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Estimation of Genetic Parameters in Barley (*Hordeum vulgare* L.)

I. Full, Half and Quarter Diallel Analysis *

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Summary. Four exotic and four indigenous strains of barley were used for making diallel crosses. The sets of parents and crosses making full, half and quarter diallel were analysed in a randomized block design for plant height, number of effective tillers, ear length, grain yield per plant, 100 grain weight and number of grains per ear.

The three alternatives of diallel were similar with respect to the estimates of degree of dominance, general combining ability and specific combining ability, indicating that all these three methods of diallel were equally efficient. However, as the number of entries are minimum in quarter diallel, it would be economical in terms of cost, time and labour to estimate genetic parameters by this method. Average degree of dominance was found in the range of overdominance. The ranking of parents on the basis of their array mean was similar to the ranking based on gca effects. Similarly, the ranking of crosses on the basis of *per se* performance was similar to the ranking based on sca effects. This suggests that the selection of best general combiner or best cross combinations may be easier and more effective through array mean for *per se* performance rather than through high gca and sca effects, respectively. From among 56 crosses, IB-226 × × C-164 was the one which showed superiority for maximum number of characters followed by AB-12/59 × PTS-57. High sca effect for plant height, ear length, grain yield, 100 grain weight and number of grains per ear was the result of cross between parents having high × low general combining ability, indicating additive × dominance type of gene interaction. For number of effective tillers, high sca was produced by low × low general combiners, indicating dominance × dominance gene interaction.

The application of diallel analysis in plant breeding to screen good combiners for exploiting heterosis was suggested by Sprague and Tatum (1942). Griffing (1956) proposed the extension of the diallel model to the characterization of gene action controlling a quantitative trait and suggested four possible ways for analysing the diallel, depending on the materials, such as (1) parents, F_1's and reciprocals (2) parents and F_1's (3) F_1's and reciprocals and (4) F_1's. Watkins *et al.* (1971) coined the terms, full, half and quarter diallel, for the (1), (2) and (4) methods, respectively. The aim of the present study was to compare the efficiency of these three methods for estimating the gene action and to identify good combiners in barley. In addition, such a study would be useful in formulating efficient breeding plans for this crop.

Material and Method

Eight diverse strains, four exotic (AB-12/59; EB-1556; PTS-57 and A-59) and four indigenous (BG-1, K-572/10; IB-266 and C-164), were used for making diallel crosses including reciprocals. The fifty-six crosses together with eight parents were sown in randomized block design with four replications at the experimental farm of the Department of Genetics, Haryana Agricultural University, Hissar. Normal agronomic practices were followed. Observations were recorded on five randomly selected plants in each replication for (i) plant height, (ii) number of effective tillers per plant, (iii) ear length, (iv) number of grains per ear, (v) 100-grain weight, and (vi) grain yield per plant.

The combining ability analysis was done on the basis of plot means using the statistical genetic model proposed by Griffing (1956) as follows:

$$Y_{ijk} = m + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc} \sum_k \sum_l e_{ijkl}$$

where,

Y_{ijk} = k^{th} observation on $i \times j^{th}$ genotype
m = population mean
g_i, g_j = general combining ability effect of i, j parent
s_{ij} = specific combining ability effect of $i \times j^{th}$ cross
r_{ij} = reciprocal effect (only in method 1)
e_{ijkl} = random error associated with $ijkl^{th}$ observation
b = number of blocks (4) and
c = number of observations in each plot (5).

The combining ability analysis and the interpretation of variance components due to *gca* and *sca* was done according to Griffing (1956) method 1, 2 and 4, model 1.

Results

The variances due to general and specific combining ability (Table 1) were highly significant for all the six characters under all the three methods of diallel, i.e., full, half and quarter. The significance of both general and specific combining ability mean sum of squares indicated the role of both additive and non-additive types of gene action in the present material. Interestingly, the relative proportions of mean sum of squares due to gca and sca were more or less the same in all the three analyses of diallel.

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Table 1. *Combining ability analysis in three sets of diallel experiments together with the degree of dominance*

Types of diallel experiment	Source	D.F.	Mean sum of squares*					
			Plant height (cm)	Ear length (cm)	Number of effective tillers	Grain yield (gm)	100-grain weight (gm)	Number of grains per ear
Full diallel	gca	7	151.50	2.05	58.07	543.64	0.33	206.89
	sca	28	82.68	1.78	140.95	787.87	0.15	108.66
	error	189	2.28	0.24	2.18	5.32	0.03	0.99
	σ_D^2/σ_A^2		5.14	22.68	7.15	15.60	3.23	4.88
Half diallel	gca	7	87.13	1.13	28.22	264.50	0.19	117.18
	sca	28	48.34	1.11	74.80	447.45	0.08	59.47
	error	105	2.28	0.24	2.18	5.32	0.03	0.99
	σ_D^2/σ_A^2		5.94	216.00	7.80	12.08	2.41	5.07
Quarter diallel	gca	7	83.93	1.40	33.61	206.27	0.17	96.40
	sca	20	37.02	1.42	152.61	468.59	0.08	44.93
	error	81	5.62	0.05	4.44	5.38	0.01	0.93
	σ_D^2/σ_A^2		2.00	146.67	3.67	5.57	2.14	2.90

* All mean sum of squares were significant at 5% level.

The estimates of average degree of dominance (σ_D^2/σ_A^2) indicated, in general, overdominance for all the six characters. This was true for all three diallels. Full diallel analysis, which provided an estimate of the reciprocal effects, indicated non-significant reciprocal differences for 100-grain weight and number of grains per ear. Other characters showed, however, significant reciprocal effects.

In order to facilitate comparison, the parents involved in the diallel crosses were ranked firstly on the basis of gca effects and secondly on the basis of array means for each character separately. The highest gca effect for plant height (Table 2) in all the three analyses of diallel was shown by C-164, whereas the lowest gca effect was recorded for BG-1 in full and half diallel. In quarter diallel, the lowest gca effect was shown by PTS-57. Comparative estimates for the three analyses of diallel indicated that all three were similar with regard to the pattern of gca effects. Ranking of the parents was found to be identical in full and half diallel.

For number of effective tillers (Table 2), the largest estimate of gca effect was recorded for BG-1 in full and quarter diallel, whereas it was greatest for IB-226 in half diallel. Similarly, the lowest estimate of gca effect in full and quarter diallel was for C-164, but in half diallel it was for the parent A-59. Ranking of parents in full and quarter diallel was more or less similar, whereas in half diallel there was considerable variation.

The highest gca effect was recorded for IB-226 and lowest for BG-1 in all the three analyses of diallel

Table 2. *General combining ability effects in three sets of diallel experiments*

Character	Type of diallel experiments	AB-12/59	EB-1556	BG-1	PTS-57	A-59	K-572/10	IB-226	C-164
Plant height (cm)	Full	−1.81	3.77	−3.60	−2.91	−0.71	1.85	−1.26	4.67
	Half	−3.03	3.05	−4.11	−1.99	−0.41	2.39	−0.65	3.93
	Quarter	−1.25	3.73	−3.29	−3.32	−0.88	1.33	−1.42	5.09
Ear length (cm)	Full	0.16	0.13	−0.49	−0.32	−0.06	0.21	0.68	−0.02
	Half	0.26	0.13	−0.56	−0.30	0.21	−0.14	0.48	−0.07
	Quarter	0.29	0.21	−0.55	−0.52	0.28	−0.17	0.60	−0.13
Number of effective tillers	Full	−0.59	−1.12	3.24	−1.41	−0.99	0.64	2.38	−1.95
	Half	−0.84	−0.61	2.16	−1.41	−1.74	1.19	2.46	−1.24
	Quarter	−1.07	−1.15	4.20	−1.72	−0.34	−0.49	3.22	−2.66
Grain yield (gm)	Full	−0.06	0.47	9.03	−3.44	−2.33	−1.94	7.24	−9.10
	Half	−0.31	2.38	5.93	−2.65	−4.71	−0.72	7.60	−7.53
	Quarter	−0.66	0.48	10.74	−5.29	−0.18	−4.40	9.51	−10.19
100-grain weight (gm)	Full	−0.16	−0.28	−0.04	0.04	0.06	0.09	0.09	0.12
	Half	−0.15	−0.28	−0.06	0.04	0.05	0.10	0.08	0.10
	Quarter	−0.16	−0.29	−0.01	0.04	0.08	0.10	0.09	0.15
Number of grains per ear	Full	2.07	6.93	1.39	−1.52	−1.14	−2.10	−0.33	−5.30
	Half	2.25	6.80	0.53	−0.93	−1.66	−2.28	−0.06	−4.66
	Quarter	2.25	6.89	1.78	−2.23	−0.76	−2.31	−0.15	−5.15

for ear length (Table 2). Rankings in half and quarter diallel were identical, while in full diallel these ranks shifted by just one position.

For grain yield (Table 2), the largest gca effect was observed for BG-1 in full and quarter diallel, whereas in half diallel the best combiner was found to be IB-226 followed by BG-1. Parent C-164 was the poorest combiner in all the three analyses of diallel. The ranking pattern was almost the same for all three analyses.

As evident from the data in Table 2, C-164 had the highest effect for 100-grain weight. The lowest gca effect was recorded for EB-1556 in all the three cases of diallel. For number of grains per ear, the highest gca effect was noted for BG-1 and the lowest for C-164 (Table 2). Ranking pattern of the parents was similar in all three diallels, both for 100-grain weight and number of grains per ear.

To make an overall comparison of these three alternative methods of diallel, the ranks over all the characters were pooled for each of the strains under these analyses, separately. The rankings of parents in each diallel were then compared with the ranking based on the array means of the parents (Table 3).

Table 3. *Ranking of parents based on their array mean and gca effects in three diallel experiments*

Parents	Array mean	Full diallel	Half diallel	Quarter diallel
AB-12/59	4	5	4	5
EB-1556	3	3	2	3
BG-1	2	2	3	2
PTS-57	8	8	8	8
A-59	6	6	7	4
K-572-10	5	5	5	6
IB-226	1	1	1	1
C-164	7	7	6	7

r_s (Array mean: Full diallel) = 1.00
r_s (Array mean: Half diallel) = 0.95
r_s (Array mean: Quarter diallel) = 0.93

Pearson's product moment correlation coefficient (Spearman's formula) was used to estimate the rank correlation (Snedecor, 1946). High rank correlation (r_s) values in each case clearly indicated that the pattern of ranking based on gca effects was the same as the one based on array means and all the three alternatives of diallel were equally efficient in estimating the gca effects. The rank correlation was 1.00, 0.95 and 0.93 for full, half and quarter diallel, respectively.

Specific combining ability (sca) effects were obtained for all the three analyses of diallel and the ranking patterns of crosses obtained on the basis of sca effects were compared with the ranking based on their *per se* performance, using rank correlation. The rank correlations between two parameters were 0.89, 0.91 and 0.87 for full, half and quarter diallel. These results indicate that all three analyses of diallel

Table 4. *Five best crosses selected on the basis of per se performances and sca effects in the full diallel experiment*

S. No.	Plant height (cm)		Ear length (cm)		Number of effective tillers per plant	
	Per se	Full diallel	*Per se*	Full diallel	*Per se*	Full diallel
1.	EB-1556 × C-164	BG-1 × C-164	BG-1 × IB-226	BG-1 × IB-226	K-572/10 × IB-226	AB-12/59 × PTS-57
2.	IB-226 × C-164	IB-226 × C-164	AB-12/59 × IB-226	AB-12/59 × K-572/10	AB-12/59 × PTS-57	K-572/10 × IB-226
3.	BG-1 × C-164	EB-1556 × IB-226	AB-12/59 × K-572/10	AB-12/59 × BG-1	BG-1 × K-572/10	EB-1556 × A-59
4.	EB-1556 × K-572/10	AB-12/59 × PTS-57	EB-1556 × A-59	EB-1556 × PTS-57	BG-1 × C-164	BG-1 × C-164
5.	EB-1556 × IB-226	PTS-57 × A-59	IB-226 × C-164	A-69 × C-164	IB-226 × C-164	BG-1 × K-572/10
S. No.	Grain yield (gm)		100-grain weight (gm)		Number of grains per ear	
	Per se	Full diallel	*Per se*	Full diallel	*Per se*	Full diallel
1.	IB-226 × C-164	IB-226 × C-164	K-572/10 × C-164	K-572/10 × C-164	EB-1556 × BG-1	EB-1556 × BG-1
2.	K-572/10 × IB-226	AB-12/59 × PTS-57	BG-1 × PTS-57	BG-1 × PTS-57	EB-1556 × K-572/10	AB-12/59 × A-59
3.	AB-12/59 × PTS-57	AB-12/59 × A-59	A-59 × C-164	EB-1556 × IB-226	AB-12/59 × A-59	EB-1556 × K-572/10
4.	BG-1 × C-164	BG-1 × C-164	A-59 × K-572/10	EB-1556 × PTS-57	AB-12/59 × EB-1556	A-59 × C-164
5.	AB-a2/59 × A-59	K-572/10 × IB-226	A-59 × IB-226	AB-12/59 × PTS-57	AB-73/59 × IB-226	PTS-57 × K-572/10

were equally efficient for estimating sca effects and good combinations could also be predicted by the *per se* performance of the crosses.

For a better comparison, a sample of the five best crosses was selected both on the basis of *per se* performance and on the sca effects of full diallel (Table 4). From this table it is evident that, out of five crosses, only three crosses for plant height, two for ear length, five for grain yield, four for number of effective tillers, two for 100-grain weight and three for grains per ear were in common under these two criteria of selection. The crosses which were common occupied, however, different positions. For example, cross 6×7 occupied second position when *per se* performance was considered but it was at the fifth position when sca effects for grain yield were considered. The crosses which were superior for grain yield did not show superiority for the component traits also. These points clearly suggest that the best performing crosses may not necessarily be selected by sca effects. The sca effects indicated that there was no cross combination which was consistently good for all the characters. However, cross IB-226×C-164 was the one which showed superiority for the greatest number of characters.

The following list gives the best cross combinations, with the general combining ability effects of the parents involved in these crosses:

Characters	Plant height	Ear length	Effective tillers
Crosses	BG-1×C-164	BG-1×IB-226	AB-12/59×PTS-57
gca effects	−3.60×4.67	−0.49×0.69	−0.59×−1.41

Grain yield	100 grain weight	Number of grains per ear
IB-226×C-164	K-572/10×C-164	EB-1556×BG-1
7.24×−9.09	0.09×0.12	6.93×1.38

From these data, it is evident that, except for number of effective tillers where a cross between low×low general combiners produced high sca effects, in all other cases the crosses between high×low general combiners were the best.

Discussion

The diallel model proposed by Griffing (1956) is such that the variance components such as σ^2_{gca} and σ^2_{sca} obtained from a diallel analysis may be interpreted genetically. It is possible, assuming no epistasis, to have the estimates of additive genetic variance (σ^2_A) and the dominance variance (σ^2_D). Average degree of dominance may thus be determined as the ratio of σ^2_D/σ^2_A. In the present study, it was observed that average degree of dominance fell in the range of over dominance. This was true for all the characters as well as under all the three diallels studied. A critical survey of the literature on degree of dominance in barley indicated a range between partial to overdominance. These estimates do not, however, seem to be reliable as the methods applied for these estimates have been faulty. For example, some workers, such as Gulati *et al.* (1969) and Yap *et al.* (1971), have reported the degree of dominance measured as the ratio of mean sum of squares due to sca to the mean sum of squares due to gca. Considering that:

$$E(MSS_{gca}) = \sigma^2_e + \sigma^2_s + (p + 2)\,\sigma^2_g$$

and

$$E(MSS_{sca}) = \sigma^2_e + \sigma^2_s$$

a ratio of $E(MSS_{sca})/E(MSS_{gca})$ would not be the estimate of degree of dominance. Clearly, it is only the σ^2_g and σ^2_s which is equal to $\frac{1}{2}\sigma^2_A$ and σ^2_D, respectively, and not the MSS_{gca} and MSS_{sca}. In some other cases, the average degree of dominance has been determined as σ^2_s/σ^2_g (Upadhyaya *et al.*, 1967). This estimate is also not appropriate, because, if we consider that:

$$\sigma^2_g = \tfrac{1}{2}\sigma^2_A + \tfrac{1}{4}\sigma^2_{AA} + \cdots$$

and

$$\sigma^2_s = \sigma^2_D + \tfrac{1}{2}\sigma^2_{AA} + \cdots$$

and the genetic variance in the base population is equal to $2\sigma^2_g + \sigma^2_s$. The degree of dominance would, therefore, be equal to $\sigma^2_s/2\,\sigma^2_g$ rather than σ^2_s/σ^2_g as has been the case in the literature cited above. Comparison of the estimates of the present investigation with those of the literature seems, therefore, meaningless.

The ranking pattern for gca effects in full diallel was identical to the ranking of the parents based on the array mean. For the half and quarter diallel also, the ranking pattern on the basis of array mean was similar to the ranking pattern for gca effects. In fact, the methods for estimation of array mean and gca effects were more or less similar so that the results are apt to be similar. To avoid more statistical computation, it is recommended that the array means should be preferred to gca effects.

High rank correlations between sca effects and the *per se* performance of crosses (0.89 for full, 0.91 for half and 0.87 for quarter diallel) indicated that ranking of crosses on the basis of sca effects and *per se* performance was similar. However, when the five best crosses were selected on the basis of *per se* performance and sca effects separately, it was found that the crosses were not necessarily the same in both cases. There were only a few common crosses (two to four) selected on the basis of *per se* performance and sca effects, except for grain yield where all the five crosses were same. This means that the choice of the best cross combination on the basis of high sca would not necessarily be the one which would give the highest *per se* performance also. Because the *per se* performance is the realized value, while the sca effect is an estimate, the former should be given preference while making the selection of cross combinations. It should also be borne in mind that the sca effect is a measure of the deviation of F_1 performance over the parental performance, so that for a given hybrid performance the sca effect may be high or low depending upon whether the parental performance is low or high. Thus, high sca would not necessarily mean a high performance by the hybrid. Keeping these points in mind, the estimation of sca effects seems to be superfluous as no additional information is obtained by doing so. Similar observations were also made by Singh *el al.* (1974) in pearl millet.

Sca effects, when analysed in correlation with gca effects, indicated epistatic gene action. For plant height, ear length, grain yield, 100 grain weight and number of grains per ear, the crosses exhibiting high sca effects involved parents with high × low gca effects. Obviously an add. × dom. type of gene interaction seems to be operative here. For the remaining characters, high sca was associated with low × low gca effects, indicating a non-additive type of gene interaction.

The three methods of diallel analysis appeared to be equally efficient, as indicated by the fact that: (i) a similar picture regarding degree of dominance (σ_D^2/σ_A^2) was observed in the three kinds of diallel; (ii) the ranking pattern for gca effects of parents was similar in all the three analyses; and (iii) the ranking of crosses on the basis of sca effects was also similar in the three analyses of diallel. These findings support the view that all the three methods of diallel provide similar results.

For a given set of parents (n) to be analysed in a diallel system, the number of entries to be handled is lowest $[n(n-1)/2]$ for quarter diallel, compared with full and half diallel. The quarter diallel would, therefore, involve less time and labour both in planning and computation. The inclusion of parental generations seems to have caused an upward bias in the estimates of combining ability variances because the degree of dominance was more or less similar in methods 1 and 2, whereas it was considerably lower in method 4. This clearly confirms the statement of Griffing (1956) that methods 1 and 2, in which the parents are considered, provide biased estimates of combining ability variances. This suggests that, in order to have precise and unbiased estimates of these variances, method 4 should be preferred to methods 1 and 2.

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