

BIOMETRICAL ANALYSIS OF A RANDOM MATING POPULATION: A COMPARISON OF FIVE EXPERIMENTAL DESIGNS

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1. INTRODUCTION AND DESIGN OF EXPERIMENTS

SEVERAL methods have been devised to estimate the components of variation in plant and animal populations, and associated with these methods has been controversy about their relative usefulness and efficiency. The present experiment was designed as a first step towards their practical evaluation.

In general these methods have evolved by the adoption and subsequent extension of crossing designs traditionally used by breeders, and involve the calculation of the variances and covariances of relatives. On the basis of some model of the genetic system, expected values are derived for these second degree statistics in terms of genetic and environmental components and by equating the observed statistics with their expectations, a series of simultaneous equations can be obtained whose solutions produce estimates of these components of variation.

The various designs in existence show a great range in the ratio of parents to progeny families, *i.e.* for the same number of progeny families produced, some designs require the use of many more parents than do others. The five designs used in the present experiments were chosen because between them they cover the whole of this range, and also because they have been widely used or discussed.

In the present experiment these five designs have been applied simultaneously to the same basic plant population with the one restriction that the number of crosses, including selfs, in each should be approximately the same. For practical reasons this number was fixed at about 45. Thus the designs can be compared on the basis of their return in terms of information yielded, for the same outlay in terms of work involved.

The techniques used were as follows:—

(i) *Biparental Progenies (B.I.P.s)*. This involves using n plants as parents and crossing them in pairs (taken at random) to yield $n/2$ progeny families. As it was decided that the number of families should be 45, 90 parents were used, and since this was the largest number of parents used by any design the population size was thus fixed at 90 plants.

(ii) *The North Carolina Design 1 (N.C.M.1)*. (Comstock and Robinson, 1952.) In this each plant used as a male parent is crossed to n female parents, no female taking part in more than one mating. Thus there are $m + mn$ plants used, m males and mn females yielding mn progeny families. Several values of m and n are possible within the restriction that mn should be approximately 45. However, the design was originally devised for situations in which the supply of female parents is greatly in excess of males, and hence it seemed appropriate to test this method when m and n were widely different. For this reason 4 male parents were each crossed to 11 female parents, so producing 44 progeny families from 48 plants.

(iii) *The Partial Diallel Cross*. (Kempthorne and Curnow, 1961.) This involves only certain crosses from all those possible between n plants used as both male and female parents, omitting selfs and reciprocals. In a full diallel cross with the same omissions there are $\frac{n(n-1)}{2}$ crosses, the number of crosses increasing rapidly with n , the number of parents used. In the partial diallel the breeder need only use $\frac{ns}{2}$ crosses, where s is a whole number equal to or greater than 2 and n and s cannot both be odd.

In the present experiment n was fixed at 14 and s at 7 yielding 49 progeny families from 14 parents.

(iv) *The North Carolina Design 2 (N.C.M.2)*. (Comstock and Robinson, 1952.) Here all the mn progeny families, obtained from crossing m males to n females, are raised. It was convenient in the present experiment to have equal numbers of male and female plants such that $m = n = 7$, $mn = 49$. Thus as for the partial diallel 49 progeny families were raised from 14 parents.

(v) *The Half Diallel Cross*. This is the most restrictive of all the designs tested as it involves all the possible crosses between n plants used as both male and female parents, but without reciprocals, *i.e.* $\frac{n(n+1)}{2}$ matings (Jinks and Hayman, 1953; Hayman, 1954; Jinks, 1954; Dickinson and Jinks, 1956). A sample of 9 parents was taken and 45 progeny families were raised from them.

There were thus 232 families produced by the five designs. The 90 plants constituting the basic population were all selfed, so giving 322 families altogether. The parents required for each of the four designs (ii)-(v) were drawn separately, and at random, from the basic population.

The experimental design consisted of 4 completely randomised blocks, two blocks being sown on 10th April 1963 and the remaining two 23 days later. Each family was represented by 5 plants per block, all 1610 plants being individually randomised within each block from the time of sowing. Altogether 6440 plants were grown in 1963.

Several factors were considered in evaluating the designs, the most important being the components of variation each yielded. Other criteria were also used such as the number of parents used, the available tests of the basic assumptions, the range of breeding material for which they can be used, the number of statistics which could be obtained and the labour involved in computation.

2. MATERIAL

The long head poppy, *Papaver dubium* was used for the experiment. It is a hexaploid ($2n = 42$) but regularly forms bivalents at meiosis, and hence probably behaves effectively as a diploid. Seed counts suggest that it produces seeds as readily on selfing as on outcrossing, and there is no reason to believe that it does not outcross widely in the wild, although detailed information is lacking about this.

The particular population used, 52A, was derived from plants collected 7 years ago on the University of Birmingham campus. The 90 parents used in this investigation and grown in 1962 were a random sample of the progeny of a biparental crossing programme carried out the previous year to simulate random mating.

Although this species is very variable morphologically much of the variation is difficult to quantify. The most suitable character, and the one in fact used here, was flowering time measured in days after 13th June, the date on which the first plant flowered.

3. ASSUMPTIONS AND NOTATION

The following assumptions are involved in deriving genetical interpretations from the designs studied.

(i) Regular diploid behaviour at meiosis. Since *P. dubium* regularly forms bivalents at meiosis this assumption is most probably valid, although it is not possible to exclude polysomic inheritance with random chromosome assortment.

(ii) No maternal effects. In the present experiment N.C.M.2 provides a test of maternal effects.

(iii) No linkage. Failure of this assumption will upset the analyses only if statistics of two or more ranks are used. Statistics of rank 1 and 2 are in fact brought into all the analyses shown except for the Hayman analysis of the diallel cross (see later).

(iv) No non-allelic interaction.

(v) No genotype-environment interactions.

(vi) No multiple alleles.

(vii) Uncorrelated gene distributions.

Assuming random mating and unequal gene frequencies, three principal notations exist to designate the components of variation, all of which are simply related to the basic formulæ set out by Falconer (1960) and Jinks and Hayman (1953) (see table 1).

For consistency in presenting the results from the various designs the components are defined as far as possible using Mather's notation (1949). However, certain statistics in the half diallel can only be described by the Dickinson and Jinks (1955) elaboration of this system.

Heritability (h^2) is measured in all cases by the ratio of additive to total phenotypic variance, *i.e.*

$$\frac{V_A}{V_P} \text{ or } \frac{\frac{1}{2}D_R}{\frac{1}{2}D_R + \frac{1}{4}H_R + nE_2}$$

(*i.e.* heritability in the narrow sense). The genetic component heritability in the broad sense) is, of course

$$\frac{V_G}{V_P} \text{ or } \frac{\frac{1}{2}D_R + \frac{1}{4}H_R}{\frac{1}{2}D_R + \frac{1}{4}H_R + nE_2}$$

TABLE 1

The relationship between the various notations used in this text

General formulæ	Mather	Lush, Lerner and Falconer	Dickinson and Jinks
$\frac{\Sigma 4uv[d+h(v-u)]^2}{\Sigma 16u^2v^2h^2}$ Σe^2	$\frac{D_R}{H_R}$ nE_2	$\frac{2V_A}{4V_D}$ V_E	$D_I + \frac{1}{2}H_I - \frac{1}{2}H_{II} - \frac{1}{2}F_I$ $\frac{H_{II}}{nE_2}$

4. RESULTS

The original data are set out in the form of family means in the appendix. The results from each design have been analysed by the methods suggested by their respective authors. The general form of each analysis and its interpretation are described in this section, and a comparative evaluation of all designs is presented in section 5.

Because of the difference between the two sowing times it was decided to analyse the data from them as different experiments in all cases and the results are shown in this form. Such an approach is justified and indeed required by the marked difference between the variances at the two sowings, those plants raised from the earlier sowing being approximately twice as variable as from the second.

As several plants failed to reach maturity some families contained only 4 or even 3 plants. The average variance within families was calculated by summing the sums of squares (SS) and the degrees of freedom (d.f.) from each family and dividing the former by the latter. All other statistics were calculated on five times the family means, *i.e.* assuming 5 plants per family.

(i) B.I.P.s (Appendix A)

Although 45 matings were made between the 90 parents, two failed to produce viable seed, and the results shown are thus based on only 43 families.

Two statistics only can be obtained from this design—the variation within and between B.I.P. families. Comparison of these two statistics (table 2) shows the latter to be very significantly greater than the

former, at both sowings, so demonstrating the presence of genetic variation in the population.

The numbers in the column headed v indicate which variances were used in the denominator of each χ^2 or variance ratio test, and

TABLE 2
Analysis of variance of B.I.P. data
Sowing 1

Item	d.f.	M.S.	v	χ^2	P	Expectation of mean squares
1. Between families (F)	42	157.13	4	133.14	< 0.001	$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2$
2. Blocks (B)	1	15.05	4	< 1	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2 + 215\sigma_b^2$
3. F × B	42	50.60	4	42.84	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2$
4. Within families	329	49.61				σ_w^2
5. Pooled within families (2, 3, 4)	372	49.63				

Sowing 2

Item	d.f.	M.S.	v	χ^2	P	Expectation of mean squares
1. Between families (F)	42	66.92	4	122.64	< 0.001	$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2$
2. Blocks (B)	1	14.52	4	< 1	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2 + 215\sigma_b^2$
3. F × B	42	18.44	4	< 42	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2$
4. Within families	334	22.91				σ_w^2
5. Pooled within families (2, 3, 4)	377	22.69				

correspond to the numbers ascribed to the various items in the first column of the table. Because of the large size of the degrees of freedom attached to the variance within families, no great advantage would be obtained from pooling any non-significant interactions with this component for the purpose of significance tests. Non-significant items are, however, pooled for the purposes of estimating σ_w^2 . This approach will be used throughout.

The expectations of mean squares in this analysis can be interpreted as follows. The item σ_w^2 is the mean variance of families, \bar{V}_{BIP} or V_{2BIP_3} , and σ_s^2 is the variance of family means, V_{BIP} or V_{1BIP_3} as defined by Mather (1949) *i.e.*,

$$\bar{V}_{BIP} = \frac{1}{4}D_R + \frac{3}{16}H_R + nE_2$$

$$V_{BIP} = \frac{1}{4}D_R + \frac{1}{16}H_R$$

where $n = \text{family size} = 5$.

As there are three parameters and only two statistics from which to estimate them, it is necessary to make the added assumption that there is no dominance, *i.e.* $H_R = 0$, or to accept that D_R is a compound measure of D and H , such that:—

$$\hat{V}_{BIP} = \frac{1}{4}D_R + nE_2$$

$$\hat{V}_{\overline{BIP}} = \frac{1}{4}D_R.$$

The values \hat{V}_{BIP} , $\hat{V}_{\overline{BIP}}$, D_R and nE_2 obtained from the above analysis of variance are shown in table 3 together with the heritabilities.

TABLE 3

Components of variation and heritabilities from B.I.P.s

Sowing 1	Sowing 2
$\hat{V}_{\overline{BIP}} = 10.75$	$\hat{V}_{\overline{BIP}} = 4.42$
$\hat{V}_{BIP} = 49.63$	$\hat{V}_{BIP} = 22.69$
$\underline{V \text{ (Total)} = 60.38}$	$\underline{V \text{ (Total)} = 27.11}$
$\frac{1}{4}\hat{D}_R = 21.50$	$\frac{1}{4}\hat{D}_R = 8.84$
$n\hat{E}_2 = 38.88$	$n\hat{E}_2 = 18.27$
$\hat{h}^2 = 0.36$	$\hat{h}^2 = 0.33$

Evidently some 30 per cent. of the variation in the population is under additive genetic control. This, however, is an approximation which becomes more accurate as H_R tends to zero.

By this method the variation can only be approximately partitioned into genetic and environmental components and no information concerning the nature of the genetic component is available.

(ii) *North Carolina Model I (Appendix B)*

This design provides a third statistic which is not available from the B.I.P.s, since we can now recognise families with a common father (paternal arrays). Comstock and Robinson (1952) suggest the following analysis of variance of the data to give comparisons between males, between females within males, and within families (table 4).

From these analyses it can be seen that the items M and F are significant, *i.e.* both σ_m^2 and σ_{mf}^2 are greater than 0. These expectations of mean squares have genetical significance as shown below (see also Falconer, 1960) and estimates of the components are presented in table 5.

$$\sigma_m^2 = \text{Cov (H.S.)} = \frac{1}{8}D_R$$

$$\sigma_{mf}^2 = \text{Cov (F.S.)} - \text{Cov (H.S.)} = \frac{1}{8}D_R + \frac{1}{16}H_R$$

$$\sigma_w^2 = V_P - \text{Cov (F.S.)} = \frac{1}{4}D_R + \frac{3}{16}H_R + nE_2.$$

In estimating the values of σ^2 , the relevant non-significant items were pooled, e.g. in sowing 1 items 3, 4 and 5 are all estimates of σ_w^2 and hence were combined to give a value σ_w^2 of 34.71.

From this analysis it would appear that approximately 70-80 per cent. of the variation in flowering time is genetically controlled, and

TABLE 4
Analysis of variance of N.C.M.1 data

Item	d.f.	M.S.	<i>v</i>	χ^2	P	V.R.	P	Expectation of mean squares
<i>Sowing 1</i>								
1. Between males (M)	3	761.43	2			5.49	<0.01	$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2 + 10\sigma_{mf}^2 + 110\sigma_m^2$
2. Between females within males (F)	40	138.63	5	152.26	<0.001			$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2 + 10\sigma_{mf}^2$
3. M × blocks	3	41.74	5	3.45	N.S.			$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2$
4. F × blocks	40	19.84	5	<40	N.S.			$\sigma_w^2 + 5\sigma_{fb}^2$
5. Within families	336	36.42						σ_w^2
<i>Sowing 2</i>								
1. Between males (M)	3	214.09	2			3.06	<0.05	$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2 + 10\sigma_{mf}^2 + 110\sigma_m^2$
2. Between females within males (F)	40	69.95	4			2.48	<0.005	$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2 + 10\sigma_{mf}^2$
3. M × blocks	3	28.02	4			<1	N.S.	$\sigma_w^2 + 5\sigma_{fb}^2 + 55\sigma_{mb}^2$
4. F × blocks	40	28.16	5	60	<0.02			$\sigma_w^2 + 5\sigma_{fb}^2$
5. Within families	336	18.76						σ_w^2

that this variation includes both additive and non-additive components. In the absence of interaction the non-additive components could be interpreted as dominance but as no test for interaction can be made, such a distinction can not be drawn.

(iii) *The Partial Diallel Cross (Appendix C)*

The analysis of these data is that suggested by Kempthorne and Curnow (1961). The diallel consisted of 14 plants used as both male and female parents with 7 crosses used in each array. The components in the analysis of variance are the variances within and

between families, the latter having 48 d.f. Of these, 13 d.f. contribute to differences between arrays and measure general combining ability (g.c.a.), the remaining 35 being concerned with estimating variation within arrays or specific combining ability (s.c.a.).

Owing to the structure of this design the only way to calculate the g.c.a. SS is to assume the absence of s.c.a. The s.c.a is then obtained by subtraction.

TABLE 5

Components of variation and heritabilities from N.C.M.1

Sowing 1	Sowing 2
$\hat{\sigma}_m^2 = 5.66$ $\hat{\sigma}_{mf}^2 = 10.39$ $\hat{\sigma}_w^2 = 34.71$ <hr/> $V_P = 50.76$	$\hat{\sigma}_m^2 = 1.31$ $\hat{\sigma}_{mf}^2 = 4.18$ $\hat{\sigma}_w^2 = 18.76$ <hr/> $V_P = 24.25$
$\hat{h}^2 = \frac{4\hat{\sigma}_m^2}{V_P} = 0.45$	$\hat{h}^2 = 0.22$
$\frac{1}{2}\hat{D}_R = 22.64$ $\frac{1}{4}\hat{H}_R = 18.92$	$\frac{1}{2}\hat{D}_R = 5.24$ $\frac{1}{4}\hat{H}_R = 11.48$
$n\hat{E}_2 = 9.20$	$n\hat{E}_3 = 7.53$
$\hat{V}_G = 41.56$	$\hat{V}_G = 16.72$
Genetic component = 81.88 per cent.	Genetic component = 68.95 per cent.

In the absence of s.c.a., the expected value of observed Y_{ij} , the flowering time of cross $i \times j$, is

$$\mu + g_i + g_j$$

where μ is the overall mean, and $g_i + g_j$ are the g.c.a.s of the i th and j th parent. To estimate the g_i s we minimise,

$$X = \sum_{ij} (Y_{ij} - \mu - g_i - g_j)^2.$$

If we write R_i for the i th array total, the normal equations take the form $\mathbf{A} \cdot \mathbf{G} = \mathbf{Q}$

where \mathbf{A} is the symmetric circulant matrix with elements a_{ij} such that $a_{ii} = s$, the number of crosses per array (in this case 7) and $a_{ij} = 1$ if cross $i \times j$ is used and $= 0$ otherwise

\mathbf{G} is the column vector with elements g_i

\mathbf{Q} is the column vector with elements $Q_i = R_i - s\mu$.

In the present case, **A** takes the form:—

7	0	0	0	1	1	1	1	1	1	1	0	0	0
0	7	0	0	0	1	1	1	1	1	1	1	0	0
0	0	7	0	0	0	1	1	1	1	1	1	1	0
0	0	0	7	0	0	0	1	1	1	1	1	1	1
1	0	0	0	7	0	0	0	1	1	1	1	1	1
etc.													
0	0	0	1	1	1	1	1	1	1	0	0	0	7

which on inversion by the method given by Kempthorne and Curnow yields,

$$\begin{aligned}
 \mathbf{A}^{-1} = & a_0 \ a_1 \ a_2 \ a_3 \ a_4 \ a_5 \ a_6 \ a_7 \ a_6 \ a_5 \ a_4 \ a_3 \ a_2 \ a_1 \\
 & a_1 \ a_0 \ a_1 \ a_2 \ a_3 \ a_4 \ a_5 \ a_6 \ a_7 \ a_6 \ a_5 \ a_4 \ a_3 \ a_2 \\
 & a_2 \ a_1 \ a_0 \ a_1 \ a_2 \ a_3 \ a_4 \ a_5 \ a_6 \ a_7 \ a_6 \ a_5 \ a_4 \ a_3 \\
 & \text{etc.} \\
 & a_1 \ a_2 \ a_3 \ a_4 \ a_5 \ a_6 \ a_7 \ a_6 \ a_5 \ a_4 \ a_3 \ a_2 \ a_1 \ a_0
 \end{aligned}$$

with values obtained for a_i of:—

i	a_i
0	0.173118
1	0.025902
2	0.019012
3	0.010154
4	-0.020358
5	-0.029216
6	-0.036106
7	-0.040465

The values for Q_i calculated from the row totals are:—

Q		
i	Sowing 1	Sowing 2
1	65.500001	46.185717
2	-32.599999	-44.114283
3	42.900001	40.985717
4	-44.499999	-18.214283
5	-24.499999	3.785717
6	28.100001	-0.714283
7	26.700001	13.585717
8	-12.299999	-9.014283
9	-41.399999	-9.014283
10	-1.299999	-14.314283
11	56.900001	59.585717
12	14.900001	-27.514283
13	-18.299999	-13.014283
14	-60.099999	-28.214283

now if a_{ij} is the element in the i th row and j th column of \mathbf{A}^{-1} , the g.c.a. SS is $\sum_{ij} a_{ij} Q_i Q_j$.

The analyses of variance obtained in this way for each sowing are shown in table 6.

From these analyses it will be seen that at neither sowing is the s.c.a. M.S. significant, and hence it is only necessary to fit σ_w^2 and σ_g^2

TABLE 6
Analysis of variance of partial diallel data

Item	d.f.	M.S.	<i>v</i>	χ^2	P	V.R.	P	Expectation of mean squares
<i>Sowing 1</i>								
1. Between families (F)	48	166.35	6	157.03	<0.001			
2. g.c.a.	13	515.28	6	131.73	<0.001			$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2 + 70\sigma_g^2$
3. s.c.a.	35	36.75	6	<35	N.S.			$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2$
4. Blocks (B) . . .	1	259.37	6	5.1	<0.05			$\sigma_w^2 + 5\sigma_{bf}^2 + 245\sigma_b^2$
5. F × B	48	52.30	6	49.37	N.S.			$\sigma_w^2 + 5\sigma_{bf}^2$
6. Within families .	383	50.85						σ_w^2
<i>Sowing 2</i>								
1. Between families (F)	48	115.43	5			2.36	<0.001	
2. g.c.a.	13	307.37	5			6.30	<0.001	$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2 + 70\sigma_g^2$
3. s.c.a.	35	44.14	5			<1	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2 + 10\sigma_s^2$
4. Blocks (B) . . .	1	82.04	5			1.68	N.S.	$\sigma_w^2 + 5\sigma_{bf}^2 + 245\sigma_b^2$
5. F × B	48	48.82	6	96.56	<0.001			$\sigma_w^2 + 5\sigma_{bf}^2$
6. Within families .	383	24.27						σ_w^2

from the expectation of mean squares. The genetical interpretation of these variances are shown below, together with σ_s^2 .

$$\sigma_g^2 = \text{Cov (H.S.)} = \frac{1}{8}D_R$$

$$\sigma_s^2 = \text{Cov (F.S.)} - 2 \text{Cov (H.S.)} = \frac{1}{16}H_R$$

$$\sigma_w^2 = V_P - \text{Cov (F.S.)} = \frac{1}{4}D_R + \frac{3}{16}H_R + nE_2.$$

The non-significance of the s.c.a. item suggests the absence of non-additive variation in the population *i.e.* $H_R = 0$.

$$\text{Thus } \sigma_g^2 = \frac{1}{8}D_R$$

$$\sigma_w^2 = \frac{1}{4}D_R + nE_2.$$

TABLE 7
Components of variation and heritabilities from partial diallel data

Sowing 1	Sowing 2
$\hat{\sigma}_g^2 = 6.65$	$\hat{\sigma}_g^2 = 3.72$
$\hat{\sigma}_w^2 = 49.94$	$\hat{\sigma}_w^2 = 24.27$
$\underline{VP = 63.24}$	$\underline{VP = 31.71}$
$\hat{h}^2 = 0.42$	$\hat{h}^2 = 0.47$
$\frac{1}{2}\hat{D}_R = 26.60$	$\frac{1}{2}\hat{D}_R = 14.88$
$n\hat{E}_2 = 36.64$	$n\hat{E}_2 = 16.83$

TABLE 8
Analysis of variance of N.C.M.2 data

Item	d.f.	M.S.	ν	χ^2	P	V.R.	P	Expectation of mean squares
<i>Sowing 1</i>								
1. Males (M)	6	404.13	3			2.76	0.025	$\sigma_w^2 + 10\sigma_{mf}^2 + 70\sigma_m^2$
2. Females (F)	6	413.35	3			2.82	0.025	$\sigma_w^2 + 10\sigma_{mf}^2 + 70\sigma_f^2$
3. M × F	36	146.53	9	111.31	<0.001			$\sigma_w^2 + 10\sigma_{mf}^2$
4. Blocks (B)	1	13.56	8	<1	N.S.			
5. M × B	6	11.47	8	<6	N.S.			
6. F × B	6	51.36	8	<7	N.S.			
7. M × F × B	36	42.24	8	<36	N.S.			
8. Within families	377	48.47						σ_w^2
9. Pooled within families (4, 5, 6, 7, 8)	426	47.38						
<i>Sowing 2</i>								
1. Males (M)	6	233.03	3			4.71	<0.01	$\sigma_w^2 + 10\sigma_{mf}^2 + 70\sigma_m^2$
2. Females (F)	6	103.53	3			2.09	<0.1	$\sigma_w^2 + 10\sigma_{mf}^2 + 70\sigma_f^2$
3. M × F	36	49.46	9	77.54	<0.001			$\sigma_w^2 + 10\sigma_{mf}^2$
4. Blocks (B)	1	24.92	8	1.08	N.S.			
5. M × B	6	24.41	8	<7	N.S.			
6. F × B	6	17.50	8	<6	N.S.			
7. M × F × B	36	21.74	8	<36	N.S.			
8. Within families	377	23.13						σ_w^2
9. Pooled within families	426	22.96						

Estimates of these together with the heritabilities are shown in table 7.

There is evidence from this analysis of considerable additive variation ($h^2 \approx 0.45$) in the population, but no evidence of non-additive effects. The estimates of h^2 are very consistent.

(iv) *The North Carolina Model 2 (Appendix D)*

In this method it is possible to distinguish both maternal and paternal arrays, any excess in variance of the former compared to the latter giving a measure of maternal effects. The analysis is partitioned into items for males, females, males \times females and within families, plus the block interactions (table 8).

With the exception of the females (F) item in sowing 2, the items M, F, and M \times F are significant at both sowings. This non-significant females item is however bordering on significance (V.R. = 2.09, P = 0.10-0.05) and hence for the purposes of estimation it has been treated as a real effect. The expectations of mean squares have the genetical significance as shown below:—

$$\begin{aligned}\sigma_m^2 &= \sigma_f^2 = \text{Cov (H.S.)} = \frac{1}{8}D_R \\ \sigma_{mf}^2 &= \text{Cov (F.S.)} - 2 \text{Cov (H.S.)} = \frac{1}{16}H_R \\ \sigma_w^2 &= V_P - \text{Cov (F.S.)} = \frac{1}{4}D_R + \frac{3}{16}H_R + nE_2.\end{aligned}$$

Thus from the analysis of variance (table 8) there is evidence of significant additive and non-additive genetic effects. Estimates of σ^2 and the components of variation are shown in table 9. Since the females item is not significantly greater than the males item, maternal effects are assumed to be absent.

The estimates of heritability are consistent (0.23) but the genetic component drops from 84 per cent. in sowing 1 to 60 per cent. in sowing 2, *i.e.* there is proportionally less non-additivity at the second sowing. However, the non-additive portion of the genetic variance is approximately twice as large as the additive portion, and thus in the absence of evidence of interaction we must infer the existence of considerable dominance in the population.

(v) *The half Diallel Cross (Appendix E)*

This design includes the parents selfed and thus enables non-additivity to be measured as the deviation of the F_1 from the mid parent.

The SS for non-additivity can be further sub-divided into b_1 testing the overall deviation of the F_1 from the mid parent (unidirectional effects), b_2 testing the interaction of non-additivity with arrays (a test of gene asymmetry), and b_3 testing for non-additive variation from other causes.

The analysis of variance used is that described by Hayman (1954), modified for the half diallel. The three non-additive components described above appear in this analysis as items " b_1 ", " b_2 " and " b_3 " respectively, while " a " tests the additive variation. This

TABLE 9

Components of variation and heritabilities from N.C.M.2 data

Sowing 1	Sowing 2
$\hat{\sigma}_m^2 = 3.68$ $\hat{\sigma}_f^2 = 3.81$ } 7.49 $\hat{\sigma}_{mf}^2 = 9.92$ $\hat{\sigma}_{wv}^2 = 47.38$ <hr/> $V_P = 64.79$	$\hat{\sigma}_m^2 = 2.62$ $\hat{\sigma}_f^2 = 0.77$ } 3.39 $\hat{\sigma}_{mf}^2 = 2.65$ $\hat{\sigma}_{wv}^2 = 22.96$ <hr/> $V_P = 29.00$
$\hat{h}^2 = 0.23$ $\frac{1}{2}\hat{D}_R = 14.98$ $\frac{1}{4}\hat{H}_R = 39.68$ } $\hat{V}_G = 54.66$ $n\hat{E}_2 = 10.13$	$\hat{h}^2 = 0.23$ $\frac{1}{2}\hat{D}_R = 6.78$ $\frac{1}{4}\hat{H}_R = 10.60$ } $\hat{V}_G = 17.38$ $n\hat{E}_2 = 11.62$
Genetic component 84 per cent.	Genetic component = 60 per cent.

TABLE 10

Analysis of variance of half diallel data

Item	d.f.	M.S.	V.R.	P
<i>Sowing 1</i>				
a	8	95.71	11.59	<0.001
b	36	23.37	2.83	<0.001
b ₁	1	15.25	1.85	
b ₂	8	17.58	2.13	<0.05
b ₃	27	25.39	3.07	<0.001
Blocks × a	8	1.97		
Blocks × b	36	9.65		
Blocks × b ₁	1	0.01		
Blocks × b ₂	8	8.16		
Blocks × b ₃	27	10.38		
Blocks × t	44	8.26		
<i>Sowing 2</i>				
a	8	31.14	7.43	<0.001
b	36	5.68	1.35	N.S.
b ₁	1	8.40	2.00	N.S.
b ₂	8	1.62	—	—
b ₃	27	6.49	1.54	N.S.
Blocks × a	8	3.19		
Blocks × b	36	4.41		
Blocks × b ₁	1	0.00		
Blocks × b ₂	8	6.93		
Blocks × b ₃	27	3.83		
Blocks × t	44	4.19		

analysis is presented in table 10. Each item is tested against the total block interaction (b_t).

The analysis gives evidence of additive and non-additive variation, the latter being almost exclusively b_3 , suggesting that only certain crosses show a significant deviation from the mid parent. Examination of the original data (Appendix E) points to crosses of parent 8, with parents 1 and 5. There is then either dominance specific to certain crosses, or, more likely, non-allelic interaction. The interaction of

TABLE 11

Analysis of variance of half diallel data omitting array 8

Item	d.f.	M.S.	V.R.	P
<i>Sowing 1</i>				
<i>a</i>	7	63.89	7.20	<0.001
<i>b</i>	28	10.33	1.16	N.S.
b_1	1	0.18	—	
b_2	7	6.41	—	
b_3	20	12.21	1.37	N.S.
Blocks $\times a$	7	3.48		
Blocks $\times b$	28	10.22		
Blocks $\times b_1$	1	0.00		
Blocks $\times b_2$	7	8.81		
Blocks $\times b_3$	20	11.23		
Blocks $\times t$	35	8.87		
<i>Sowing 2</i>				
<i>a</i>	7	21.54	4.67	<0.005
<i>b</i>	28	2.62		
b_1	1	4.00		
b_2	7	2.58		
b_3	20	2.56		
Blocks $\times a$	7	2.54		
Blocks $\times b$	28	5.13		
Blocks $\times b_1$	1	0.46		
Blocks $\times b_2$	7	8.91		
Blocks $\times b_3$	20	4.03		
Blocks $\times t$	35	4.61		

array 8 with arrays 1 and 5 is more pronounced in the first sowing and is probably the cause of the significant b_2 item in this sowing.

On the assumption that there is interaction present, the analysis was repeated omitting the interacting parent 8. The results are presented in table 11, each item, as before, being tested against the total block interaction.

After removing the presumed interacting array we are now left with only additive variation. Thus it is suggested that the significant non-additive item in the previous analysis was caused by non-allelic interaction.

A separate test of dominance can be carried out on these data, namely the W_r/V_r analysis of Jinks (1954). This depends on calculating the variance of each array (V_r) and the covariance of the array

on the non recurrent parent (W_r) and plotting the regression of W_r on V_r so that each parent is represented by one point on the graph. In the presence of dominance and additivity only, the points should be dispersed along a line of slope one, with the dominant parents towards the origin and the recessive parents towards a limiting parabola described by $W_r = \sqrt{V_{p2}V_r}$. In the absence of dominance the arrays would be clustered at random around the mid point of the line. Thus a test for dominance is the consistency of the arrangements of arrays over blocks and for this purpose an analysis of variance on $W_r + V_r$ was carried out, as suggested by Allard (1956). This analysis was made before omitting array 8 (table 12).

TABLE 12

Analysis of variance of $W_r + V_r$ data from complete half diallel

Item	d.f.	Sowing 1		Sowing 2	
		M.S.	V.R.	M.S.	V.R.
Arrays (r) . . .	8	355.45	2.22	27.32	1.5
Blocks (B) . . .	1	1164.36	7.26*	10.76	—
$B \times r$	8	160.28	—	18.47	—

* $P < 0.05$.

The non-significance of the array items shows that there is no consistent arrangement of points on the W_r/V_r graph and hence no significant dominance. The same is true on omitting array 8. However, it is worth noting here the danger of plotting W_r/V_r graphs without testing for consistency of the array positions over blocks. Testing for the significance of the regression line one would not detect the presence of different dominance relations in each block. Thus we can conclude from this design that there is significant additive and non-additive variation in the population, the latter very probably being non-allelic interaction.

The diallel provides us with six statistics from which to estimate the components of variation. With random mating and unequal gene frequencies there are five such components $D_1, H_1, H_{11}, F_1, E_2$ as defined by Dickinson and Jinks (1956) *i.e.*

$$D_1 = \Sigma 4uvd^2$$

$$H_1 = \Sigma (8uv - 16u^2v^2)h^2$$

$$H_{11} = \Sigma 16u^2v^2h^2$$

$$F_1 = \Sigma 16uv(u-v)dh$$

and occur in the statistics with the following coefficients.

$$\begin{aligned} \bar{V}_{BIP} &= \frac{1}{4}D_1 + \frac{1}{8}H_1 + \frac{1}{16}H_{11} - \frac{1}{8}F_1 + nE_2 \\ \bar{V}_r &= \frac{1}{8}D_1 + \frac{1}{16}H_1 - \frac{1}{16}F_1 \\ \bar{V}_{\bar{r}} &= \frac{1}{8}D_1 + \frac{1}{16}H_1 - \frac{1}{16}H_{11} - \frac{1}{16}F_1 \\ W_{\rho_2/r} &= \frac{1}{4}D_1 + \frac{1}{16}H_1 - \frac{1}{16}H_{11} - \frac{3}{32}F_1 \\ V_{\rho_2} &= \frac{1}{2}D_1 + \frac{1}{16}H_1 - \frac{1}{8}F_1 \\ \bar{V}_{\rho_2} &= \frac{1}{4}D_1 + \frac{1}{16}H_1 + \frac{1}{16}H_{11} + nE_2. \end{aligned}$$

These components assume an infinite population. For a finite population such as the present, all statistics except those within families,

TABLE 13

Statistics obtained from half diallel omitting array 8

Statistic	Sowing 1		Sowing 2	
	Block 1	Block 1	Block 1	Block 2
\bar{V}_{BIP} =	41.8540	38.4784	20.7634	26.9301
\bar{V}_r =	18.9464	7.7275	4.7346	4.6606
$\bar{V}_{\bar{r}}$ =	4.3678	3.1661	1.5737	0.7557
$W_{\rho_2/r}$ =	5.2173	5.1557	3.4625	1.2769
V_{ρ_2} =	9.1955	16.4229	10.4114	9.0641
\bar{V}_{ρ_2} =	30.1145	37.5250	8.8125	28.9226

contain a sampling component equivalent to $1/n$ th of the appropriate "within family" variance, where n is the number of individuals summed over to calculate that statistic.

In the present analysis, as there was no reason to assume the existence of dominance, only the components D_1 and E_2 were fitted, and then only after omitting array 8, as interaction invalidates the operation. The values for the 6 statistics are shown in table 13 for each block separately.

Least squares estimates of D_1 and E_2 were obtained from the statistics averaged over two blocks for each sowing. The relevant C matrix obtained for solving D_1 and E_2 and the estimates of these components are shown in table 14.

An approximate test of goodness of fit of the model fitting only the estimates of D_1 and E_2 shown above, can be obtained in a manner similar to that described by Mather and Vines (1952). The process involves carrying out an analysis of variance on the statistics at each sowing. There is no expected mean for the statistics as each is composed of six parameters, none having the same coefficient in all statistics. Thus the SS for sitting six statistics has 6 d.f. The other components are blocks—1 d.f., blocks \times statistics—5 d.f. Of the 6 d.f. concerned with statistics, 2 d.f. are taken up by fitting D_1 and E_2 .

This SS is calculated as the SS for observed minus expected statistics and subtracting this from the SS for fitting statistics. These variances are shown in table 15.

TABLE 14
C matrix and variance components for half diallel

D_1	E_2	Sowing 1	Sowing 2
2.983223 -0.187390	0.030993	$\begin{pmatrix} 29.692750 \\ 397.070917 \end{pmatrix}$	$\begin{pmatrix} 17.614120 \\ 228.400110 \end{pmatrix}$
Sowing 1	$\hat{D}_1 = 14.1730$ $\hat{E}_2 = 6.7423$	$\hat{h}^2 = \frac{\frac{1}{2}D_1}{\frac{1}{2}D_1 + 5E_2} = 0.17$	
Sowing 2	$\hat{D}_1 = 9.7470$ $\hat{E}_2 = 3.7781$	$\hat{h}^2 = 0.21$	

TABLE 15
Analysis of variance for fitting D_1 and E_2 only to statistics

Item	n	Sowing 1		Sowing 2	
		M.S.	V.R.	M.S.	V.R.
Fitting 6 statistics (S)	6	1046.7130	42.76***	349.5050	9.44*
Fitting D_1 and E_2	2	1025.6052	41.89***	342.5320	9.25*
Remainder after fitting D_1 and E_2	4	21.1088		6.9730	
Blocks (B)	1	0.1240		39.7922	
B x S	5	24.4810		37.0128	

* P = 0.05-0.01. *** P < 0.001.

The residual SS after fitting D_1 and E_2 is insignificant and hence the variation in the population, after omitting array 8, can be explained assuming only that D_1 and E_2 are present with the values shown in table 14.

5. DISCUSSION AND CONCLUSIONS

The experimental techniques investigated can be compared using various criteria. It is proposed first to discuss their relative merits under each criterion separately—specific evaluation, and then to attempt to draw overall conclusions—general evaluation.

I. SPECIFIC EVALUATION

(i) *Size of population sampled*

It is obvious that the larger the sample of parents used in any technique, the closer any estimate of a parameter will become to the population value, other factors being equal. The actual number of plants used as parents in any design are shown in table 16.

It can be seen that B.I.P.s use the most parents, in fact ten times as many as does the diallel.

TABLE 16

Number of parents used and number of families raised in each design

	B.I.P.s	N.C.M.1	Partial diallel	N.C.M.2	Half diallel
Sample size . . .	86*	48	14	14	9
Families raised . .	43**	44	49	49	45

* Originally 90 } but 2 crosses failed.
 ** Originally 45 }

For many studies, however, the relevance of this criterion may be doubtful. For instance a breeder may only be interested in the genetic properties of a small selected sample of lines and not with a whole population of possible lines. In such cases the small sample techniques may be able to include most, if not all, the material under investigation.

However, as the populations become larger and more variable, either large samples or repeated samples are necessary.

(ii) *Suitability for different breeding material*

Owing to the breeding behaviour some experimental material permits only a limited number of families to be raised from each female. Most animals fall into this category and many plants do not produce sufficient flowers, for a single plant to be used as a recurrent female parent. In such situations the B.I.P. and N.C.M.1. techniques are eminently suitable in that only one family per female is required.

In many domesticated animals the sex ratio is kept extremely unequal for economic reasons and hence raising B.I.P.s is not practical and the N.C.M.1. is superior having indeed been designed for just such situations.

If it is possible to raise more than one family per female and the necessary corrections for parity are made, then the other three techniques may also be used. If the experimental population consists of inbred lines, strains, or distinct sub-populations the partial diallel, N.C.M.2 and the half diallel are all possible. When the material is a

random mating population the half diallel cannot be used unless the population consists of monoecious plants, because of the problem of selfing. Using *Papaver dubium* all programmes were equally easy to carry out.

(iii) *Labour of computation*

The amount of computation involved in estimating the components of variation increases with the restraint the programme imposes on the arrangement of matings, but all are basically simple analyses of variance. However, in the partial diallel there is a complex 14×14 matrix inversion followed by the calculation of a series of sums of products which on a desk calculator at least amounts to a computationally arduous procedure.

(iv) *Number of statistics obtained and possible number of components estimated*

Of the five designs used B.I.P.s yield the fewest statistics—two—and hence allow only two parameters to be estimated. This only permits an approximate breakdown of the phenotypic variance into a genetic and environmental component. However, one can partition the genetic variance by using the covariance of B.I.P. family means on the parental values. Very often, however, it is impossible to grow parents and offspring at the same time, as in this experiment, and hence the covariance may be upset by the effects of different seasons. Also if the parents or the parents selfed are grown at the same time as the progeny it means that the size of the experiment is also increased, or alternatively the number of parents used must be decreased to maintain equality with other programmes. For example, in this investigation the number of families was arbitrarily fixed at 45, and if the parents selfed and B.I.P. families are to be included, then only 30 parent plants could be used, and the advantage of a large parental sample would be reduced.

The North Carolina models 1 and 2 and the partial diallel all yield 3 statistics by allowing the between families statistics to be subdivided. This allows the genetic and environmental components to be separated and the genetic component to be broken down into additive and non-additive components. Furthermore, the N.C.M.2 allows one to discriminate between maternal and paternal arrays and so obtain a measure of maternal effect.

The half diallel, however, also allows the detection of the direction of dominance, the estimation of the relative frequency of dominant increasing and decreasing genes, the grouping of parents in terms of the number of dominant genes they carry by means of the W_r/V_r graph and a test of the adequacy of an additive dominance model. Altogether six statistics can be obtained from this design to give least squares estimates of the five components D_1 , H_1 , H_{11} , F_1 and E_2 as defined earlier. Also it is the only design to give Σd^2 for V_A and hence

a dominance ratio that is not biased by unequal gene frequencies. Thus the diallel is superior on the grounds of absolute amount of information provided.

(v) *Tests of assumptions*

The basic assumptions inherent in the interpretations of the data from these designs are listed in section 3.

Of the designs used in this experiment only N.C.M.2 provides a test for maternal effects: it suggests they are absent. However, in the diallel this test was deliberately excluded as a full diallel with reciprocals would have halved the number of independent F_1 families that could be raised. Similarly in the B.I.P.s and N.C.M.1, the use of the covariance of B.I.P. families on to male and female parents would necessitate a much larger experiment. In the partial diallel the authors have not suggested a sampling procedure to take in reciprocals, nor have they produced an analysis which could measure maternal effects in the design as it exists at present.

Dickinson and Jinks (1955) have discussed tests for linkage, correlated gene distributions, and non-allelic interaction for the heterozygous diallel. No other design includes a test of the presence of these effects nor do they detect the presence of multiple alleles. In the present case the diallel is also unable to detect disturbances due to multiple alleles.

(vi) *Observed results*

The estimates of the components of variation from all the designs are presented in table 17 together with the means and variances of the flowering times of the parents used. In this table D_R , H_R and E_2 have been converted to V_A , V_D and V_E using the relationships set out in table 1.

The total phenotypic variance (V_P) is consistent over designs at each sowing with the exception of that from the half diallel, which is lower than the rest. This lower phenotypic variance in the half diallel is also shown by the sample of plants from which it was derived (bottom line of table 17). Furthermore, inspection of the mean flowering times of these parents shows them to consist of later flowering plants, the effect of which will be discussed later. It would appear, therefore, that the small sample of 9 plants chosen for the half diallel is unrepresentative of the population as a whole.

In every design the total phenotypic variance can be partitioned into genetic (V_G) and environmental (V_E) components. It can be seen that the V_E items fall into two groups on the basis of their magnitudes. In the B.I.P.s, the partial diallel and half diallel they are large, and in the two North Carolina designs they are small, at both sowings. Since, however, all the designs consisted of approximately the same number of plants individually randomised over the same range of

environments, the V_E items should be the same within the limits of sampling error. How then could these differences come about?

The partitioning of V_G into additive (V_A) and non-additive components (V_D) throws light on the source of this discrepancy. In all the cases in which the V_E item is high, there is no evidence of V_D ,

TABLE 17

Summary of individual component analyses of the various designs together with the means and variances of the parents. (Sowing 1 upper line, Sowing 2 lower line)

	B.I.P.s	N.C.M.1	Partial diallel	N.C.M.2	Half diallel	
V_P	60.38 27.11	50.76 24.25	63.24 31.71	64.79 29.00	40.80 23.76	
V_G	21.50 8.84	41.56 16.72	26.60 14.88	54.66 17.38	7.09 4.87	
V_A	21.50 8.84	22.64 5.24	26.60 14.88	14.98 6.78	7.09 4.87	
V_D	— —	18.92 11.48	0 0	39.68 10.60	0 0	
V_E	38.88 18.27	9.20 7.53	36.64 16.83	10.13 11.62	33.71 18.89	
V_G as percentage of V_P .	36 33	82 69	42 47	84 60	17 21	
h^2	0.36 0.33	0.45 0.22	0.42 0.47	0.23 0.23	0.17 0.21	
Within family variance .	49.63 22.69	34.71 18.76	49.94 24.27	47.38 22.96	40.07 23.09	
Parents {	Number of parents used	86	48	14	14	9
	Mean flowering time	42.86	43.60	42.79	40.29	45.67
	Variance	29.46	33.14	34.18	23.45	14.50

while V_D is present in the cases of low V_E . This suggests either that the designs with high V_E items have not extracted all the genetic variance from V_P , so leaving some confounded with V_E , or that the other designs have ascribed to the non-additive components, variation which is not in fact due to dominance. It is also possible that both factors are acting together.

Let us now consider each design, with these possible sources of error in mind. It will be remembered that the B.I.P.s yielded only two statistics, \bar{V}_{BIP} and $V_{\bar{BIP}}$, from which to estimate the components of variation, and hence we could only estimate two parameters, V_G and

V_E . To do this, however, we had to assume the absence of non-additive effects. In the presence of non-additivity, then, our estimate of $\frac{1}{4}D_R$ would contain $\frac{1}{16}H_R$, and nE_2 would contain $\frac{1}{8}H_R$, *i.e.* both $\frac{1}{2}D$ and $nE_2(V_A$ and $V_E)$ would be overestimated by the same amount, thus:—

$$\begin{aligned}V_A &= \frac{1}{2}D_R + \frac{1}{8}H_R \\V_E &= nE_2 + \frac{1}{8}H_R.\end{aligned}$$

However, if we neglect the V_A from the diallel there is no suggestion from the other designs that V_A from B.I.P.s is too high. Further evidence on this point can be obtained by using the supplementary information yielded by the data from the parents selfed which, though not part of the present trial, were grown for a selection experiment. The covariance of B.I.P. means on the mid-parental (selfed) value

TABLE 18

Revised components of variation from B.I.P.s

Sowing 1	Sowing 2
$\overline{V_{BIP}} = 10.75 = \frac{1}{4}D_R + \frac{1}{16}H_R$	= 4.40
$\overline{W_{BIP/p_2}} = 8.74 = \frac{1}{4}D_R$	= 3.33
$\overline{V_{BIP}} = 49.61 = \frac{1}{4}D_R + \frac{3}{16}H_R + nE_2$	= 22.91
$V_A = 17.48 = \frac{1}{2}D_R$	= 6.66
$V_D = 8.04 = \frac{1}{4}H_R$	= 4.28
$V_E = 34.84 = nE_2$	= 16.37

provides a direct estimate of $\frac{1}{4}D_R$. This together with the other two statistics obtained from the B.I.P.s is shown in table 18.

As the V_D item is low and the V_E item still high when compared with these components estimated in the two North Carolina designs, we must assume that our second hypothesis is causing the discrepancy, *i.e.* the presence of variation other than dominance inflating V_D in these latter designs.

From the half diallel statistics it was possible to carry out a least squares estimation of the components of variation. This design, as mentioned before, has the added advantage of estimating V_A as Σd^2 . The Hayman analysis of variance on the complete data from the half diallel showed the presence of both additive and non-additive variation, but it was shown that this non-additivity was probably due to complementary gene interaction. Also after removing the interacting arrays a good fit could be obtained with the data using only D_1 and E_2 , thus any non-additivity in the phenotypic variance was not of a type to be ascribed to dominance, and hence was forced into E_2 . It is suggested then that much of the non-additive variation of the other designs, is also likely to be of an epistatic nature. It must be

borne in mind, however, that as was pointed out earlier, the parents used in the half diallel were a late flowering sample and showed less phenotypic variance than those in other designs. Since the genuine environmental variation is probably constant over all designs this will have the effect of reducing the proportion of the variation ascribable to the genetic components.

Further evidence that the North Carolina designs are ascribing variation other than dominance to V_D can be obtained by comparing

TABLE 19

The expected mean squares from the half diallel and their genetic interpretation

$$\begin{aligned}
 a &= \sigma_w^2 + 10\sigma_s^2 + 10p\sigma_g^2 \\
 b &= \sigma_w^2 + 10\sigma_s^2 \\
 \text{VBIP} &= \sigma_w^2
 \end{aligned}$$

where $p = n + 2^*$
and $n =$ the number of parents

$$\begin{aligned}
 \sigma_g^2 &= \frac{1}{2}V_A \\
 \sigma_s^2 &= \frac{1}{4}V_D \\
 \sigma_w^2 &= \frac{1}{2}V_A + \frac{1}{2}V_D + V_E
 \end{aligned}$$

* Wearden—personal communication.

the estimates of the components of variation yielded by the half diallel data using both the least squares method described previously and the North Carolina approach. The latter method depends on estimating the components from the Hayman analysis of variance, the expectations of the a and b items being as shown in table 19.

As the a and b mean squares were originally calculated from the means of sets of five measurements, it is necessary to multiply them by five before solving. This was done with both the complete data, and the data after removing parent 8. The components of variation obtained from both sets of data are shown in table 20 together with values obtained by least squares estimation. For comparison the components obtained from the N.C.M.2 are also shown.

The V_A item is of approximately the same order of magnitude in all the analyses shown in table 20. However, the V_D and V_E items show marked differences. The North Carolina approach to the complete data from the diallel yields values of V_D and V_E of magnitudes similar to N.C.M.2 while after omitting the interacting parent, the same approach yields values of V_D and V_E similar to those from the conventional analysis. As the earlier diallel analysis had suggested the presence of non-allelic interaction in the complete data, it must surely be this interaction which is inflating V_D relative to V_E . If this is true of the diallel data, then it is likely to be true of the data from the North Carolina designs also.

Any failure of the assumptions on which the genetic model is based will upset the estimation of components. It is not easy to visualise how the V_E item could be underestimated, and thus it must be assumed that the estimates of V_E yielded by the two North Carolina designs give a closer approximation to the true value.

TABLE 20

The components of variation obtained from the Hayman analysis of variance of the half diallel data, before and after removing array 8, using expectations of mean squares. The values of the components from the N.C.M.2, and, by least squares, from the half diallel are shown for comparison. (Sowing 1 upper line, Sowing 2 lower line)

	Half diallel			North Carolina model 2
	Conventional analysis	N.C. approach (omitting parent 8)	N.C. approach (complete data)	
V_A	7.09 4.87	4.87 1.54	6.58 2.31	14.98 6.78
V_D	0 0	4.73 0	30.72 2.12	39.68 10.60
V_E	33.71 18.89	31.73 22.32	13.74 20.34	10.13 11.62

II. GENERAL EVALUATION

The raising of B.I.P.s would appear to be a technique of wide application under most breeding systems and permits the testing of a large part of the population. However, it provides little information about the variance components of the population beyond allowing an approximate partition of the total variance into genetic and environmental components.

The N.C.M.1 allows one to test a large number of plants from the population, and is especially useful when the sex ratio is unequal. Both this and the N.C.M.2 appear to extract the additive variation adequately, but the non-additive component appears to be greatly affected by epistasis, so giving an inflated estimate of dominance and a correspondingly lower estimate of V_E . No unambiguous tests of additivity or dominance are suggested by the authors of these designs. The design has been subsequently modified to estimate additive-additive interaction (Matzinger and Cockerham, 1963) but only in restricted circumstances not applicable here. However, both designs provide simple methods of estimating V_A and V_D and allow tests of significance to be applied to them.

The partial diallel appears to yield no more information than the two North Carolina designs, while enforcing a crossing programme that is complicated to devise, and lengthy and awkward to analyse.

These disadvantages appear to outweigh its sole advantage namely the larger sample of parents it employs compared with a complete diallel.

The half diallel has the advantage of using only a small number of parents resulting in the possibility that, as in the present case, an unrepresentative sample is taken. However, it can be applied to a wide range of breeding systems and within the restriction of its small sampling power, provides a great deal of information about the components of variation of those individuals selected. It allows one to test for the presence of non-allelic interaction, and estimates additivity and dominance unambiguously.

Thus where it is practical to carry out the half diallel cross it is to be preferred because of the large amount of precise information it provides about the components of variation. If this is not practical then the two North Carolina techniques are most useful.

6. SUMMARY

Estimates of the components of variation in flowering time in a population of *Papaver dubium* have been obtained from five breeding programmes, with approximately the same number of families (45) raised in every design to facilitate comparisons between them. The designs used were B.I.P.s, the North Carolina models 1 and 2, the partial diallel and the half diallel.

Several criteria were used to compare the methods the most important being the estimates they yielded of the components of variation. The B.I.P.s had the advantage of using the largest sample of parents from the population but had the disadvantage of only yielding two statistics from which to estimate the components. This drawback could be overcome either by using the covariance on the parental means in the previous year, which would result in complications due to different seasons, or by using the covariance on the parents or parents selfed in the same season. This latter modification of the design would result in using only a third of the number of parents.

The two North Carolina designs were well suited to certain breeding systems, but had the disadvantage of providing no test of non-allelic interaction. There was evidence that this type of interaction was present and had upset the estimates of the components from these designs.

The partial diallel appears to have no advantage over the other designs, and the analysis associated with it was computationally arduous.

The half diallel gave the most information about the small number of plants used in it. It demonstrated additive and non-additive variation, but showed the non-additive variation to be mainly due to non-allelic interaction. After removing this interaction, good agreement with the observed statistics was obtained by fitting D_I and E_2 only. The estimates of these components were obtained by least squares, and hence are likely to be the most reliable estimates of all

the designs. The small sample of parents used, however, appeared to be unrepresentative of the population as a whole.

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8. APPENDICES

APPENDIX A

Mean flowering times of B.I.P. families. (Block 1 upper line, Block 2 lower line)

	Sowing			Sowing			Sowing	
	1	2		1	2		1	2
1	28.6 27.8	30.4 30.2	16	26.8 17.4	34.8 37.0	31	35.4 24.6	27.8 31.0
2	32.3 29.8	33.0 30.2	17	29.6 27.0	41.0 35.0	32	35.5 32.6	33.6 31.6
3	31.8 31.6	33.2 29.2	18	29.8 33.4	27.0 33.0	33	16.8 23.8	28.0 28.0
4	28.4 30.0	31.0 32.5	19	34.0 27.8	29.0 26.2	34	23.6 25.2	35.0 33.6
5	31.2 27.2	33.5 30.0	20	24.8 27.6	29.2 28.6	35	31.8 34.3	33.2 35.6
6	22.6 28.0	31.4 27.8	21	30.4 26.0	36.2 33.8	36	10.2 16.6	25.8 23.0
7	29.6 25.0	31.8 31.4	22	27.6 36.0	34.8 31.6	37	28.6 28.6	30.0 35.2
8	26.2 18.4	28.2 30.8	23	32.2 27.0	29.8 30.4	38	23.0 27.6	28.0 28.2
9	28.0 30.4	28.4 32.0	24	27.4 23.0	30.8 30.0	39	29.8 30.4	35.0 31.0
10	30.4 27.2	30.6 30.4	25	28.6 28.5	32.4 36.2	40	29.5 29.6	33.5 35.8
11	34.6 30.4	34.6 31.5	26	28.0 34.0	26.8 29.8	41	27.0 28.4	31.2 31.6
12	24.4 24.4	31.2 31.6	27	31.0 28.0	30.4 28.0	42	34.2 33.8	32.7 33.6
13	30.8 31.2	35.0 32.2	28	22.4 20.0	27.4 28.4	43	31.6 26.4	30.8 27.8
14	28.4 28.0	32.4 31.5	29	26.0 32.6	32.4 31.8			
15	27.8 31.4	34.6 32.4	30	25.6 29.2	32.0 32.6			

APPENDIX B

Means flowering times of North Carolina model 1 families. (Block 1 upper line, Block 2 lower line)

♂												
	1			2			3			4		
	Sowing			Sowing			Sowing			Sowing		
	1	2		1	2		1	2		1	2	
♀	1	21.6 23.2	31.2 28.6	12	33.0 35.6	35.6 35.0	23	18.4 26.4	21.4 24.2	34	33.6 33.8	32.4 33.5
	2	30.8 19.0	34.4 30.8	13	29.8 28.0	32.0 33.0	24	19.8 23.8	25.4 30.0	35	36.0 31.0	29.6 32.2
	3	27.8 31.0	29.6 34.6	14	24.8 27.0	30.2 30.2	25	29.0 32.7	29.7 34.4	36	32.0 31.0	39.3 39.0
	4	28.8 24.4	28.6 34.2	15	33.4 31.4	32.0 31.8	26	26.8 28.4	32.4 28.8	37	31.0 31.4	36.2 34.8
	5	27.8 30.4	36.0 32.3	16	29.8 30.4	34.0 30.8	27	24.8 26.8	31.4 31.6	38	28.4 29.2	33.4 35.8
	6	23.6 25.4	30.6 25.4	17	26.4 29.6	32.0 32.2	28	28.8 29.6	29.8 32.2	39	33.7 28.6	33.0 25.2
	7	30.2 31.8	33.2 33.2	18	31.0 31.0	32.0 30.8	29	15.2 18.6	28.2 24.0	40	23.2 25.2	28.4 33.4
	8	28.8 21.2	30.0 30.8	19	33.0 29.6	32.2 32.2	30	29.0 32.6	33.0 35.2	41	29.6 34.0	31.4 30.3
	9	32.7 31.8	32.8 25.6	20	33.5 33.4	30.4 29.6	31	33.4 31.2	33.8 32.4	42	27.0 30.0	31.8 27.6
	10	17.6 21.0	31.0 25.4	21	30.4 30.0	33.0 32.0	32	28.3 25.4	27.6 30.6	43	34.6 27.6	35.2 32.0
	11	19.0 20.2	25.8 25.4	22	29.2 26.0	29.0 33.6	33	23.2 21.0	29.8 27.4	44	32.5 31.6	35.0 30.8

APPENDIX D

Mean flowering times of North Carolina model 2 families. (Block 1 upper line, Block 2 lower line)

♀ \ ♂	1		2		3		4		5		6		7	
	Sowing		Sowing		Sowing		Sowing		Sowing		Sowing		Sowing	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2
8	25.6	31.6	29.4	30.4	29.8	27.2	21.0	31.2	27.4	26.6	33.0	31.8	25.6	28.4
	29.6	33.4	27.0	31.2	25.6	30.2	30.2	23.0	29.0	33.0	34.8	31.6	24.8	28.0
9	25.6	34.3	28.6	28.4	23.8	31.6	23.0	31.8	31.0	32.0	30.3	32.0	21.0	26.0
	23.0	31.8	29.0	29.6	33.0	35.6	22.6	27.0	30.8	31.2	31.0	32.4	22.8	25.2
10	34.2	31.6	31.6	30.4	22.6	30.8	29.8	29.2	25.4	32.2	21.8	26.8	12.0	24.2
	26.4	33.2	26.0	34.0	26.2	31.0	25.2	29.0	28.2	34.0	17.0	25.8	10.8	19.6
11	29.6	34.2	27.2	31.2	19.6	29.4	29.0	29.0	27.0	31.6	25.4	27.0	23.0	27.0
	26.8	31.8	28.2	32.0	22.2	32.6	28.0	33.2	26.8	34.4	30.0	28.0	16.0	23.8
12	27.8	30.6	27.2	29.2	30.6	34.8	17.8	31.0	31.0	32.0	28.6	32.8	27.0	29.6
	32.0	33.0	24.4	28.2	29.4	33.2	19.5	26.0	30.8	30.6	29.2	28.8	31.3	30.4
13	26.0	36.8	28.6	27.2	26.2	30.4	19.6	29.0	27.2	32.8	26.8	35.0	25.8	26.8
	31.8	32.6	28.8	31.2	22.0	27.0	18.4	29.4	30.0	30.2	25.4	31.6	22.6	29.2
14	23.2	31.6	17.2	23.8	23.8	30.4	27.2	27.8	18.8	25.2	32.0	30.2	14.2	29.0
	20.8	29.6	15.6	23.4	21.4	25.6	19.6	27.4	17.6	23.4	23.2	28.6	18.8	26.8

