

A comparison of different diallel analyses*

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Summary. Five different methods of diallel analysis have been compared using data from a half-diallel cross of a fixed set of nine homozygous varieties and one set of their single cross progenies in chickpea. The interrelationships among various parameters obtained from these analyses are reviewed and the advantages and disadvantages of each method discussed. The analysis proposed by Gardner and Eberhart (1966) appears to be superior as in addition to gca and sca effects and variances it provides information on the additive effects of varieties and their average and individual contribution to heterosis in crosses.

Key words: Half diallel – Griffing models – Jones model – Gardner and Eberhart model – Walters and Morton model

Introduction

One of the several biometrical techniques available to plant breeders for evaluating and characterizing genetic variability existing in a crop species is diallel analysis. The several distinct advantages of a half-diallel experiment that includes one set of single cross progeny (no reciprocals) and the parents require no further comment. There are several methods for analyzing data from a set of p parents and their p(p-1)/2 single-cross progenies. The analyses proposed by Morley Jones (1965) and Walters and Morton (1978), and two of the four methods described by Griffing (1956), Method-2 and Method-4, can be used with data from a halfdiallel. Similarly, Analysis II and Analysis III proposed by Gardner and Eberhart (1966) are essentially meant for the same type of data and could easily be combined together for statistical purposes.

In considering these five alternative methods for analysis of data from a half-diallel mating, it becomes essential to evaluate just how the various genetic parameters obtained are inter-related and what is the extent of the advantages or disadvantages of either of these analyses. For this purpose the above five methods have been used and compared in the present investigation by utilizing the data from a fixed set of nine varieties and their half-diallel crosses in chickpea (*Cicer arietinum* L.).

Materials and methods

The material consisted of nine varieties of chickpea namely L-550(1), GL-629(2), K-850(3), H-208(4), ICCC-2(5), RS-11(6), F-404(7), P-993(8) and K-1189(9), and all their possible 36 F_1 single crosses, excluding reciprocals. Sowing was done in a Randomized Block Design comprising three replications at the experimental farm of The Haryana Agricultural University, Hissar, during *rabi* season in 1978–79. Each parent and F_1 had a single row plot accommodating 15 plants spaced 20 cm apart. The row to row distance was 60 cm. Ten competitive plants were harvested from each plot and data on grain yield per plant were recorded. The plot mean data were subjected to various diallel analyses, the statistical models of which are presented here:

Griffing (1956) – Model I, Method-2

Model: $V_i = \mu + 2g_i + S_{ii}$ for parents, and

 $C_{ij} = \mu + g_i + g_j + S_{ij}$ for single cross progeny

where, μ is the population mean, $g_i(g_j)$ is the gca effect for the $i^{th}(j^{th})$ parent, S_{ij} is the sca effect of the cross between the i^{th} and j^{th} parents, and S_{ii} is the specific effect of i^{th} parent when crossed with itself.

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Griffing (1956) – Model I, Method-4

Model: $C_{ij} = \mu + g_i + g_j + S_{ij}$ for single cross progeny.

Morley Jones (1965)

Model: $V_i = m + 2j_i - (p-1)l - (p-2)l_i$ for parents, and $C_{ij} = m + j_i + j_j + 1 + l_i + l_j + l_{ij}$ for single cross progeny

where, m is the grand mean of the population, j_i is the mean deviation from the grand mean due to ith parent ('a' component), l is the overall mean dominance deviation ('b₁' component), l_i is the further dominance deviation due to ith parent ('b₂' component), and l_{ij} is the dominance deviation that is unique to each F₁ and unexplained by above two dominance deviations ('b₃' component). Also, b₁ + b₂ + b₃ = b.

Gardner and Eberhart (1966) – Analysis III

Model: $V_i = \mu_v + v_i$ for parents, and

 $C_{ij} = \mu_c + g_i + g_j + S_{ij}$ for crosses

where, μ_v is the parental mean, v_i is the deviation from μ_v associated with ith parent and μ_c is the mean of all single cross progenies.

Gardner and Eberhart (1966) – Analysis II Model: $V_i = \mu_v + v_i$ for parents, and $C_{ij} = \mu_v + v_i + \bar{h} + h_i + h_j + S_{ij}$

where, \bar{h} is the average heterosis contributed by a particular set of varieties used in the crosses, $h_i(h_j)$ is the average heterosis contributed by $i^{th}(j^{th})$ variety in its crosses measured as a deviation from average heterosis \bar{h} , and $\bar{h} + h_i + h_j + S_{ij} =$ h_{ij} , the overall heterosis effect.

Walters and Morton (1978)

Model: $V_i = m + 2 g_i$ for parents, and

 $C_{ij} = m + g_i + g_j + 1 + 1_i + 1_j + 1_{ij}$ for crosses

where, m is parameter for the mean response level, $g_i(g_j)$ is the additive contribution of $i^{th}(j^{th})$ variety, and 1, l_i and l_{ij} are equivalents to \bar{h} , hi and S_{ij} of Gardner and Eberhart's Analysis II.

Results and discussion

Mean grain yields per plant for nine varieties of chickpea and one set of all their possible 36 F_1 single crosses are presented in Table 1. The genetic constants

estimated from these data and the corresponding analysis of variance for five diallel methods are presented in Tables 2 and 3. In this paper results have been discussed only to compare the different methods as far as genetic constants and variance estimated are concerned. Hence, no effort has been made to discuss the results on combining ability variances and effects of the genotypes studied.

Genetic constants

1. ' g_i 's of Griffing's Method-4 are equal to ' g_i 's of Gardner and Eberhart's model.

2. 'v_i's of Gardner and Eberhart are equivalent to 'g_i's of Walters and Morton, i.e., $g_i = \frac{1}{2} v_i$.

3. ' \bar{h} ', and ' h_i 's of Gardner and Eberhart are equal to '1' and ' l_i 's of Walters and Morton.

4. ' S_{ij} 's of Griffing's Method-4 are equal to the ' S_{ij} 's of Gardner and Eberhart and Walters and Morton.

5. The estimates of all genetic constants in Griffing's Method-2 are dissimilar to those from the other three methods.

The model proposed by Morley Jones considers the homozygous varieties as taken at random from some base population about which the conclusions are to be drawn. Consequently, his model is concerned with variances and not the estimates of genetic constants.

Analysis of variance

1. The estimates of mean squares for gca of Griffing's method-2 are equal to v_i of Gardner and Eberhart and equivalent to 'a' of Morley Jones. The value of 'a' was three times that of gca, i.e. 'a' = $3 \times$ gca, since gca value is based on mean of three replications. Both parameters measure additive variance.

2. Mean squares for 'b' of Morley Jones are equivalent to sca of Griffing's Method-2 and ' h_{ij} ' of Gardner and Eberhart, i.e., 'b'=3×sca=3× h_{ij} . All these parameters measure dominance or heterosis components.

3. Mean squares of ' b_1 ' of Morley Jones are equal to parents vs. crosses contrast of RBD analysis, and both

Table 1. Mean grain yield (g/plant) of 9 self-pollinated varieties of chickpea and one set of all possible single crosses among them

	1	2	3	4	5	6	7	8	9
1	23.83	26.40	30.69	33.40	36.16	26.25	31.23	27.07	19.13
2		24.96	26.81	32.99	34.06	28.90	32.01	28.19	20.67
3			23.41	35.01	36.13	31.78	30.28	32.45	24.02
4				30.55	35.00	29.72	33.37	27.95	25.06
5					31.29	30.75	37.95	33.96	28.05
6						27.17	32.03	30.23	23.15
7							24.26	29.18	28.04
8								26.76	24.18
9									12.42

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Griffing's N	fethod-2									Grif	fing's Me	ethod-4									
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	9 S S S S S S S S S S S S S S S S S S S	3.137 2.364 6.467 5.975 5.975 7.184 1.7461 3.484 3.484	S ₁₂ -0.7 S ₁₃ 2.2 S ₁₅ 4.0 S ₁₆ -1.5 S ₁₆ -1.5 S ₁₆ -0.6 S ₁₉ -0.6 S ₁₉ -2.3 S ₁₉ -1.7 S ₂₃ -1.7 S ₂₄ -1.7 S ₂₅ -1.7 S ₂₆ -1.7 S ₂₆ -1.7 S ₂₆ -1.5 S ₂₇ -1.5 S ₂₆ -1.5 S ₂₇ -1.5 S ₂₆ -1.5 S ₂₆ -1.5 S ₂₇ -1.5 S ₂₆ -1.5 S ₂₆ -1.5 S ₂₇ -1.5 S ₂₇ -1.5 S ₂₇ -1.5 S ₂₆ -1.5 S ₂₇ -1.5 S	82883644224 828836442248 82888888888888888888888888888888	2.535	⁸ ⁸ ⁸ ⁹ ⁸ ⁸ ⁸ ⁸ ⁸ ⁹ ⁸ ⁹ ¹	-0.377 3.236 1.135 -0.347 -1.317 -1.317 -1.317 -3.048 -3.048 -3.048 -2.195	ື « ແລະ	3.597 1.050 1.465 1.994 1.644 0.886 0.886 4.374 1.954	వా బా బ్లా బా బా బా బా బా బా బా	29.79 -1.135 1.177 1.269 2.033 4.825 0.782 0.782 2.258 2.258 -0.725	× × × × × × × × × × × × × × × × × × ×	1.072 0.768 2.721 2.685 0.322 0.322 0.322 0.351 0.352	S S S S S S S S S S S S S S S S S S S	2.350 0.631 1.071 1.144 0.307 1.367 1.367 1.247 0.247	$\begin{array}{rrrr} S_{35} & -3.035\\ S_{35} & 2.177\\ S_{35} & 2.177\\ S_{45} & -1.639\\ S_{45} & -1.639\\ S_{47} & -0.702\\ S_{48} & -0.187\\ S_{48} & -0.187\\ S_{48} & -0.187\\ S_{56} & -3.078\\ S_{56} & -3.078\\ \end{array}$	% % % % % % % % % %	1.079 0.072 0.004 - 0.766 1.955 0.714 - 2.141 2.568 1.687			
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Table 2. Estimates (g/plant) of genetic constants from the data in Table 1 using different models of diallel analysis

4. Mean squares for ' b_2 ' of Morley Jones are equivalent to ' h_i ' of Gardner and Eberhart and ' l_i ' of Walters and Morton. These items estimate the difference between H_1 and H_2 (H_1-H_2), indicating the asymmetry in the gene distribution and/or parental contribution to variety heterosis.

5. Mean squares for ' b_3 ' of Morley Jones are equivalent to ' S_{ij} ' of Gardner and Eberhart, ' 1_{ij} ' of Walters and Morton, and, ' S_{ij} ' of Griffing's Method-4. These items measure specific dominance/combining ability.

6. Mean squares for gca of Griffing's Method-4 are equal to gca of Gardner and Eberhart. Both items measure general combining ability of the parents in crosses.

7. Mean squares for 'g_i' of Walters and Morton are equivalent to those for 'Varieties' of Gardner and Eberhart, i.e., 'g_i'= $3 \times$ Varieties. These two items measure the additive contribution of the parents in crosses.

The mean squares for additive parameter 'a' in the Morley Jones' model is higher when compared with that of the corresponding 'g_i' in the Walters and Morton model. The parameter 'a' appears to contain some portion of a dominance component for 'a'=D-F+ H_1-H_2 (Hayman 1954), and when the 'b₂' item ['b₂'= (H_1-H_2)] is significant, 'a' gets confounded with the dominance mean square. In Walters and Morton's model, there is no such confounding of additive and dominance mean squares because of the non-orthogonality of the model, and thus it gives unbiased estimates of additive component of variance together with other genetic constants.

The relationship between the 'a' of Morley Jones and the gca of Griffing's Method-2 shows that the gca is a direct function of 'a' and, since the latter may be confounded with dominance variance, the gca may also contain the dominance variance. Hayman (1954), Jinks (1955), Hayman and Mather (1955), Matzinger (1963), Chung and Stevenson (1973) and Singh (1980) also expressed similar opinion. Jugeneheimer (1976) emphasized the need for more experiments to prove the validity of the assumption that gca variance was due to additive variance only. Sokol and Baker (1977) have also demonstrated that when gene frequencies are not equal to one-half, dominance variance also contributes to gca variance regardless of correlation between loci.

The various parameters in the analyses of variance of these five diallel methods are inter-related as shown by Baker (1978) and give similar genetic information. However, Griffing, in his Method-2, did not subdivide heterosis and called it sca. He included a specific effect of the parent when crossed with itself in both of his gca

 Table 3. Analyses of variance of 9 varieties and their 36 crosses

 for design of the experiment and five different diallel methods

Design of the exper	iment	(BRD)		
Source		DF		MS
Entries		44		74.22
Parents		8		94.26
Crosses		35		57.37
Parents vs. crosses		1		503.38
Error		88		4.95
Griffing				
Source	Meth	od-2	Meth	od-4
Source	DF	MS	DF	MS
gca	8	93.94	8	70.94
sca	36	9.37	27	4.17
Error	88	1.65	70	1.70
Morley Jones	^.			
Source		DF		MS
a		8		281.80
b		36		28.11
b,		1		503.38
b,		8		21.32
h-		27		12.52
Error		88		4.95
Gardner and Eberh	art			
Source		DF		MS
Varieties		8		31.42
vi		8		95.25
gca		8		70.94
ĥii		36		9.37
		1		167.79
h:		8		7 11
S		27		4 17
Error		88		1.65
Walters and Morton	n			
Source		DF		MS
gi	_	8		94.26
Ĭ		1		503.38
li		8		21.32
lii		27		12.52
Ĕrror		88		4.95

and sca effects. Since the parents generally represent an extremely different yield level, the inclusion of their effects per se may cause a bias in the estimated of gca and sca effects. Moreover, the breeders are generally interested in knowing the performance of the parents in crosses rather than their effects per se. Thus, Griffing's Method-2 fails to give a clear picture of heterosis and the various genetic effects involved.

Morley Jones subdivided heterosis and defined his parameters in terms of deviation around the experimental mean and was not concerned about the estimates of various genetic constants. When the varieties represent a fixed set, the estimates of variance components in that case would have little value because they do not apply to any base population. Griffing's Method-4 provide similar estimates of gca and sca as those provided by Gardner and Eberhart but, unlike the latter model, it does not provide either any information on average or any specific contribution of the parents to heterosis. Both these methods estimate the gca and sca based only on the progeny performance and thus remove the bias that may come due to the inclusion of parents themselves. Hayes and Paroda (1974) also concluded that the exclusion of the parents from diallel analysis increases the precision of gca and sca estimates. But the problem of Griffing's Method-4 is that the mean squares due to sca is the only component used for the nonadditive gene effects, whereas the average heterosis, which is not estimated in this method, is also attributable entirely to non-additive gene effects.

The model proposed by Walters and Morton provides various information similar to that found in the model of Gardner and Eberhart except that the gca of the parents in this model are not based on progeny performance; its 'g_i' parameter gives only the additive contribution of varieties based only on the parental data.

In view of the above facts, it becomes clear that although all these five methods of diallel analysis are inter-related with each other and have many parameters in common, the Gardner and Eberhart's combined analysis provides the maximum information. The parameters obtained from the other four methods can be expressed as simple linear functions of the various parameters in this method. The combined analysis of Gardner and Eberhart has the following distinct advantages over the others:

1. Since this model assumes arbitrary gene frequencies at all loci between the parents, it is equally applicable to a fixed set of both homozygous varieties as well as those mating at random.

2. The variety and cross means can be predicted, and if S_{ij} and h_i heterosis effects are negligible, the predicted variety cross means have smaller standard errors than the observed variety cross means.

3. The estimates of various genetic effects from a halfdiallel cross and related populations are defined more clearly as functions of gene frequencies and additive and dominance effects for individual loci. Heterosis effects are further sub-divided to provide additional inO. Singh and R. S. Paroda: A comparison of different diallel analyses

formation about the varieties involved. The estimates obtained are particularly useful in making predictions and choosing breeding materials and breeding methodologies.

4. An analysis of variance with appropriate F-tests is provided for various types of gene action involved.

5. The variety effects, as presented by Gardner and Eberhart, depend only on additive and additive \times additive gene action regardless of the gene frequencies or correlated gene distribution (Sokol and Baker 1977).

6. Heterosis can easily be calculated from the estimates obtained in this model, as $h_{ii} = 2S_{ii} - S_{ii} - S_{ii}/2$.

These findings emphasize the fact that the data from a diallel cross can completely be summarized following the combined analysis of Gardner and Eberhart. A few reports have appeared in the literature comparing this model with others (Gupta and Ramanujam 1974; Baker 1978; Singh 1980). In view of the facts discussed above, it appears that the conclusions drawn by Gupta and Ramanujam (1974) from their studies do not seem to hold true. The observations of Baker (1978) and Singh (1980), however, support the findings of the present investigation.

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