METHODS OF ANALYSIS AND THE ESTIMATION OF THE GENETIC PARAMETERS FROM A DIALLEL SET OF CROSSES

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SUMMARY

The relationships between the estimates of general (σ_g^2) and specific (σ_s^2) combining abilities obtained from the four methods of diallel analysis described by Griffing (1956) and estimates of D_R and H_R, the additive and dominance components of variability, are compared both theoretically and experimentally for model II situations. Theoretically they are compared by deriving the expectations of the variance components for the general and specific combining abilities for each method in terms of the genetical parameters $\sum u_i v_i d_i^2$, $\sum u_i v_i h_i^2$, $\sum u_i^2 v_i^2 h_i^2$ and $\sum u_i v_i (u_i - v_i) d_i h_i$. Experimentally they are compared by extracting data from a diallel set of crosses between a random sample of $29F_9$ families derived from the F_2 of the cross of varieties 1 and 5 of *Nicotiana rustica* by pedigree inbreeding.

The theoretical results show and the experimental results confirm that the genetical expectations of σ_g^2 and σ_s^2 for method 1 are identical with the general definitions of $\frac{1}{4}D_R$ and $\frac{1}{2}H_R$. This method, therefore, gives consistent estimates of D_R and H_R in all situations. In contrast, methods 2, 3 and 4 give close approximations to $\frac{1}{4}D_R$ and $\frac{1}{4}H_R$ only when estimates from diallels involve large numbers of parents.

The limitations of diallel analysis as a source of estimates of genetically defined as opposed to statistically defined parameters are discussed.

1. INTRODUCTION

Griffing (1956) has described methods for analysing (a) full diallel with selfs; (b) half diallel with selfs; (c) full diallel without selfs and (d) half diallel without selfs: and estimating the components of variance for general (σ_g^2) and specific (σ_s^2) combining abilities. However, little has been published either about the genetical expectations of these components $(\sigma_g^2$ and $\sigma_s^2)$ or how their estimates relate to the values of $\frac{1}{4}D_R$ and $\frac{1}{4}H_R$, which are the additive and dominance components of a randomly mating population. With this objective we shall compare the genetical expectations of the σ_g^2 and σ_s^2 components obtained from all four methods for model II situations using genetical parameters defined by Hayman (1954), Jinks (1954) and Mather and Jinks (1982) and illustrate the theory by analysing a 20×20 diallel produced by Breese (1955) from a random sample of inbred lines which were extracted from the F_2 of the cross of varieties 1 and 5 of *Nicotiana rustica*.

2. THEORY

We shall compare the four methods of Griffing (1956), which we shall refer to as 1 to 4, by obtaining the theoretical expectations of their σ_g^2 and

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σ_s^2 components in terms of $\sum u_i v_i d_i^2$, $\sum u_i v_i h_i^2$, $\sum u_i^2 v_i^2 h_i^2$, $\sum u_i v_i (u_i - v_i) d_i h_i$ and $\sum u_i^2 v_i^2 h_i^2$, respectively, (see Jinks, 1954 and Mather and Jinks, 1982, for definitions). Following Griffing we shall use U_i and V_i as the actual numbers of inbred parents in which the alternative alleles are fixed with respect to the ith locus with a further proviso that $U_i/u_i = V_i/v_i = p$, the number of parents in a diallel crossing programme. However, to make the expectations valid for a population we shall assume p to be large and finite. We shall also assume that epistasis, genotype environmental interaction, linkage, multiple allelism, reciprocal differences, differential gametic selection etc. are absent.

We obtain the estimates of σ_g^2 and σ_s^2 as the variances of individual gca and sca effects which in turn are estimated from the formulae given by Griffing (1956). To illustrate the method used to obtain these variances we shall present the derivation procedure for method 1.

For any locus i for which alternative alleles (A and a) are fixed amongst the sample of inbred lines, the diallel set of crosses produced from them have the following expectations:

♀ parent	♂ parent	AA	aa	
		(U_a)	(V_a)	Row total
AA	Frequency	U_a^2	$U_a V_a$	
	Genotype	AA	Aa	
(U_a)	Score	$m + d_a$	$m + h_a$	$pm + U_a d_a + V_a h_a$
aa	Frequency	$U_a V_a$	V_a^2	
	Genotype	Aa	aa	
(V_a)	Score	$m + h_a$	$m - d_a$	$pm - V_a d_a + U_a h_a$
Column total		$pm + U_a d_a + V_a h_a$	$pm - V_a d_a + U_a h_a$	$p^2 m + p(U_a - V_a)d_a + 2U_a V_a h_a$

Here U_a and V_a are the actual numbers of inbreds with AA and aa genotypes respectively, whereas m, d_a and h_a are the mean, additive genetic and dominance effects as defined by Mather and Jinks (1982). Using Griffing's formulae we obtain

$$gca(AA) = \frac{1}{2p}\{2pm + U_a d_a + V_a h_a\} - \frac{1}{p^2}\{p^2 m + p(U_a - V_a)d_a + 2U_a V_a h_a\}$$

$$= \frac{V_a d_a}{p} - \frac{V_a(U_a - V_a)h_a}{p^2};$$

and

$$gca(aa) = \frac{1}{2p}\{2pm - V_a d_a + U_a h_a\} - \frac{1}{p^2}\{p^2 m + p(U_a - V_a)d_a + 2U_a V_a h_a\}$$

$$= -\frac{U_a d_a}{p} + \frac{U_a(U_a - V_a)h_a}{p^2}$$

and their respective frequencies are U_a and V_a. The variance of these values

is obtained as $\{U_a gca(AA)^2 + V_a gca(aa)^2\}/p$ which is equal to

$$\frac{U_a V_a d_a^2}{p^2} + \frac{U_a V_a h_a^2}{p^2} - \frac{4U_a^2 V_a^2 h_a^2}{p^4} - \frac{2U_a V_a(U_a - V_a)d_a h_a}{p^3}$$

Similarly we obtain the *sca* values for *AA*, *Aa* and *aa* as

$$-\frac{2V_a^2 h_a}{p^2}, \qquad \frac{2U_a V_a h_a}{p^2} \quad \text{and} \quad -\frac{2U_a^2 h_a}{p^2}$$

respectively and their variance as $\frac{1}{2}\{U_a^2(-2V_a^2 h_a)^2 + 2U_a V_a(2U_a V_a h_a)^2 + V_a^2(-2U_a^2 h_a)^2\}/p^6$ which is equal to $(4U_a^2 V_a^2 h_a^2)/p^4$.

For many loci these expectations become

$$\sigma_g^2 = \frac{\sum U_i V_i d_i^2}{p^2} + \frac{\sum U_i V_i h_i^2}{p^2} - \frac{4\sum U_i^2 V_i^2 h_i^2}{p^4} - \frac{2\sum U_i V_i(U_i - V_i)d_i h_i}{p^3}$$

and

$$\sigma_s^2 = \frac{4\sum U_i^2 V_i^2 h_i^2}{p^4},$$

which are the sums over all loci.

These expectations together with those for methods 2, 3 and 4 are listed in table 1. The contributions of the various components to σ_g^2 and σ_s^2 obviously differ between methods. For example, the cross product $d_i h_i$ has a coefficient of $2\sum U_i V_i(U_i - V_i)/p^3$ for the full diallel (method 1); $2\sum U_i V_i(U_i - V_i)/p^2(p+2)$ for half diallel with selfs (method 2); $2\sum U_i V_i(U_i - V_i)/p^2(p-2)$ for full diallel without selfs (method 3) and $2\sum U_i V_i(U_i - V_i)/p^2(p-2)$ for half diallel without selfs (method 4). These differences and those for the other components of σ_g^2, however, depend only on the number of parents in the diallel. In contrast, coefficients of h_i^2 for σ_s^2 are affected in a more complicated manner.

To quantify these effects for σ_g^2 the coefficients for $\sum u_i v_i d_i^2$, $\sum u_i v_i h_i^2$, $4\sum u_i^2 v_i^2 h_i^2$ and $2\sum u_i v_i(u_i - v_i)d_i h_i$ have been obtained by substituting p equals 4, 8, 10, 20 and 100 into the formulae to cover a whole range of possible diallel crossing programmes after substituting $U_i = u_i p$ and $V_i = v_i p$ to standardise the parameters. The values of these coefficients are given in table 2. For the smaller values of p it is unlikely in practice that the gene frequencies in the sample of parents would be the same as in the parental population, we have, however, assumed them to be the same.

For σ_s^2 the same range of values have been substituted for p and in addition gene frequencies have been varied between $u = v = \frac{1}{2}$ and $u = \frac{3}{4}$ and $v = \frac{1}{4}$. These gene frequencies have, however, been assumed to apply to all loci for which the parental population varies. The coefficients, standardised in each case to apply to $4\sum u_i^2 v_i^2 h_i^2$ so that the actual values of σ_s^2 can be compared between methods, are given in table 3.

3. MATERIALS

(i) *The experiment*

During 1943 a cross between two inbred varieties V1 and V5 of *Nicotiana rustica* was initiated by Mather and Vines at Merton, South

TABLE 1

Theoretical expectations of σ_g^2 and σ_s^2 for methods 1 to 4 of diallel analysis proposed by Griffing (1956)

Method	Expectation
	(a) *General combining ability σ_g^2*
1. Full diallel with selfs	$\dfrac{\sum U_i V_i d_i^2}{p^2} + \dfrac{\sum U_i V_i h_i^2}{p^2} - \dfrac{4 \sum U_i^2 V_i^2 h_i^2}{p^4} - \dfrac{2 \sum U_i V_i (U_i - V_i) d_i h_i}{p^3}$
2. Half diallel with selfs	$\dfrac{\sum U_i V_i d_i^2}{p^2} + \dfrac{\sum U_i V_i h_i^2}{(p+2)^2} - \dfrac{4 \sum U_i^2 V_i^2 h_i^2}{p^2(p+2)^2} - \dfrac{2 \sum U_i V_i (U_i - V_i) d_i h_i}{p^2(p+2)}$
3. Full diallel without selfs	$\dfrac{\sum U_i V_i d_i^2}{p^2} + \dfrac{\sum U_i V_i h_i^2}{(p-2)^2} - \dfrac{4 \sum U_i^2 V_i^2 h_i^2}{p^2(p-2)^2} - \dfrac{2 \sum U_i V_i (U_i - V_i) d_i h_i}{p^2(p-2)}$
4. Half diallel without selfs	$\dfrac{\sum U_i V_i d_i^2}{p^2} + \dfrac{\sum U_i V_i h_i^2}{(p-2)^2} - \dfrac{4 \sum U_i^2 V_i^2 h_i^2}{p^2(p-2)^2} - \dfrac{2 \sum U_i V_i (U_i - V_i) d_i h_i}{p^2(p-2)}$
	(b) *Specific combining ability σ_s^2*
1. Full diallel with selfs	$\dfrac{4 \sum U_i^2 V_i^2 h_i^2}{p^4}$
2. Half diallel with selfs	$\dfrac{4 \sum U_i(U_i+1) V_i(V_i+1) h_i^2}{p(p+1)^2(p+2)}$
3. Full diallel without selfs	$\dfrac{4 \sum U_i(U_i-1) V_i(V_i-1) h_i^2}{p(p-1)^2(p-2)}$
4. Half diallel without selfs	$\dfrac{4 \sum U_i(U_i-1) V_i(V_i-1) h_i^2}{p(p-1)^2(p-2)}$

* U_i and V_i are the actual numbers of inbreds which have alternative alleles fixed in them for the ith locus.

TABLE 2

Expected coefficients of $\sum u_i v_i d_i^2$, $\sum u_i v_i h_i^2$, $4 \sum u_i^2 v_i^2 h_i^2$ and $2 \sum u_i v_i (u_i - v_i) d_i h_i$ for various sizes of diallel crosses

No. of parents in a diallel	$\sum u_i v_i h_i^2$	coefficients of $\sum u_i v_i h_i^2$	$4 \sum u_i^2 v_i^2 h_i^2$	$2 \sum u_i v_i (u_i - v_i) d_i h_i$
	Method 1: Full diallel with selfs			
Any	1·0000	1·0000	1·0000	1·0000
	Method 2: Half diallel with selfs			
4	1·0000	0·4444	0·4444	0·6666
8	1·0000	0·6400	0·6400	0·8000
10	1·0000	0·6944	0·6944	0·8333
20	1·0000	0·8264	0·8264	0·9090
100	1·0000	0·9612	0·9612	0·9804
∞	1·0000	1·0000	1·0000	1·0000
	Methods 3 and 4: Full and half diallel without selfs			
4	1·0000	4·0000	4·0000	2·0000
8	1·0000	1·7777	1·7777	1·3333
10	1·0000	1·5625	1·5625	1·2500
20	1·0000	1·2346	1·2346	1·1111
100	1·0000	1·0412	1·0412	1·0204
∞	1·0000	1·0000	1·0000	1·0000

TABLE 3

Expected coefficients of $4 \sum u_i^2 v_i^2 h_i^2$ for various sizes of diallel when u and v take values of $\frac{3}{4}$ and $\frac{1}{4}$, and $\frac{1}{2}$ and $\frac{1}{2}$, respectively

Method	$u:v$	Number of parents in the diallel					
		4	8	10	20	100	∞
1. Full diallel	$\frac{3}{4}:\frac{1}{4}$	1·0	1·0	1·0	1·0	1·0	1·0
with selfs	$\frac{1}{2}:\frac{1}{2}$	1·0	1·0	1·0	1·0	1·0	1·0
2. Half diallel	$\frac{3}{4}:\frac{1}{4}$	1·1380	1·1067	1·0932	1·0555	1·0135	1·0
with selfs	$\frac{1}{2}:\frac{1}{2}$	0·96	0·9876	0·9916	0·9976	1·0000	1·0
3. Full diallel	$\frac{3}{4}:\frac{1}{4}$	0·0	0·7257	0·8026	0·9194	0·9863	1·0
without selfs	$\frac{1}{2}:\frac{1}{2}$	0·8888	0·9796	0·9876	0·9972	0·9999	1·0
4. Half diallel	$\frac{3}{4}:\frac{1}{4}$	0·0	0·7257	0·8026	0·9194	0·9863	1·0
without selfs	$\frac{1}{2}:\frac{1}{2}$	0·8888	0·9796	0·9876	0·9972	0·9999	1·0

London (Mather and Vines, 1952). Subsequently a controlled programme of pedigree inbreeding was carried out to produce a random sample of the inbred lines which can be extracted from the cross. In 1954 twenty F_9 lines, each produced from a separate F_2 plant, were diallely crossed to produce 20 selfs and 190 pairs of reciprocal F_1's. These families were raised during the summer of 1955 in a randomised layout in two blocks where each family was allocated a single row plot of 5 plants at random. Adequate guards were provided to avoid differential competition between the experimental plants and each plant was scored for flowering time in days from an arbitrary date and for final height in inches at the end of the season.

4. ANALYSES

Before we submit the data to the combining ability analyses we shall test for some important assumptions made in section 2. These tests we can carry out by applying the analysis of variance of Hayman (1954a) and the W_r/V_r graphic analysis and component estimation of Jinks (1954) and Hayman (1954b). These analyses have already been carried out by Jinks, Perkins and Breese (1969) and published with the analyses on test crosses. The results they obtained for final height point to the absence of gene interaction and linkage disequilibrium and provide a strong hint of allelic inequality with recessive alleles being more frequent than dominants. For flowering time there is, however, some evidence for epistasis or a linkage disequilibrium or both and gene frequencies are more likely to be equal than different. Jinks *et al.*, (1969) also estimated various parameters which we summarise thus:

	$4 \sum u_i v_i d_i^2$	$4 \sum u_i v_i h_i^2$	$16 \sum u_i^2 v_i^2 h_i^2$	$8 \sum u_i v_i (u_i - v_i) d_i h_i$
Flowering time	14·20	1·91	1·29	6·07
Final height	36·49	3·60	0·28	12·20

The most appropriate combining ability analysis for our data is Griffing's Method 1 because it utilises information derived from every one of the

TABLE 4

Mean squares of the analyses of variance of a 20×20 and four 5×5 diallels of Nicotiana
rustica *for methods 1 to 4 proposed by Griffing (1956)*

| | | 20×20 diallel | | | 5×5 diallel | |
| | | Flowering | Final | | Flowering | Final |
Item	df	time	height	df	time	height
		Method 1: Full diallel with selfs				
GCA	19	86·98***	268·41***	16	27·24***	77·98***
SCA	190	2·39***	6·46***	40	2·28***	9·36***
Recip. diffs	190	2·00**	5·49**	40	2·32***	5·94***
Error	384	0·99	3·71	92	0·78	3·27
		Method 2: Half diallel with selfs				
GCA	38	51·41***	150·30***	32	21·85***	56·07***
SCA	380	2·23***	6·46**	80	2·50***	8·59
Error	384	0·99	3·71	92	0·78	3·27
		Method 3: Full diallel without selfs				
GCA	19	73·50***	241·09***	16	12·85***	52·22***
SCA	170	2·31***	5·57***	20	1·36*	5·55***
Recip. diffs	190	2·00***	5·49***	40	2·32***	5·94***
Error	384	0·99	3·71	92	0·78	3·27
		Method 4: Half diallel without selfs				
GCA	38	37·99***	122·17***	32	6·96	29·07***
SCA	340	2·13***	5·67**	40	2·24***	5·58***
Error	384	0·99	3·71	92	0·78	3·27

*** $p < 0.001$; ** $0.01 \geqslant p \geqslant 0.001$; * $0.05 \geqslant p > 0.01$; NS $p > 0.05$.

families raised in the experiment. Method 3 can, however, be applied simply by excluding the selfs on the leading diagonal of the diallel table. This exclusion also allows the two halves of the diallel to be analysed as two independent experiments using method 4. By reinstating the selfs with either of these halves two separate sets of data are produced which can be analysed by method 2.

The results of these analyses for each character using plot means are summarised in table 4. For methods 1 and 3 the mean squares for *gca*, *sca* and reciprocal effects are tabulated for 19, 190 and 190 degrees of freedom respectively. For methods 2 and 4 the sum of squares from the two sets are pooled and the combined mean squares for *gca* and *sca* are presented for 38 and 380 degrees of freedom. In each case there is a common error variance obtained from the blocks × families interactions as $\frac{1}{5} \times ms_{(b \times f)}$ and the significance of various mean squares is tested according to Model II.

It is clear from tables 1, 2 and 3 that the magnitudes of σ_g^2 and σ_s^2 can vary with p, the number of parents in the diallel. To see if it is true in practice our 20×20 diallel has been arbitrarily split into four 5×5 diallels and the analyses repeated for each diallel separately. To summarise these four analyses the relevant *ss*'s and degrees of freedom over the diallels have been pooled to obtain cumulative mean squares. These are presented in table 4 for comparison. Again the tests of significance have been carried out according to Model II using $\frac{1}{5} \times ms_{(b \times f)}$ for 92 degrees of freedom as error variance.

Each item in table 4 is highly significant except the *sca* mean square for flowering time in the 5×5 diallels which is significant only at the 5 per

TABLE 5

Estimates of σ_g^2 and σ_s^2 for 20×20 and 5×5 diallels as obtained from Methods 1 to 4 analyses

Method	σ_g^2		σ_s^2	
	$p=5$	$p=20$	$p=5$	$p=20$
(a) *Flowering time*				
1. Full diallel with selfs	2·5031	2·1149	0·8928	0·7349
2. Half diallel with selfs	2·7645	2·2350	1·7231	1·2388
			(0·9531)	(0·7328)*
3. Full diallel without selfs	1·9169	1·9773	0·2915	0·6610
4. Half diallel without selfs	1·5754	1·9923	1·4631	1·1416
			(0·6931)	(0·6366)
(b) *Final height*				
1. Full diallel with selfs	6·8910	6·5500	3·6250	1·4450
2. Half diallel with selfs	6·7823	6·5388	5·3183	2·7488
			(3·9841)	(1·8588)
3. Full diallel without selfs	7·7779	6·5421	1·1391	0·9299
4. Half diallel without selfs	7·8319	6·4720	2·3083	1·9612
			(0·9741)	(1·0712)

* Values in brackets are obtained by subtracting the σ_{recips}^2 (from table 4) from the values given.

cent level. In every case the relevant component of variance (σ_g^2 or σ_s^2) is, therefore, significantly greater than zero. The estimates of σ_g^2 and σ_s^2 obtained for these comparisons are given in table 5.

5. RESULTS

A number of patterns emerge from the theoretical expectations (tables 1, 2 and 3) which are relevant to our practical results. Firstly, estimates of σ_g^2 are expected to differ between different methods only when the number of parents in the diallel is small ($p < 10$). They should, therefore, have the same value when obtained by any of the methods from diallel crosses involving a large number of parents (say $P > 20$). Secondly, even when p is small the differences between the estimates of σ_g^2 are expected to occur mainly (a) between those obtained from methods 1 and 2 and (b) between these estimates and those from methods 3 and 4, the latter pair of estimates are themselves not expected to differ.

Method 1 should provide consistent estimates of σ_g^2 even when p, the number of parents, is reduced. This is because of a consistency of the coefficients of the genetical components of σ_g^2 which is independent of p. This, however, is not true for the other methods because the coefficients of $\sum u_i v_i h_i^2$, $4\sum u_i^2 v_i^2 h_i^2$ and $2\sum u_i v_i(u_i - v_i)d_i h_i$ either decrease as in the case of method 2 or they increase as for methods 3 and 4 when p is reduced. The contributions of $\sum u_i v_i d_i^2$ to the estimates of σ_g^2 in the four methods, on the other hand, remain the same as those for method 1 and are consistent over all methods. Consequently we expect either

$$\sigma_g^2(\text{method 2}) > \sigma_g^2(\text{method 1}) \gg \sigma_g^2(\text{method 3}) \simeq \sigma_g^2(\text{method 4})$$

or

$$\sigma_g^2(\text{method 2}) < \sigma_g^2(\text{method 1}) \ll \sigma_g^2(\text{method 3}) \simeq \sigma_g^2(\text{method 4})$$

to be true when both additive and dominance effects are significant and p is small ($p < 10$). The four estimates, however, should gradually become equal to each other either as p becomes very large ($p > 100$) or as the dominance becomes very small.

The coefficient of σ_s^2 when estimated by method 1 is again independent of change in p. For the remaining methods estimates of σ_s^2 seem to be equally affected by unequal gene frequencies and the size of the diallel. For example approximately equal estimates of σ_s^2 are obtained when p is large or when $u_i = v_i$ and p is small ($5 < p < 10$). On the other hand when p is small and $u_i \neq v_i$ σ_s^2 from method 2 has the largest value while estimates from methods 3 and 4 have the smallest value. In general, however, σ_s^2(method 1) and σ_s^2(method 2) are expected to be marginally larger than σ_s^2(method 3) and σ_s^2(method 4) when $u_i = v_i$. These differences increase when $u_i \neq v_i$ but within each pair σ_s^2(method 2) > σ_s^2(method 1) and σ_s^2(method 2) $\simeq$ σ_s^2(method 4) for all situations.

In interpreting the experimental results in table 5 it must be borne in mind that the differences between the 20×20 and 5×5 diallels and among the four methods of analysis are not subjected to the normal sampling errors. Within the 20×20 and 5×5 diallels the four methods are using the same data although the 5×5 diallels use only about a quarter of the data of the 20×20 diallel. As a result differences attributable to the four methods of analysis within the 20×20 or the 5×5 diallels are subject to very small sampling errors, hence small differences are real; and, while the sampling errors for differences between the 20×20 and 5×5 diallels will be larger, they will still be smaller than normal.

In general our experimental results (table 5) support the conclusions based upon theoretical expectations. For example, both for flowering time and final height estimates of σ_g^2 differ less when they are obtained from a 20×20 than from a 5×5 diallel (table 5). Thus while no systematic sequencing of the σ_g^2 estimates is possible when $p = 20$, the expected trend is apparent when $p = 5$, that is, for flowering time

$$\sigma_g^2(\text{method 2}) > \sigma_g^2(\text{method 1}) > \sigma_g^2(\text{method 3}) > \sigma_g^2(\text{method 4})$$

and for final height

$$\sigma_g^2(\text{method 2}) < \sigma_g^2(\text{method 1}) < \sigma_g^2(\text{method 3}) < \sigma_g^2(\text{method 4}).$$

Also, as expected, the estimates of σ_g^2 are relatively larger for both methods 1 and 2 when $p = 5$ but smaller when $p = 20$ for both characters. The same pattern, however, holds for methods 3 and 4 in respect of final height only, the reverse being true for flowering time.

Estimates of σ_s^2 also conform to our theoretical expectations but only when the comparisons are restricted to those between methods 1 and 3 and methods 2 and 4. When $p = 20$ σ_s^2 takes smaller values for methods 3 and 4 than for methods 1 and 2. These differences, as expected, are increased when p is reduced to 5. Furthermore, for both characters σ_s^2 increases in value when estimated from methods 1 and 2. The estimates from methods 3 and 4 however, as expected, show no distinct pattern.

A marked feature of these analyses is that the estimates of σ_s^2(method 2) and σ_s^2(method 4) are always nearly twice those of σ_s^2(method 1) and σ_s^2(method 3) which is contrary to the theoretical expectation that they should be approximately equal (when $p = 20$). However, σ_s^2 represents *sca*

effects for methods 2 and 4 only when differences between reciprocal crosses and plot errors are non-significant. While these effects can be allowed for in the design of the analysis for methods 1 and 3, this is not possible for methods 2 and 4 especially when both reciprocal differences and plot errors are confounded as they are in the present experiment. Estimates of σ_s^2 however are reduced to approximately their true values when they are corrected by subtracting σ_{recips}^2 (see table 5).

6. DISCUSSION

Table 1 shows that the genetical expectations of σ_g^2 and σ_s^2 differ for methods 1 to 4. For σ_g^2 these differences are confined to the relative contributions made by the four constituent components while these constituent components themselves remain unchanged as $\sum u_i v_i d_i^2$, $\sum u_i v_i h_i^2$, $\sum u_i^2 v_i^2 h_i^2$ and $\sum u_i v_i (u_i - v_i) d_i h_i$, respectively. For σ_s^2, on the other hand, the differences are more complex involving the number of parents p, the gene frequencies u_i and v_i and the dominance effects $\sum h_i$ in ways that are not readily reducible to functions of a single component, $\sum u_i^2 v_i^2 h_i^2$. These differences, however, merely reflect the unique experimental situation presented by each method.

The genetical expectations of σ_g^2 and σ_s^2 for method 1 are identical with the general definitions of additive and dominance components of variation in a randomly mating population. Method 1 should therefore always provide consistent estimates of $\frac{1}{4}D_R$ and $\frac{1}{4}H_R$. This is not true, however, of methods 2, 3 and 4. They will give close approximations of $\frac{1}{4}D_R$ and $\frac{1}{4}H_R$ only if they are estimated from diallels involving at least 20 parents. They are unlikely to do so, however, if the involvement of a large number of parents is accompanied by the use of a partial design for reducing the total number of families in the diallel.

The relationships between σ_g^2 and σ_s^2 and D_R and H_R are conditional upon the assumptions in section 2 being met. Methods 1 and 3 provide tests for one of these assumptions, no differences between reciprocal crosses, and an experimental design could be adopted for all of the methods that would allow for the failure of another assumption, no genotype × microenvironment interactions. None of the methods, however, provide tests for the assumptions of no non-allelic interaction and linkage equilibrium. Nevertheless the data of methods 1 and 2 if analysed by the alternative method of Hayman (1954) and Jinks (1954) provide a test for these two assumptions. Furthermore, if the assumptions are met their analysis partitions the statistically defined additive and dominance components, D_R and H_R, into gene action defined components which provide estimates of gene frequencies and of the dominance ratio.

It has often been argued (Gilbert, 1958; Kempthorne, 1976; Hinkelmann, 1976; Bulmer, 1980; Mayo, 1980) that the assumptions that must be satisfied for this partitioning to yield interpretable estimates of the genetical components are too stringent and that a genetically uninformative but relatively assumptionless analysis such as that of Griffing is, therefore, to be preferred. This argument on the one hand ignores the provision of tests of the additional assumptions made by Jinks and Hayman, and on the other hand the regularity with which users of the Griffing's analysis attempt to extend the interpretation beyond the narrow limits it imposes. For

example, the equation of general combining ability with additive gene action and of specific combining ability with dominance makes implicit assumptions about gene action and interaction, and allele frequency and distribution that go beyond even those of the Jinks and Hayman analysis without providing justification for any of them. If, however, the primary purpose of an investigation is to measure the genetical components of variation and to test the assumptions on which the estimates are based, the diallel should not be the preferred design. The triple test cross (Kearsey and Jinks, 1968) in one or more of its many forms (Jinks, Perkins and Breese, 1969; Pooni, Jinks and Jayasekara, 1978; Pooni, Jinks and Pooni, 1980) will always be more appropriate. Indeed, the kind of information that the breeders of many crops should be seeking to guide their breeding policy can be obtained from little more than a simple analysis of random F_3 families (Jinks and Pooni, 1980; Pooni and Jinks, 1981; Jinks 1983).

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