅ GCA component for these traits and SCA component for grain yield remained almost constant. For grains/spike, the SCA component in the F₂ was low and in the F₃ it was abnormally high. GCA component was stable over generations for spikes/plant but the SCA component for this trait

Grains/spike				100-grain weight			
F ₂	F ₃	F ₄	F ₅	F ₂	F ₃	F ₄	F ₅
.928**	.750	.786*	.786*	.893**	.857*	.825*	.821*
-.107	-.214	.071	.036	.928**	.607	.714	.750
	.893*	.928**	.928**		.964**	.928**	.928**
	.964**	.786*	.893**		.678	.571	.714
		.928**	.928**			.964**	.964**
		.857*	.928**			.321	.321
			1.000*				1.000**
			.964**				.893**

*, **Significant at 5 and 1% respectively

diminished in F₄ and F₅. The persistence of SCA component up to F₅ for grain yield, grains/spike and grain weight, indicated that the additive × additive component was important. For 100-grain weight, there was a consistent decrease in SCA component as generation advanced indicating the decreasing importance of the dominance component and epistatic components involving dominance.

For grain yield, grains/spike and grain weight, the GCA component decreased in F₂ but thereafter showed relatively a good level of constancy indicating that advancing from F₁ to F₂ is critical. The estimates of GCA components in F₂ were more reliable as these were obtainable even in latter generations. Estimates of GCA effects showed more instances wherein F₁ estimates rather than any other generation did not fit in the general trend (table 2). Two such examples were C 273 for grain yield and Sharbati Sonora for grains/spike. This suggested that an analysis of the F₂ will be more useful than F₁ provided large samples are taken and efforts are made to avoid conscious or unconscious selection.

Graphical Analysis

The interpretation of W_r, V_r graphs (W_r is

the covariance of offspring in the rth array with non-recurrent parent and V_r is the variance of the offspring in the rth array) given by Hayman (1954) and Jinks (1954) is relevant to F₁ generation. In the later generations the distribution of array points would be congested. The expectations of W_r and V_r in F₁ are:

$$W_r = \frac{1}{2} D - \frac{1}{2} F, \text{ and } V_r = \frac{1}{2} D + \frac{1}{2} H - \frac{1}{2} F$$

As the generations advance the dominance component (H₁) will decrease (being 1/16 H₁ in F₂) and when H₁=0, all the array points congregate at the point of contact (1/2 D, 1/4 D). The regression line forms a tangent at this point to the limiting parabola $W_r^2 = V_r V_p$.

The W_r, V_r graph indicated overdominance for grain yield in the F₁ (figure 1). The regression was significant and as good as unity in latter generations even though the expectations may be that non-fulfilment of assumptions may have more pronounced effect on the graph in the latter generations when the contribution of dominance is reduced (Tandon et al. 1976). In all the generations S 413 was located away from the origin. S 413, thus, possessed higher number of recessive alleles. Argelto was also generally located away from the origin. In F₂ to F₅

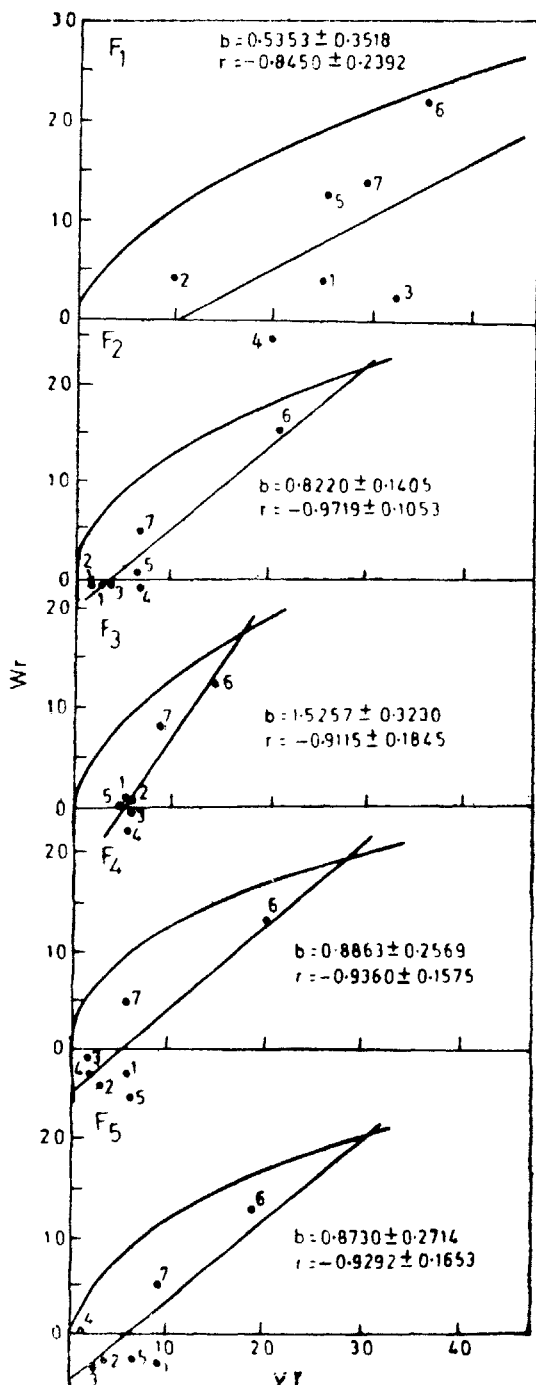


Figure 1 Variance (Vr), covariance (Wr) graphs for grain yield/plant over different generations

generations, the other five parents were congregated near the origin. The regression estimates did not differ from unity for the three component traits in all generations except F₃ for spikes/plant and F₅ for grain weight (figures 2 to 4). Considering the F₁ generation, nearly complete dominance was observed for spikes/plant and 100-grain weight whereas there was overdominance for grains/spike. The spread of array points along the regression line for grains/spike suggested that C 273 and K 68 had a greater proportion of dominant alleles as they were located close to the origin. Kalyansona was located away from origin except in F₁. It seemed to possess maximum number of recessive genes and along with it Sharbati Sonora and Argelto also were generally located away from the origin. In the case of 100-grain weight, the parents S 413 and Argelto possessed more recessive alleles. The array point for the parent K 68 usually showed an excess of dominant genes. Sonalika, C 273 and Sharbati Sonora were also located generally near the origin. There was no consistent spread of array points for spikes/plant in various generations.

The magnitude of regression coefficients did not show any trend as generations advanced. However, the point where regression line intersected the 'Y' axis generally moved up as the generations advanced except for grain yield for which it remained below the origin in all generations. The distribution of array points became congested in the F₂. After the F₂ successive congregation of points was not realised particularly for grain yield and grains/spike. Most of these observations suggest that genetic analysis does not fit a simple additive-dominance model or the various other assumptions of the graphical analysis are not met with.

The rank correlations among different generations with respect to Wr + Vr values were mostly non-significant and did not

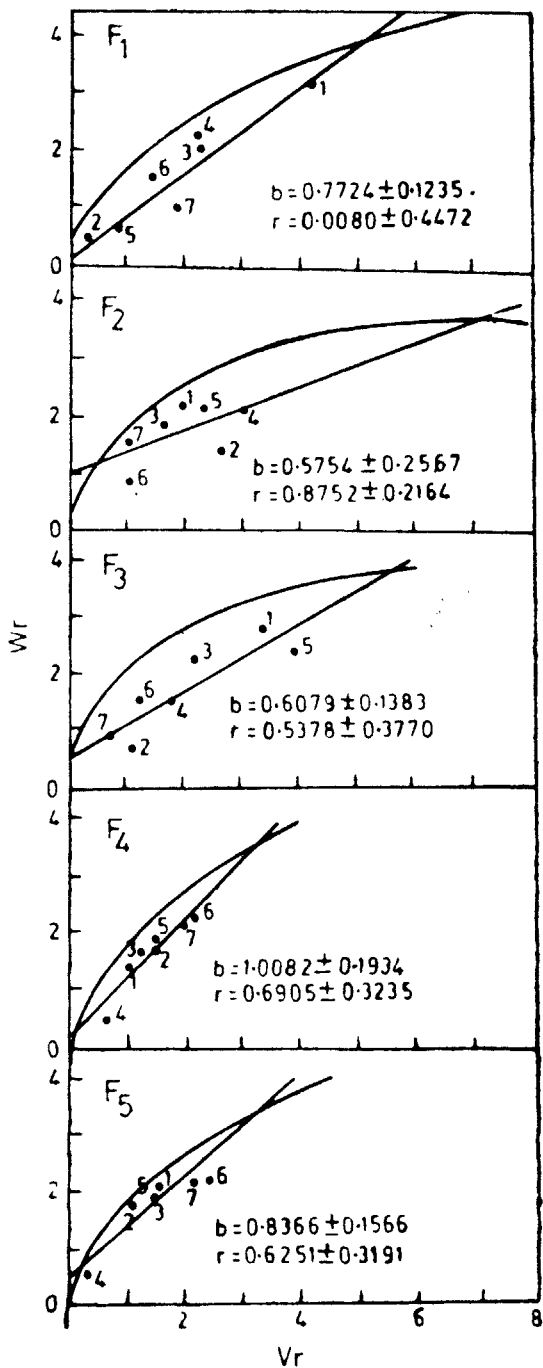


Figure 2 Variance (Vr), covariance (Wr) graphs for spikes/plant over different generations

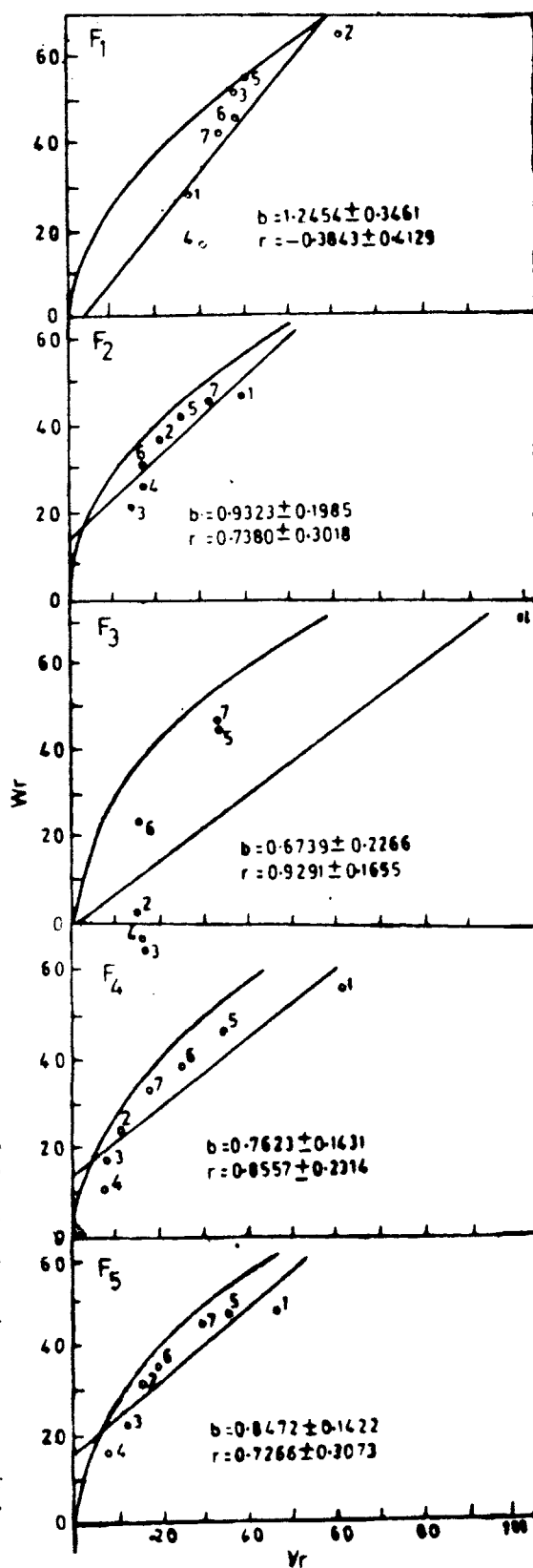


Figure 3 Variance (Vr), covariance (Wr) graphs for grains/spike over different generations. →

indicate any trend for grain yield, spikes/plant and grain weight except that $W_r + V_r$ values in the F_4 and F_5 generations were

significantly correlated (table 3). For spikes/plant, correlations were sometimes negative. Rank correlations with respect to W_r and V_r values separately did not provide any further clue regarding their constancy over generations. For grains/spike, $W_r + V_r$ values in the F_4 to F_5 generations were positive and significantly correlated. A perusal of figures 1 to 4 indicated that the genetic diversity among the parents as revealed by the analysis of F_2 generation rather than that of F_1 generation was being generally confirmed by the latter generations. For example, congestion near the origin of all the parents except S 413 and Argelto for grain yield and location of Kalyansona away from the origin for grains/spike. It is interesting because the analysis applies to the F_1 generation rather than the F_2 . A consistency of results obtained from F_2 to F_5 was also obtained in the combining ability analysis.

The correlation between Y_r (parental measurement) and $W_r + V_r$ values was negative for grain yield and 100-grain weight in all generations suggesting that higher expression of these characters was controlled by dominance alleles (figures 1-4). In the case of grain number, positive correlation was obtained in the F_2 to F_5 , the correlation being non-significant in the F_1 . A positive correlation indicated that the manifestation of greater number of grains was governed by recessive genes. For spikes/plant, no consistent trend was obtained. The estimates did not differ from zero in F_1 , F_3 and F_5 but were significantly negative in F_2 and significantly positive in F_5 generation. Such variable relationships in different generations are not understandable. It may be added that the correlation coefficients were based on only 5 degrees of freedom.

Relative Importance of Additive and Non-additive Variation

The results obtained in the F_1 generation

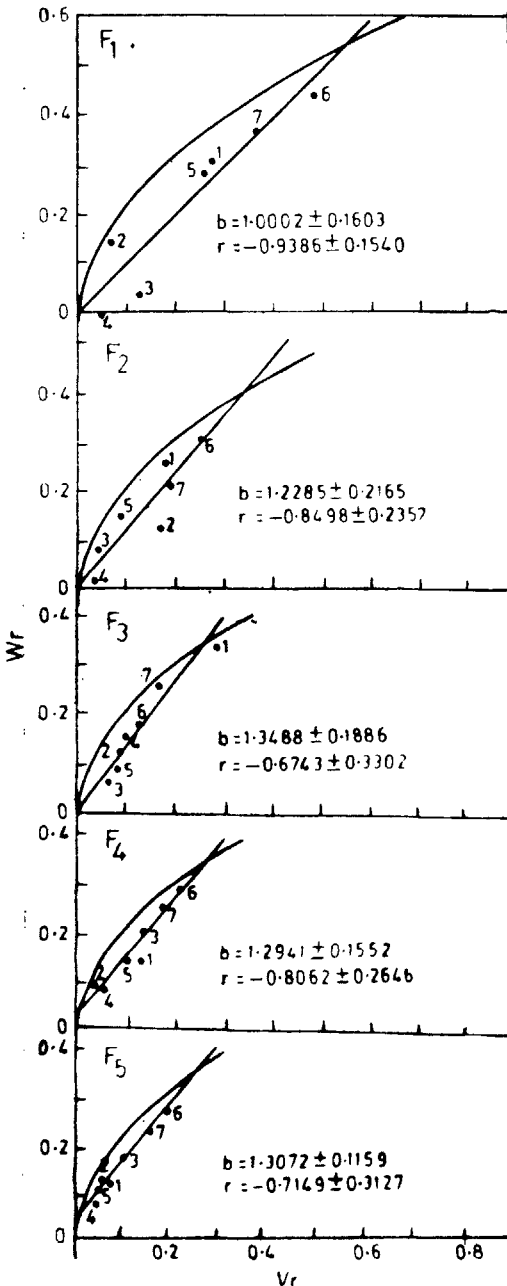


Figure 4 Variance (V_r), covariance (W_r) graphs for 100-grain weight over different generations

were significantly negative in F_2 and significantly positive in F_3 generation. Such variable relationships in different generations are not understandable. It may be added that the correlation coefficients were based on only 5 degrees of freedom.

Relative Importance of Additive and Non-additive Variation

The results obtained in the F_1 generation by the two techniques were in agreement regarding the relative importance of additive and non-additive components in the inheritance of grain yield and spikes/plant. For grain yield both the analyses indicated predominance of non-additive genetic variation. For spikes/plant there was nearly complete dominance. For grains/spike and grain weight combining ability revealed a greater role of additive variation whereas the graphical analysis in the F_1 generation showed complete dominance to overdominance.

The graphical analysis had the advantage that it can detect epistasis and isolate the parents contributing to it. In the present study, complementary type of epistasis was observed for grain yield in the F_1 generation but this was not borne by the analysis of the latter generations.

Combining ability analysis of the diallel cross on the other hand is incapable of providing this type of information. In this analysis, genetic variation is partitioned in to fixable ($2\sigma_p^2 = \sigma_A^2 + \frac{1}{2}\sigma_{AA}^2 \dots$) and non-fixable ($\sigma_S^2 = \sigma_D^2 + \frac{1}{2}\sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 \dots$) components (Griffing 1956 b). This partitioning provides most of the information practically utilised by the plant breeders. Moreover, there are many assumptions of graphical analysis which seem to be untenable (Gilbert 1958, Arunachalam 1976, Dhillon et al: 1976). It is not clear, therefore, how much reliance can be placed on graphical analysis. On the other hand combining ability analysis is based on more general model.

Table 4 Parents transmitting higher and lower expression of various traits as revealed by combining ability and graphical analyses

Character	Combining ability analysis		Graphical analysis	
	Good	Poor	Good	Poor
Grain yield/plant	Kalyansona Sonalika Sharbati Sonora	C 273 S 413	Kalyansona Sonalika Sharbati Sonora K 68 C 273	S 413
Spikes plant	S 413 Argelto	Sonalika Kalyansona K 68 Sharbati Sonora		
Grains/spike	Kalyansona Sharbati Sonora	Sonalika C 273 K 68	Kalyansona Sharbati Sonora Argelto	C 273 K 68
100-grain weight	C 273 K 68 Sonalika	Kalyansona S 413 Argelto	K 68 Sonalika Sharbati Sonora C 273	S 413 Argelto Kalyansona

Selection of Parents

Based on previous discussions, all the generations are considered for the selection of good and poor parents instead of considering only the F_1 (table 4). Both procedures generally enabled selection of parents that transmitted good and poor performance to their progenies for grain yield, grains/spike, and 100-grain weight, except for C 273 for grain yield. The graphical analysis indicated C 273 to be a better parent but it had negative GCA effects in F_2 to F_5 generations.

In the breeding programmes at this University, Kalyansona has been extensively used in hybridization and has contributed in the development of the cultivars such as 'WG 377', 'WL 711' and 'WL 1562', all with high numbers of grains/spike. Kalyansona had GCA effects significantly higher than all other parents in all the generations for this character. The graphical analysis of F_2 to F_5 also showed Kalyansona to be the best parent and that the expression of higher number of grains/spike was controlled by recessive genes. Then a question arises that how a parent having recessive alleles can be a good general combiner in F_1 generation of the diallel cross unless dominance is absent ($h=0$) which is not borne by the graphical as well as combining ability analyses. This brought out a discrepancy in graphical analysis even though nothing conclusive was evident in the graphical analysis of F_1 generations.

It was feasible to isolate good and poor general combiners with respect to spikes/plant using combining ability analysis. In the graphical analysis, however, there was no consistency in dispersion of array points and it is difficult to assign any factor for the inconsistent results for this trait.

In the present study combining ability analysis seemed to provide precise and consistent information than the graphical analysis and was better for selection of parents for their prepotency. These analyses have been used and comparable results obtained by some while most of workers recorded different results (Arunachalam 1976). Tandon et al. (1970) compared graphical and combining ability analyses and observed the latter to be better and similar observations were made by Dhillon (1974) who in addition also estimated D and H components. Arunachalam (1976) discussed at length the models on which the two approaches are based and pointed out that combining ability analysis is more realistic from the stand point of assumptions and information needed by the breeders. Baker (1978) had also discussed different approaches in diallel cross analysis. He concluded that generally it is difficult to meet the assumptions underlying the genetic interpretations of diallel statistics and, therefore, combining ability analysis should be preferred.

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