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A comparison of different methods of half-diallel analysis

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Summary. A comparison among various forms of half-diallel analysis was made. The different half-diallel techniques used were: Griffing's model I, method 2 and 4, Morley-Jones' model; Walters and Morton's model, and Gardner and Eberhart's model. All these methods of diallel analysis were found to be interrelated. However, as the Gardner and Eberhart's model partitioned heterosis into different components as well as gave information about combining ability, this method had certainly some advantages over the others. The results further indicated the possibility of dominance variance being confounded with the additive variance of general combining ability.

Key words: Half diallel – Heterosis – Combining ability – Half-diallel models – Genetic components – Mungbean

Introduction

From the practical point of view, diallel mating designs provide a very simple and convenient method for the estimation of genetic parameters. Among various diallel forms, the half diallel techniques have certain advantages over others, giving maximum information about genetic architecture of a trait, parents and allelic frequency (Kearsey 1965). Different forms of half diallel analysis have been proposed by various workers. Griffing (1956) used the half diallel analysis for combining ability while Gardner and Eberhart (1966), using the step-up multiple regression approach, partitioned heterosis in terms of average, general and specific heterosis effects. Morley-Jones (1965) extended the analysis of variance of a full diallel table to a half diallel table. However, Walters and Morton (1978) criticized the Morley-Jones approach on the basis of non-orthogonality of the model used and suggested improvement in the model. In the present paper, a comparative view of these models has been presented and discussed in light of their practical significance.

Materials and methods

To start with, 8 × 8 half diallel crosses of mungbean (*Vigna radiata* (L.) Wilczek) were produced. The varieties used were: 1. 'H-70-16' ('Varsha'), 2. 'H-70-21', 3. 'B-105', 4. 'K-851', 5. 'PS-7', 6. 'Russian', 7. 'PSG', 8. 'P. B.' ('Pusa Baisakhi'). These crosses, along with their parents, were evaluated in a randomized block design with three replications over two years. The observations were recorded on five randomly selected plants in each replication for 100 seed weight. The data were analysed using the following models.

Griffing's model I

(i) Method 2: $X_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b} \sum_k e_{ijk}$.

(ii) Method 4: $X_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b} \sum_k e_{ijk}$

$(i = j = 1, \dots p; k = 1, \dots b)$

where,

u = the population mean;
g_i = the general combining ability effect of the i^{th} parent;
g_j = the general combining ability effect of the j^{th} parent;
s_{ij} = the specific combining ability effect of the cross between i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$ and
e_{ijk} = the environmental effect associated with ijk^{th} observation.

The restrictions $\sum_i g_i = 0$ and $\sum_i s_{ij} + s_{ii} = 0$ (for each i in method 2), $\sum_{i \neq j} s_{ij} = 0$ (for each j in method 4) are imposed.

Morley-Jones model

$y_{ii} = m + 2J_i - (p-1)\,l - (p-2)\,l_i$ for parents and
$c_{ij} = m + J_i + J_j + l + l_i + l_j + l_{ij}$ for single cross progeny;

where,

m = grand mean;
J_i = mean deviation from the grand mean due to the i^{th} parent = 'a' component;
l = mean dominance deviation = b_1;
l_i = further dominance deviation due to the i^{th} parent = b_2 and
l_{ij} = dominance deviation that is unique to each F_1 and unexplained by above two dominance deviations = b_3.

Walters and Morton's model

$y_{ii} = m + 2\,g_i$ for parents;
$y_{ij} = m + g_i + g_j + l + l_i + l_j + l_{ij}$ for crosses;

where,

m = parameter for the mean response level;
g_i = additive contribution of the i^{th} lines;
l = average dominance deviation;
l_i = an additional dominance deviation due to the i^{th} line and
l_{ij} = dominance deviation due to the ij^{th} cross.

Gardner and Eberhart's model

For a comprehensive analysis of heterosis Gardner and Eberhart's model III analysis and Model II analysis were used:

a. Model III analysis

$y_{ii} = u_v + v_i$ for parents;
$y_{ij} = u_c + g_i + g_j + s_{ij}$ for crosses;

where,

y_{ii} = is the observed value of parent i;
u_v = the parental mean;
v_i = the deviation from u_v associated with parent i;
y_{ij} = the observed value of ij^{th} cross between parent i and j;
g_i, g_j and s_{ij} are general and specific combining ability effects of parents i and j and their cross, respectively.

b. Model II analysis

$y_{ij} = u_v + (v_i + v_j)/2 + r\,(\bar{h} + h_i + h_j + s_{ij})$;

where,

v_i and v_j are variety effects when parents are included in the analysis.
$\bar{h}$ = average heterosis of all crosses;
h_j = the parental heterosis contributed by variety j in its crosses measured as a deviation from $\bar{h}$, average heterosis, $\left(\sum_j h_j = 0\right)$;
s_{ij} = the same as in model III;
r = 0 if i = j and 1 if i $\neq$ j and
$\bar{h} + h_i + h_j + s_{ij} = h_{ij}$, the overall heterosis effect.

Results and discussion

The analysis of variance for 100-seed weight carried out for the year 1975 and 1976 for testing the significance of genotypic differences is given in Table 1. The entries' (genotypic) variance was also partitioned into its appropriate orthogonal components viz., parents vs F_1's etc. The genotypic differences were foundsignificant in both years. Likewise, the significant differences were also observed among the parents and F_1's. However, the absence of significance of mean square associated with parents vs F_1 indicated lack of average heterosis for 100-seed weight in both years.

In both of Griffing's methods, the variances due to gca effects were highly significant. However, the variance due to sca effects was significant only in method 2 but not in method 4. This suggested the predominant role of additive type of gene effects for this character. In Morley-Jones' model, only two components, 'a' and 'b_2', were significant. Here 'a' signifies additive genetic variance in the absence of the b_2 item. Since b_2 is significant, the 'a' item will not measure additive variance unambiguously, but it will be contaminated with non-additive variance also. The b_1 item measures the mean deviations of the F_1's from the mid-parental values and becomes significant when the dominance effects at various loci are predominantly in one direction. The absence of significance of this item in this case suggested an ambidirectional nature of dominance. The significance of the b_2 item indicated that the mean dominance deviations of the F_1's from their mid-parental values differed significantly over the F_1 arrays and these arrays differ if some parents contain more dominant alleles than others, implying asymmetry of gene distribution (i.e. $H_1 \neq H_2$; Hayman 1954). The item b_3 is equivalent to specific combining ability variance and was not significant for this character during 1975. A similar situation was also indicated by Griffing's method 4.

In case of Walters and Morton's model, the g_i (the additive genetic variance) and l_i (which is equivalent to the b_2 item of Morley-Jones' model) were significant, giving almost similar picture as that described by the Morley-Jones' model. Here l_{ij} which is equivalent to b_3/sca and l (equivalent to b_1) were significant and not significant respectively.

As regards Gardner and Eberhart's model, the variances due to gca effects, h_i (parental heterosis which is equivalent to b_2) and h_{ij} (the overall heterosis) were significant. The other components such as $\bar{h}$ (average heterosis equivalent to b_1, l and parents vs F_1's) in both the years and s_{ij} (the sca variance equivalent to b_3/l_{ij}) during 1975 were not significant.

Thus from this analysis the following comparison was obvious: The additive parameter (a) in Morley-

Table 1. Comparison of different diallel models for 100-seed weight

Simple ANOVA (RBD)				Griffing's method 2				Griffing's method 4			
Source	D.F.	MS		Source	D.F.	MS			D.F.	MS	
		1975	1976			1975	1976			1975	1976
Entries	35	0.87**	0.92**	gca	7	1.24**	0.97**		7	0.61**	0.40**
Parents	7	2.13**	2.20**	sca	28	0.05*	0.14*		20	0.04	0.13*
F_1's	27	0.56**	0.61**	Error	70	0.03	0.07		70	0.03	0.07
P vs F_1's	1	0.22	0.35								
Error	70	0.09	0.21								
Morley-Jones' model				Walters and Morton's model				Gardner and Eberhart's model			
a	7	3.71**	2.90**	g_i	7	2.14**	2.20**	gca	7	0.61**	0.40**
b_1	1	0.22	0.35	l	1	0.22	0.35	h_{ij}	28	0.05*	0.14*
b_2	7	0.27**	0.49*	l_i	7	0.27**	0.49*	$\bar{h}$	1	0.07	0.12
b_3	20	0.12	0.40*	l_{ij}	20	0.67**	0.65**	h_i	7	0.09**	0.16*
bt (Error)	70	0.09	0.21	Error	70	0.09	0.21	s_{ij}	20	0.04	0.13*
								Error	70	0.03	0.07

* $P = 0.05 - 0.01$
** $P = 0.01 - 0.001$

Jones' model was higher than its corresponding value (g_i) in Walters and Morton's model. The higher value of 'a' over 'g_i' may be due to the presence of some portion of dominance in 'a', as shown by Hayman (1954). The theoretical value of $a = D - F + H_1 - H_2$ and of $b_2 = H_1 - H_2$. If b_2 is significant, obviously a substantial portion of dominance will be present in the 'a' item. With b_2 being significant in the present case, the estimate of additive variance (a) could not be unbiased.

The values of mean squares of 'a' in Morley-Jones' model were 3.71 and 2.90 while the values of gca mean squares in Griffing's method 2 were 1.24 and 0.97 in 1975 and 1976, respectively, showing a relationship between the two parameters, since $a = 3 \times \text{gca}$. In fact, these two estimates would have been equal, had these been estimated on the mean values over three replications. In the present case, however, 'a' was estimated on the basis of totals over replications whereas gca variance was estimated on means. The gca variance being equal to 'a' of the Morley-Jones' model, it may contain some portion of dominance. Thus the belief that gca is purely a function of additive variance appears to be contradicted (Matzinger 1963; Chung and Stevenson 1973; Jugenheimer 1976).

Item 'b_1' of Morley-Jones' model was equal to that of the 'l' in the Walters and Morton model and $\bar{h}$ in Gardner and Eberhart's model ($\bar{h} \times 3$; because the M.S. values were based on means of 3 replications), and the P vs F_1 contrast in the simple analysis of variance table. All these measured average heterosis or mean dominance variance. None of these parameters were significant. The 'b_2' in Morley-Jones' model (which is equal to $H_1 - H_2$) was equal to the l_i in Walters and Morton's model and h_i in Gardner and Eberhart's model and all these estimated asymmetrical gene distribution or parental contribution towards variety heterosis. The magnitude of the 'b_3' item of Morley-Jones' model was not equal to that of the l_{ij} in Walters and Morton's, but was equal to the s_{ij} of Gardner and Eberhart's model and the sca of Griffing's method 4. The gca of Gardner and Eberhart's model was equal to the gca of Griffing's method 4.

Obviously, all these methods of diallel analysis are interrelated. However, the method of Gardner and Eberhart (1966) appears to have some advantages over the others. Firstly, it gives a clear-cut idea about the genetic aspect of heterosis by partitioning the total sum of squares of heterosis (h_{ij}) into different components as well as furnishing information on combining ability of the parents as obtained in Griffing's method 4. Secondly, since in this analysis parents are also included, and there is a simple relationship between heterosis (h_{ij}) and specific combining ability (s_{ij}) as $h_{ij} = \frac{2 s_{ij} - s_{ii} - s_{jj}}{2}$, heterosis can be easily calculated, if the s_{ij} of crosses and parents is known.

There are a few reports on the comparison of Gardner and Eberhart's method with Griffing's model (Gupta et al. 1974; Gupta and Ramanujam 1974). Keeping in view the facts discussed above, it appeared that the conclusions drawn by these authors do not hold true.

The results in the present case have further suggested that Griffing's method 2 and 4 give a more or less similar picture with respect to combining ability effects and variances. However, there are reports that by exclusion of parental generation from diallel analysis the precision of estimates is increased (Hayes and Paroda 1974). An in-depth study of some of these reports, however, indicate that the errors were committed by these authors in computing various statistics (gca/sca) and thus wrong conclusions were drawn about the superiority of one model over the other.

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