ANALYSIS OF RECIPROCAL DIFFERENCES IN DIALLEL CROSSES

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1. PRELIMINARY OBSERVATIONS

METHODS of analysing genetic diallel tables by Jinks (1954) and Hayman (1954a), based on the biometrical analysis of quantitative variation of Mather (1949), and their further extension, have been mainly developed for the analysis of the summed reciprocals, but there are also ways of examining the reciprocal differences. If a pronounced difference is observed between the reciprocal crosses of two parents, examination of the W/V graph (Jinks, 1954) of the reciprocal means, and substitution of each reciprocal in turn in both reciprocal cells, will give information on the gene/cytoplasm inter- action. In other cases where reciprocal differences are more general, information may be obtained by comparing Hayman's (1954b) *c* and *d* items, or each of these with the error variation, the biometrical significance of which, together with that of a factorial analysis (Jinks and Broadhurst, 1963) and of Henderson's (1952) analysis, is con- sidered by Wearden (1964). Cases arise where these methods are insufficient for the recognition of some patterns of reciprocal differences.

Unlike the analysis of summed reciprocals where the model is supplied by knowledge of the segregational and recombinational properties of nuclear genes there is no one universally recognised mechanism determining reciprocal differences. The object of an analysis would be, in part, to obtain information about such mechan- isms. There are, however, two rather more obvious forms of inherit- ance which will be considered, here termed alpha and beta inheritance, which can be sub-divided into multifactor inheritance and associated, or group, inheritance.

Table 1 (*a*) is a diallel table with $n = 4$ parents where, in the absence of reciprocal differences, $y_{12} = y_{21}$, etc., or more generally, $y_{rs} = y_{sr}$ for reciprocal crosses between the rth female parent and the sth male parent. Table 1 (*b*) symbolises a full table of reciprocal differences, $y_{12} - y_{21} = g_{12}$, etc., or $y_{rs} - y_{sr} = g_{rs}$. $G_1' = y_1. - y._1$, etc., are the differences between reciprocal array totals and $\Sigma G = 0$.

Other symbols are used:

P_r', the rth parental value measured from the mean of all n parents
V_r, variance of the reciprocal means of the rth parental arrays.
V_{r2} variance of the female array of the rth parent.

$V_{r\male}$ variance of the male array of the rth parent.

W_r covariance of the reciprocal means of the rth parental array onto all parents.

$W_{r\female}$ covariance of the female array of the rth parent onto all parents.

$W_{r\male}$ covariance of the male array of the rth parent onto all parents.

$w_r = W_{r\female} - W_{r\male}$, or covariance of reciprocal differences of the rth parent male and female arrays onto all parents.

$w_r' = w_r - \bar{w}$.

TABLE 1 (a)

Diallel table

	♂ parents				♀ array totals
	1	2	3	4	$y_{1.}$
♀ parents					
1 . .	y_{11}	y_{12}	y_{13}	y_{14}	$y_{1.}$
2 . .	y_{21}	y_{22}	y_{23}	y_{24}	$y_{2.}$
3 . .	y_{31}	y_{32}	y_{33}	y_{34}	$y_{3.}$
4 . .	y_{41}	y_{42}	y_{43}	y_{44}	$y_{4.}$
♂ array totals .	$y_{.1}$	$y_{.2}$	$y_{.3}$	$y_{.4}$	$y_{..}$

TABLE 1 (b)

Diallel table of reciprocal differences

	♂ parents				Differences between reciprocal array totals
	1	2	3	4	♀ array—♂ array
♀ parents					
1 . .	...	g_{12}	g_{13}	g_{14}	G_1
2 . .	g_{21}	...	g_{23}	g_{24}	G_2
3 . .	g_{31}	g_{32}	...	g_{34}	G_3
4 . .	g_{41}	g_{42}	g_{43}	...	G_4

Some symbols differ from those used by some writers because the same symbol has hitherto been used for more than one item, and some items have been symbolised in more than one way by different writers.

2. MULTIFACTOR BETA INHERITANCE

Multifactor beta inheritance occurs when each of any number of genes has different amounts of dominance in the reciprocal crosses concerned.

(i) Formulæ

Using the notation of Mather (1949) and Jinks (1954) and considering two alleles, $A-a$, at one locus, which occur with frequencies

u, v, $(u+v = 1)$ respectively among the parents, their contributions to the parents and reciprocal crosses in terms of d, the additive deviation, and h, the average dominance deviation of the two reciprocals from the mid-parent value, are given in table 2. An additional

TABLE 2

Beta inheritance model

Parent . . .	AA	aa
Frequency . .	u	v
Mean . . .	d	$-d$
	AA	Aa
AA u d . . .	u^2	uv
	d	$h+\beta$
	Aa	aa
aa v $-d$ . . .	uv	v^2
	$h-\beta$	$-d$

quantity, β, is also entered. This is the deviation of each reciprocal cross from the average dominance deviation due to a change in dominance between the reciprocal crosses. β is positive when the reciprocal difference is in a maternal direction, negative when it is in a paternal direction and zero for equilinear inheritance. There

TABLE 3

Variances and covariances given by the single gene beta
inheritance model

Variance of female array means . .	$uv[d+h(v-u)+\beta]^2$
Variance of male array means . .	$uv[d+h(v-u)-\beta]^2$
Mean variance of female arrays . .	$uv[d+h(v-u)-\beta]^2+4u^2v^2h^2$
Mean variance of male arrays . .	$uv[d+h(v-u)+\beta]^2+4u^2v^2h^2$
Variance of female AA array . .	$uv(d-h-\beta)^2$
Variance of female aa array . .	$uv(d+h-\beta)^2$
Variance of male AA array . .	$uv(d-h+\beta)^2$
Variance of male aa array . .	$uv(d+h+\beta)^2$
Covariance of female AA array . .	$2uvd(d-h-\beta)$
Covariance of female aa array . .	$2uvd(d+h-\beta)$
Covariance of male AA array . .	$2uvd(d-h+\beta)$
Covariance of male aa array . .	$2uvd(d+h+\beta)$
Male/female AA array covariance .	$uv[(d-h)^2-\beta^2]$
Male/female aa array covariance .	$uv[(d+h)^2-\beta^2]$
Variance of reciprocal differences .	$2uv\beta^2$

is no answer to the question as to whether beta inheritance influences the reciprocal crosses to the same extent on each side of the mean dominance value, only whether it is in a maternal or paternal direction.

Variances and covariances formulated in terms of u, v, d, h and β are given in table 3. Certain criteria, cited for example by Hayman (1954a, section 4) need to be met for summation over all genes to give useful estimates of the biometrical components, D, H, etc. Where

additional factors determining reciprocal differences are involved it is doubtful whether these are met, but the consequences of the model are briefly shown by writing

$$B_1 = 4\Sigma uv\beta^2$$
$$B_2 = 4\Sigma uvd\beta$$
$$B_3 = 8\Sigma uv(u-v)h\beta$$

and putting $\beta = d$ for all genes, when

$$\female\ V_{1L1} = \tfrac{1}{4}H_1$$
$$\male\ V_{1L1} = D + \tfrac{1}{4}H_1 - \tfrac{1}{2}F$$
$$\female\ V_{0L1} = D + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2 - \tfrac{1}{2}F$$
$$\male\ V_{0L1} = \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2$$

which reduce to $\tfrac{1}{4}H_1$, $D + \tfrac{1}{4}H_1$, D and 0, respectively when $u = v$, omitting the error term. $\beta = -d$ gives the same expressions with the male and female signs reversed.

(ii) Covariance graph

In the single gene model the AA—aa array covariance difference is $-4uvdh$ for both male and female arrays so that if female array covariances, $W\female$, are plotted against male array covariances, $W\male$, fig. 1, the points should lie on a line of unit slope. The $W\female - W\male$ difference is $-4uvd\beta$ so that the line passes through the origin only when β (or d) is zero. The line is depressed when β has the same sign as d (maternal inheritance) and raised when they have different signs (paternal inheritance). It will be shown in section 3 (iii) that no matter what the distribution, directions or magnitudes of the individual β values of the different genes the points will lie on a straight line of unit slope. Consequently if reciprocal differences occur the covariance graph will show immediately any deviations from multifactor beta inheritance by the spread of the points off the line. Conversely, if multifactor beta inheritance does occur throughout the data the graph will not show which parents have greater or less amounts of beta inheritance, or the direction in which it operates for each parent, although the direction of displacement of all the points will give the average direction of inheritance, paternal (raised) or maternal (depressed). If these are equal in amount the points will lie on a line which passes through the origin simulating no reciprocal differences.

In the single gene model, a positive value of β obviously gives reciprocal differences in a female direction for all parents. The same result occurs with many genes and the differences between reciprocal array totals are then positively correlated with the parental values. Similarly negative β values give a negative correlation, and positive and negative values together a reduced or no correlation. Some information which can be extracted about the behaviour of individual parents is more conveniently dealt with in the next section which describes multifactor alpha inheritance.

Specific crosses, or entire arrays, of parents deviating from the line can be removed to determine the source of the deviations from multifactor beta inheritance. The deviations of parents from the line may indicate associated beta inheritance described in a later section. Insofar as the covariances of the summed reciprocals supply
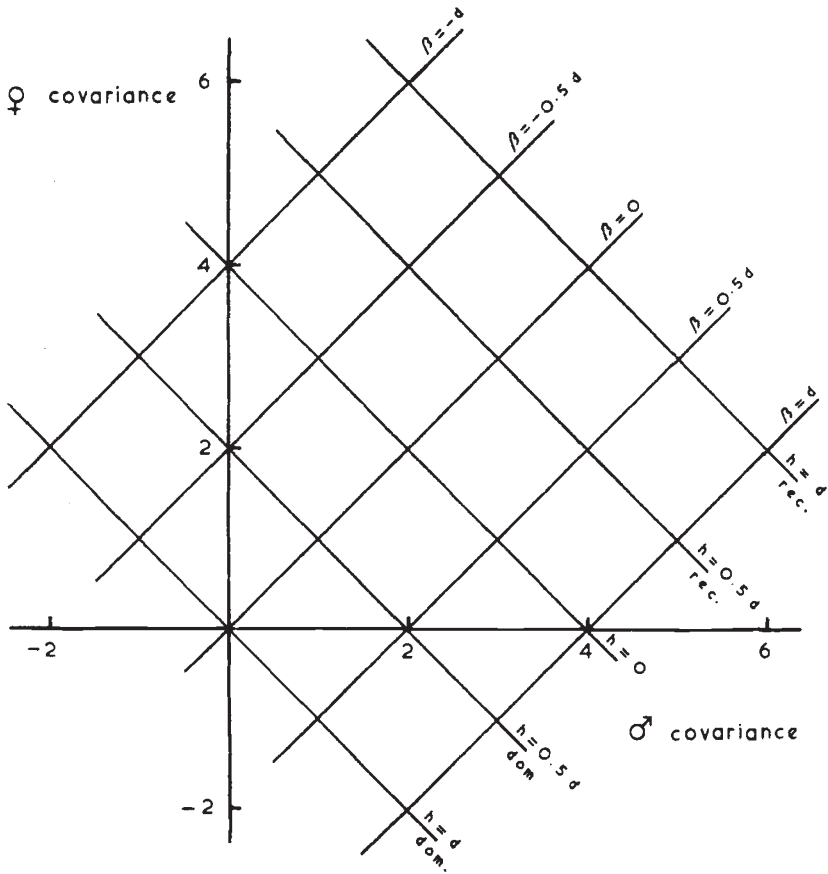

FIG. 1.—Female covariance/male covariance graph for beta inheritance, for single gene model, for unit value of d/uv.

information on the average dominance relations of the individual parents these relations are displayed on the same covariance graph and the difference between the male and female covariance is a measure of the average change in dominance due to multifactor beta inheritance.

(iii) Variance graphs and covariance/variance graphs

The analysis of reciprocal differences yields a multiplicity of formulæ and some observations on the graphical relations of only a few will be given. None of the graphs gives a clear picture of the distribution, direction and magnitude of the β values among the

parents because the parents either fall on a straight line or the deviations from the line are dependent in part on the distribution of dominant and recessive alleles among the parents. The covariance/variance graph of the reciprocal means will be in no way different from that given by a diallel cross without reciprocal differences where beta inheritance is symmetrical as in the model. If it is asymmetric this merely shifts dominance in the appropriate direction without distorting the graph.
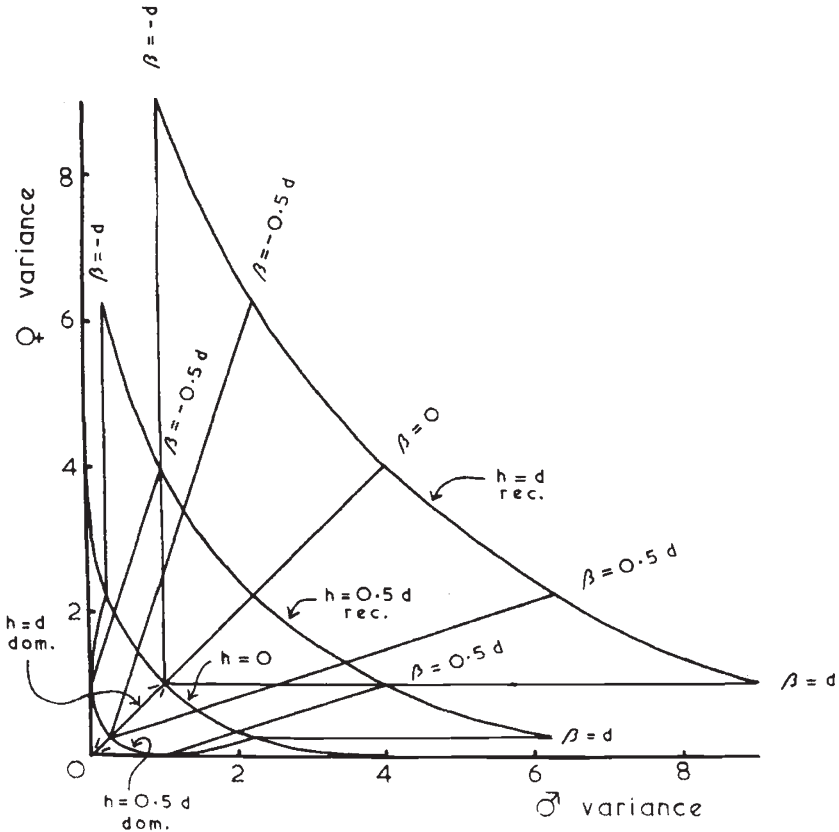

FIG. 2.—Female variance/male variance graph for beta inheritance, for single gene model, for unit value of d/uv.

For the single gene model the female array variances plotted against the male array variances give a slope of $(d-\beta)/(d+\beta)$ which is therefore greater than one for beta inheritance in a male direction and less than one when it is in a female direction. In the general case with many genes, parents carrying most recessive alleles will be displaced from a line of unit slope through the origin more than those with more dominant alleles, the parents tending to fan out the further they are situated from the origin (fig. 2). Depending on their distribution, beta factors in maternal and paternal directions could cancel out to give a line of unit slope through the origin.

The covariance/variance graph for the female arrays, using the single gene model, has been split into two parts in figs. 3 (*a*) and 3 (*b*).
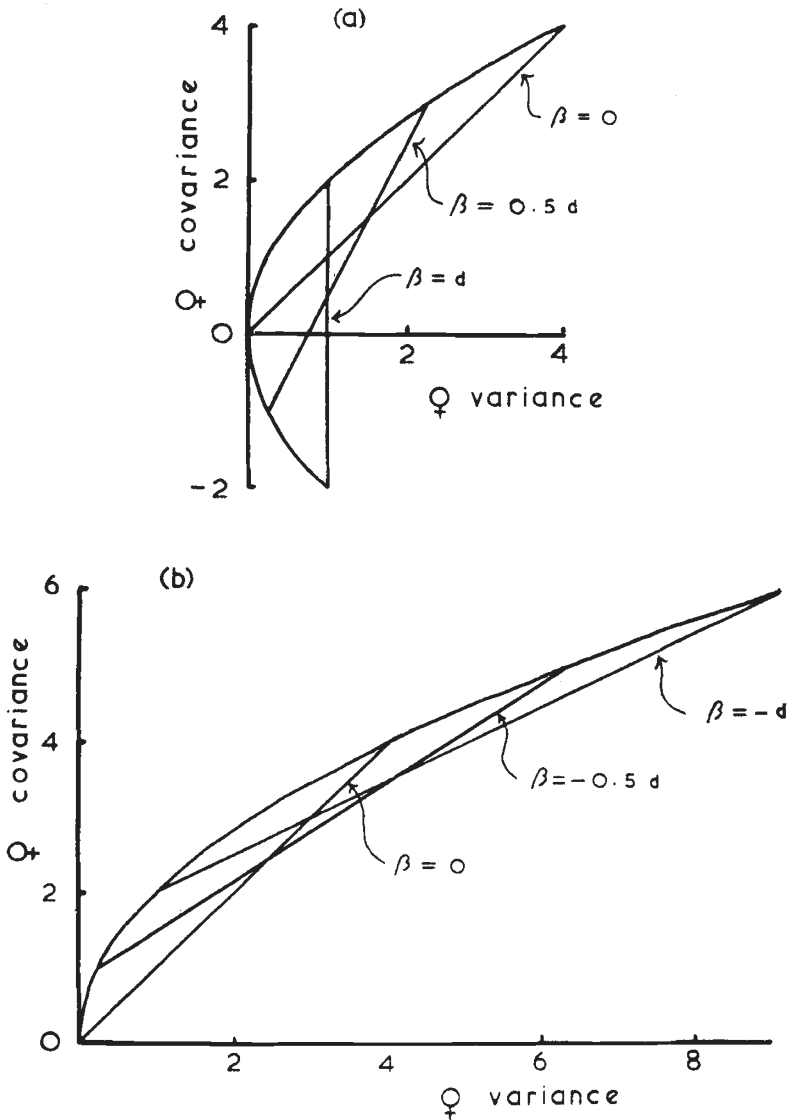

FIG. 3.—(*a*) Covariance/variance graph, for single gene model, for female arrays with positive values of β (shown) or for male arrays with negative values of β, for unit value of d/uv.

    (*b*) Covariance/variance graph, for single gene model, for female arrays with negative values of β (shown) or for male arrays with positive values of β, for unit value of d/uv.

    Lines for $h = d$ only are shown; other values of h give lines parallel to those shown, also meeting the parabola, for each value of β.

Fig. 3 (*a*) shows the pattern for beta inheritance in a maternal direction, and fig. 3 (*b*) in a paternal direction. With many genes, the parents

would lie on a straight line if the β values were the same for all genes but with a slope greater than one for maternal inheritance and less than one for paternal inheritance. If the β values are of different magnitudes and directions the parents are dispersed; with maternal inheritance the recessive parents are depressed and dominant parents raised; with paternal inheritance recessive parents are raised and dominant parents are depressed. The covariance/variance graphs for the male arrays are the same as those for the female arrays except that fig. 3 (*a*) and 3 (*b*) are interchanged. Deviations from multifactor beta inheritance are best examined on the covariance graph in sub-section (ii).

The male/female array covariances, $W\male/\female$, plotted against the array variances of reciprocal means give a line of unit slope which is displaced from the origin by $-uv\beta^2$ for the single gene model. Male array covariances and female array covariances plotted respectively against the array variances of the reciprocal means also give lines of unit slope deviating from the origin by $uv(d^2-h^2+2d\beta)$ for the male covariances and by $uv(d^2-h^2-2d\beta)$ for the female covariances. With many genes the points will lie on a straight line of unit slope independently of direction, magnitude and distribution of the β components provided, in the last two named graphs, the array covariance/variance graph of the reciprocal means itself gives a line of unit slope.

3. MULTIFACTOR ALPHA INHERITANCE

(I) *Formulæ*

In multifactor alpha inheritance the contributions of the homozygotes and heterozygotes of any one gene are increased, or decreased, to the same extent on the male side, or on the female side, or by unequal amounts on both male and female sides, for any number of genes.

In the single gene model of table 4 (*a*), α adds to the AA female array. If α is positive, *i.e.* in the same direction as d, alpha inheritance is in a maternal direction and the difference between the parents is increased. If α is negative, *i.e.* in the opposite direction to d, inheritance is in a paternal direction and the parental difference is decreased, unless $\alpha \geqq -2d$. Models 4 (*b*), (*c*), (*d*), give similar directions and differences so that these may also be represented by 4 (*a*). Similarly, model 4 (*e*), where α is added to the male AA array, is representative of models where alpha inheritance operates on the male arrays. In 4 (*e*), if α is positive, *i.e.* in the same direction as d, the parental difference is again increased as in 4 (*a*) but the inheritance is now in a paternal direction, and so on. In 4 (*a*), therefore, maternal inheritance is associated with an increase in parental differences, and paternal inheritance with a decrease, whereas in 4 (*e*) maternal inheritance is associated with a decrease in parental difference, and paternal inheritance with an increase. One consequence of these models is that if,

for example, α is negative and operates on a female array, inheritance is apparently in a paternal direction.

TABLE 4

Alpha inheritance models.   Column and row headings, parents and frequencies for each model are the same as in table 2

$d+\alpha$	$h+\alpha$
h	$-d$

(a)

d	h
$h-\alpha$	$-d-\alpha$

(b)

d	h
$h+\alpha$	$-d+\alpha$

(c)

$d-\alpha$	$h-\alpha$
h	$-d$

(d)

$d+\alpha$	h
$h+\alpha$	$-d$

(e)

Array variances and covariances, formulated in terms of d, h and α for the single gene model 4 (a) are given in table 5.   They are also

TABLE 5

Array variances and covariances given by the single gene alpha inheritance model

Variance of female AA array	$uv(d-h)^2$
Variance of female aa array	$uv(d+h)^2$
Variance of male AA array	$uv(d-h+\alpha)^2$
Variance of male aa array	$uv(d+h+\alpha)^2$
Covariance of female AA array	$uv(d-h)(2d+\alpha)$
Covariance of female aa array	$uv(d+h)(2d+\alpha)$
Covariance of male AA array	$uv(d-h+\alpha)(2d+\alpha)$
Covariance of male aa array	$uv(d+h+\alpha)(2d+\alpha)$
Male/female AA array covariance	$uv(d-h)(d-h+\alpha)$
Male/female aa array covariance	$uv(d+h)(d+h+\alpha)$
Variance of AA array reciprocal means	$\frac{1}{4}uv(2d-2h+\alpha)^2$
Variance of aa array reciprocal means	$\frac{1}{4}uv(2d+2h+\alpha)^2$
Variance of reciprocal differences	$\frac{1}{2}uv\alpha^2$

applicable to model 4 (e) provided male and female signs in the table are interchanged.

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(ii) *Graphical relations*

The female covariance/male covariance graph for the single gene model 4 (*a*) is given in fig. 4. The points lie on a line of unit slope, as was the case with multifactor beta inheritance, but the displacement is $-uv\alpha(2d+\alpha)$. Positive values of α, *i.e.* maternal inheritance, depress the line, negative values, *i.e.* paternal inheritance, raise the line which are the same directions given by multifactor beta inheritance. When $\alpha = -2d$ the differences between the parents in respect of the gene considered disappears, and both covariances are zero. When
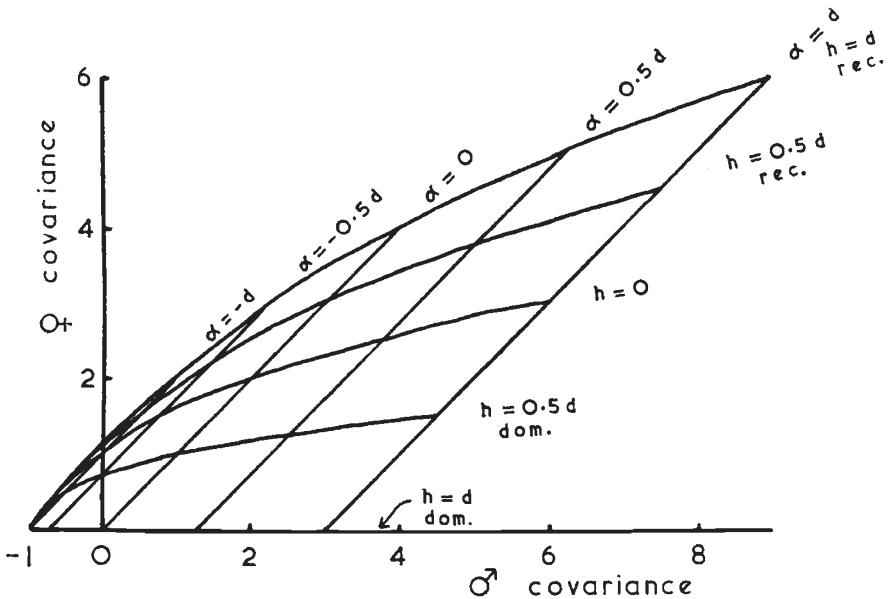
Fig. 4.—Female covariance/male covariance graph for alpha inheritance, for single gene model, for unit value of *d/uv*.

$\alpha > -2d$ the parental values are reversed and the consequent maternal inheritance depresses the line once more.

The female covariance/male covariance graph for model 4 (*e*) where alpha operates on the male arrays is the same as fig. 4 with the axes interchanged. If plotted on fig. 4 without change of axes the lines of unit slope would intermix with those shown, illustrating the ambiguity in the data; for example, alpha inheritance could be either positive and operate on the female array, or negative and operate on the male array.

With a number of genes the points remain on a line of unit slope independently of distribution, directions and magnitudes of the factors so that in this respect alpha is indistinguishable from multifactor beta inheritance. Consequently deviations from the line of unit slope indicate deviations from both forms of inheritance. In the same way multifactor alpha inheritance gives variance graphs and

variance/covariance graphs with similar, though not identical, characteristics as those given by multifactor beta inheritance. The reason for this is considered in the following sub-section.

(iii) Estimating multifactor beta and alpha inheritance

If a quantity α_1, is added to the female array of P_1', α_2 to the female array of P_2' etc., then

$$g_{12} = \alpha_1 - \alpha_2$$
$$g_{13} = \alpha_1 - \alpha_3$$
$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot$$
$$g_{24} = \alpha_2 - \alpha_4, \text{ etc.}$$

The difference between the female and male array covariances of P_1' is

$$w_1 = \frac{1}{n-1} \Sigma \alpha P'.$$

Similarly

$$w_2 = \frac{1}{n-1} \Sigma \alpha P',$$

etc., and the female covariance/male covariance graph gives a line of unit slope diplaced from the origin by $-\dfrac{1}{n-1} \Sigma \alpha P'$ which is equal to $-\dfrac{1}{n(n-1)} \Sigma G P'$.

This situation obtains with multifactor alpha inheritance. Further, if α is added to the male arrays this is equivalent, in respect of the reciprocal differences, to a negative value of α added to the female arrays. With many genes each contributing to alpha inheritance the total quantity, a_1, added to the female array of P_1' is the sum of all α factors added to that array, and so on, so that

$$g_{12} = a_1 - a_2, \text{ etc.,}$$

and

$$w_1 = -\frac{1}{n-1} \Sigma a P' = -\frac{1}{n(n-1)} \Sigma G P'$$

$$= w_2, \text{ etc.}$$

which is the uniform displacement of the parents on the W_φ/W_δ graph.

$\Sigma a P'$ is positive if alpha inheritance is mainly in a maternal direction, negative if mainly in a paternal direction and the correlation coefficient $r_{aP'} = \Sigma a P'/\sqrt{\Sigma a^2 \Sigma P'^2}$ is a useful measure of the extent of maternal or paternal inheritance. The least squares estimates of the a values are given by

$$a_1 = \frac{1}{n} G_1$$

$$a_2 = \frac{1}{n} G_2, \text{ etc.}$$

and

$$\Sigma a = 0.$$

A test of significance of the differences between the a values is the same as testing the c item against the d item in Hayman's (1954b) analysis of variance. The total sum of squares for the full table of reciprocal differences is $\frac{1}{4}\Sigma g_{rs}^2$ with $\frac{1}{2}n(n-1)$ degrees of freedom. Alpha sum of squares, c, is $\frac{n}{2}\Sigma a^2 = \frac{1}{2n}\Sigma G^2$ with $(n-1)$ degrees of freedom, the difference between them being the residual sum of squares, d. There may be highly significant differences between the a values even though the $W_{\female}/W_{\male}$ line shows no deviation from the origin, i.e. $\Sigma aP' = 0$ when maternal and paternal inheritance cancel out.

The a values are the relative amounts by which alpha inheritance of the respective parents adds to each member of their female arrays or subtracts from each member of their male arrays. Consequently alpha inheritance can be removed from the data in a number of ways, by subtracting from one array or adding to its reciprocal array independently for each parent. Since each parent is also independently adjusted in either of two ways there is ambiguity in interpreting the parental values as well as the W/V graph of the adjusted reciprocal means which changes for each combination of adjustments.

The relationship between alpha and beta multifactor inheritance is seen by comparing models of tables 2 and 4 (a). Suppose for illustrative purposes $\alpha = \beta$, then table 2 is the same as 4 (a) except that β is subtracted from the male array as well as being added to the female array, giving twice the reciprocal difference and leaving the AA parental value and average dominance unchanged. Consequently, insofar as the reciprocal differences are considered, beta is basically the same as alpha multifactor inheritance but where

$$g_{12} = 2(\beta_1 - \beta_2) \text{ etc.}$$

With many genes, if b_1'' is the total quantity added to the female array of P_1' etc., $2b''$ replaces a in the above expressions; the b'' values may now be estimated, and the correlation coefficient, $r_{b''P'}$ calculated. The expressions are also applicable if the beta components are asymmetric. The comparison of Hayman's c and d items therefore leads to a test of significance for both alpha and beta multifactor inheritance.

The adjustment for beta inheritance is made by subtracting the b'' values from all members of the respective female arrays and adding them to all members of the respective male arrays leaving the parental values unchanged. If it be supposed that the β factors show extreme asymmetry then twice the b'' values can be subtracted from each member of the female arrays, or added to each member of the male arrays, except for the parents, and change of dominance noted on the W/V graph of the reciprocal means.

In summary, these methods give estimates of the average direction of alpha or beta multifactor inheritance and of the average contributions of each parent; they do not permit the separation of one form from the other, and there is ambiguity in the interpretation of the

parental values and dominance, but they show up deviations from either of them.

4. ASSOCIATED INHERITANCE

Although individual parents may contain many genetic factors these may nevertheless act as groups in determining reciprocal differences. A simple example from the alpha type of inheritance is where the parental genetic constitution as a whole determines seed size or ripening propensities thereby adding, or subtracting, a constant amount to the members of the female array. Similarly cytoplasmic particles could contribute an additive amount to all members of an array. With beta type inheritance, the male and female genetic environments may increase or decrease dominance in the whole of the female or male array. In all these cases there is associated action. Some genetic factors may have an associated type of action on the reciprocal means, which will be considered in another paper.

(i) *Associated alpha inheritance*

Associated alpha inheritance is analysed in the same way as multifactor alpha inheritance and is indistinguishable from it, for the average contribution of a parent to multifactor inheritance is equivalent to associated alpha inheritance and the above expressions and interpretations are the same. Therefore if the $W_{\female}/W_{\male}$ graph gives points on a straight line of unit slope, associated or multifactor alpha inheritance or multifactor beta inheritance may be present. Parents deviating from this line deviate from all three forms.

For the remainder of this paper " alpha inheritance " will imply associated alpha inheritance, but multifactor alpha or multifactor beta inheritance is not ruled out. The consequences of models 4 (a) and 4 (e) are also relevant here. A large plant may, for example, produce small seed, either characteristically or because of an inability to ripen them properly in certain environments, and give small offspring in crosses where it is the female parent thereby displaying apparent paternal inheritance.

(ii) *Associated beta inheritance*

If parent P'_1 shows greater dominance (not over dominance) along its female array than along its male array then its female covariance will be smaller than its male covariance. If all parents show associated beta inheritance to a greater or less degree the points on the $W_{\female}/W_{\male}$ graph will no longer be on a line of unit slope but will be thrown off by amounts proportional to the amounts of beta inheritance of the individual parents. Parents with greater dominance in their female arrays will be displaced downwards and show maternal inheritance; parents with greater dominance in their male arrays will be displaced upwards and show paternal inheritance. Consequently the $W_{\female}/W_{\male}$ graph spreads the parents out in the direction of the line of unit

slope through the origin in the order of their dominance relations averaged over the reciprocals, $W_{(\male+\female)} = W$, and at right angles to this line in the directions and magnitudes of associated beta inheritance, $W_{(\female-\male)} = w$, the w values being measures of the change in dominance of the individual parents in the male and female arrays.

The $W_\female/W_\male$ graph therefore separates associated beta inheritance from the other forms of inheritance and for the remainder of the paper " beta inheritance " infers associated beta inheritance. The deviations from the line of unit slope could on the other hand be due to exceptional crosses, or to erratic reciprocal differences throughout the data. Sometimes these may be picked out by examination of the data but in general further analysis may be required to establish the presence of associated beta inheritance.

Beta inheritance of any one parent is measured as the difference between the regression coefficients of its male and female arrays respectively onto the parents. If b_1 is the regression of the differences between reciprocal cells of the reciprocal arrays of P_1' onto all the parents due to beta inheritance of P_1' alone, and b_2 that of P_2' etc., then

$$g_{12} = (b_1+b_2)(P_2'-P_1')$$
$$g_{13} = (b_1+b_3)(P_3'-P_1')$$
$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot$$
$$g_{24} = (b_2+b_4)(P_4'-P_2'), \text{ etc.}$$

The least squares equations are

$$b_1(\Sigma P'^2+nP_1'^2)+b_2(P_2'-P_1')^2...+b_n(P_n'-P_1')^2 = (n-1)w_1-P_1'G_1$$
$$b_1(P_1'-P_2')^2+b_2(\Sigma P'^2+nP_2'^2)...+b_n(P_n'-P_2')^2 = (n-1)w_2-P_2'G_2$$
$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot \quad \cdot$$
$$b_1(P_1'-P_n')^2+b_2(P_2'-P_n')^2...+b_n(\Sigma P'^2+nP_n'^2) = (n-1)w_n-P_n'G_n$$

and
$$b = \frac{(n-1)\bar{w}-\Sigma bP'^2}{\Sigma P'^2}.$$

The sum of squares taken out by associated beta inheritance is $\frac{1}{2}\Sigma b_r[(n-1)w_r-P_r'G_r]$ with n degrees of freedom.

A negative value of b indicates beta inheritance in a maternal direction for that parent, i.e. greater dominance in the female array; a positive value indicates that the parent is more dominant in its male array and beta inheritance is in a paternal direction. In an extreme situation where all cells in the female array have parental values $b = -0.5$ for all parents. The sum of squares taken out by beta inheritance is subtracted from the total reciprocal differences sum of squares leaving a residual sum of squares for testing beta inheritance. If the beta inheritance variance is significant when tested against its error variation obtained from replication but not when tested against the residual reciprocal variance this is indicative of erratic reciprocal differences in specific crosses; the residual reciprocal differences may also be significant when tested against its error. The

assessment of beta inheritance from the spread of the points on the $W_{\female}/W_{\male}$ graph is interpreted in the next sub-section. When all b values are equal the points are on a line of unit slope.

(iii) *Separation of alpha and beta inheritance*

Alpha and beta inheritance are not completely separable if they occur together. Even if they were, a decision would still have to be made as to whether beta inheritance should be estimated using the observed parental values, P', or using those values adjusted for alpha inheritance, P'_a. As previously mentioned, the diallel table, and therefore the parental values, can be corrected in two ways for each value of a, either by subtracting from the female array or adding to the male array, so that the parents can be corrected in 2^n ways. Alternatively, alpha inheritance may be symmetrical, equal amounts being added to the male and female arrays but with opposite signs, requiring no adjustment of the parents, or there may be some measure of asymmetry requiring only partial adjustment of the parents.

There is also ambiguity in interpreting that portion of alpha inheritance taken out by the regression of a on P' on the one hand, and mean beta inheritance on the other since

$$\frac{\Sigma a P'}{\Sigma P'^2} = -2b.$$

Consequently this portion of alpha inheritance could be interpreted as twice the mean beta inheritance with negative sign, or mean beta inheritance could be considered part of alpha inheritance, in which case there would be an additional 2^n ways of adjusting the parent values. Hence uniform beta inheritance gives points on a straight line of unit slope on the $W_{\female}/W_{\male}$ graph simulating alpha inheritance.

A third ambiguity is given by that portion of beta inheritance taken out by the regression of b on P' for this also can be interpreted as alpha inheritance since if k is the regression coefficient then

$$k(P'^2_2 - P'^2_1) = a_1 - a_2, \text{ etc.}$$

If this part of beta inheritance is apportioned to alpha inheritance its contribution to $\Sigma a P'$ is dependent upon $k\Sigma P'^3$ which is zero when the parental values are symmetrically distributed, although the a values may be considerably altered.

In the general case the parents will not be symmetrically distributed and $\Sigma a P'$ due to correlated beta inheritance, written $\Sigma (aP')_b$, will not be zero, wherein lies another ambiguity for this $\Sigma (aP')_b$ portion of correlated beta inheritance could be transferred back to b. The amounts, kP'_1, kP'_2, etc., taken out by the regression of b on P' sum to zero, $i.e.$ $k\Sigma P' = 0$, but when transferred to alpha inheritance they may be repartitioned to give a mean value, $\Sigma (aP')_b$, for this portion of beta inheritance and residual alpha deviations about $\Sigma (aP')_b$.

Furthermore it can be shown that reciprocal differences due to cor-related beta inheritance give constant values of $w = \dfrac{1}{n-1}\, k\Sigma P'^3$ for all arrays. Therefore differences in beta inheritance that are correlated with the parents do not displace the points from a line of unit slope on the W_φ/W_δ graph, but they do displace the line from the origin by an amount dependent upon $\Sigma(aP')_b$. In short, correlated beta inheritance can either be estimated as beta inheritance, transferred entirely to alpha inheritance, or split into a mean beta inheritance and non-correlated alpha inheritance.

The following method is proposed for obtaining some separation. Assume in the first instance that alpha inheritance operates sym-metrically, *i.e.* the parental values are unchanged. The reciprocal differences in terms of alpha and beta inheritance are

$$g_{12} = a_1 - a_2 + (b_1 + b_2)(P_2 - P_1)$$
$$\cdots \quad \cdots \quad \cdots \quad \cdots \quad \cdots$$
$$g_{24} = a_2 - a_4 + (b_2 + b_4)(P_4 - P_2), \text{ etc.}$$

The least squares equations can be solved if mean beta inheritance and both alpha and beta inheritance correlated with the parents are transferred to a common mean value, $\bar{b} = -\dfrac{\Sigma aP'}{2\Sigma P'^2}$ by replacing b with b', $\Sigma b' = \Sigma b'P' = 0$, and a with a', $\Sigma a' = \Sigma a'P' = 0$, the b' and a' values being deviations, due to beta and alpha inheritance, around the common mean value. The least squares equations then reduce to

$$b_1' = \frac{1}{\Sigma P'^2}\,(n-1)w_1',$$

$$b_2' = \frac{1}{\Sigma P'^2}\,(n-1)w_2', \quad \text{etc.,}$$

$$\bar{b} = \frac{1}{2\Sigma P'^2}\,[(n-1)\bar{w} - \Sigma b'P'^2]$$

$$a_1' = \frac{1}{n}\,G_1 + P_1'(b_1' + 2\bar{b})$$

$$a_2' = \frac{1}{n}\,G_2 + P_2'(b_2' + 2\bar{b}), \text{ etc.}$$

The b' values are calculated first and are substituted in to obtain $\bar{b}$ with further substitution to obtain the a' values. That part of correlated beta inheritance, $\Sigma(aP')_b$, which influences $\Sigma aP'$ is included in $\bar{b}$, and that part which influences the residual alpha inheritance is included in the a' values. Illustrations of the interpretations of a', b' and $\bar{b}$ are given in the next section.

If the data contain only alpha and beta inheritance in any combination the estimated values will give an exact fit when substituted in to give the estimated reciprocal differences, $\hat{g}_{rs}$, where,

$$\hat{g}_{12} = a'_1 - a'_2 + (b'_1 + b'_2 + 2\bar{b})(P'_2 - P'_1), \text{ etc.}$$

The best checks are $\Sigma a' = \Sigma b' = \Sigma b'P' = \Sigma a'P' = 0$. If the data contained only beta inheritance this method would partition it into alpha inheritance and beta inheritance, giving an exact fit. If the data contained only alpha inheritance an exact fit would also be obtained; all b' values would be zero and alpha inheritance could be expressed as a values only or as a' values and $\bar{b}$. If alpha inheritance is not symmetrical and is superimposed on, rather than underlies, beta inheritance exact fits should not be expected. If the parents were given adjusted values such as would be obtained if all the a' values were subtracted from the female arrays, or all were added to the male arrays, the order of the b' values would remain unchanged but their magnitudes would be changed by a constant factor of $\Sigma P'^2/(\Sigma P'^2 + \Sigma a'^2)$. If some a' values were subtracted from the female arrays and others added to the male arrays there would be changes in their relative magnitudes. Adjusting the parental values is not an ideal procedure and no account is taken of that part of alpha inheritance contained in $\bar{b}$.

Leaving on one side deviations due to erratic reciprocal differences and error variation the $W_{\female}/W_{\male}$ graph may now be interpreted. The overall deviation of the parents from a line of unit slope through the origin is a mean value, $\bar{b}$, compounded of mean beta inheritance, correlated beta inheritance the contribution of which is in part dependent upon the amount of asymmetry among the parents, and correlated alpha inheritance, which together give the average, overall direction of inheritance, maternal or paternal, and its amount. The deviations of individual parents from a line of unit slope, whether through the origin or not, are the deviations due to beta inheritance, b', of individual parents from the mean value $\bar{b}$. Residual alpha inheritance, a', is not shown by the graph.

The overall sum of squares taken out by alpha and beta together is calculated most easily from

$$\tfrac{1}{2}\Sigma(n-1)w'_r b'_r + \frac{1}{2n}\Sigma G^2$$

with $2n-3$ degrees of freedom. The two parts of this expression do not apportion the sum of squares correctly to alpha and beta inheritance as estimated; the second part is the same as Hayman's (1954b) c item and contains some beta as well as alpha inheritance. The sums of squares for a', b' and $\bar{b}$ are given in table 6, and these with twice the sums of products of $b'/\bar{b}$ and b'/a' add up to the alpha plus beta sum of squares. The correlation coefficient, $r_{a'b'}$, is useful and with replication the residual variation can also be tested.

5. EXAMPLES

Analyses of four diallel tables, sufficient to illustrate the method and to assess the type of result obtained, will be given rather than a detailed account of any one experiment.

TABLE 6

Sums of squares of a', b' *and* b

Item	Sum of squares	d.f.
Total	$\frac{1}{2}\Sigma g_{rs}^{2}$	$\frac{n}{2}(n-1)$
Alpha plus beta . .	$\frac{1}{2}\Sigma(n-1)w_{r}'b_{r}' + \frac{1}{2n}\Sigma G^{2}$	$2n-3$
a'	$\frac{n}{2}\Sigma a'^{2}$	$n-2$
b'	$\frac{1}{2}\Sigma b'^{2}\Sigma P'^{2} + \frac{n}{2}\Sigma b_{r}'^{2}P_{r}'^{2}$	$n-2$
$\bar{b}$	$2n\bar{b}^{2}\Sigma P'^{2}$	1
Residual . . .	$\frac{1}{2}\Sigma g_{rs}^{2} - \frac{1}{2}\Sigma(n-1)w_{r}'b_{r}' - \frac{1}{2n}\Sigma G^{2}$	$\frac{1}{2}(n-3)(n-2)$
$b'/\bar{b}$	Sum of products $\times 2$ $2n\bar{b}\Sigma b_{r}'P_{r}'^{2}$	
b'/a'	$-n\Sigma a_{r}'b_{r}'P_{r}'$	

(i) F_2 variances of a diallel cross with Linum

Durrant and Tyson (1964) have described a diallel cross between six types of *Linum* comprising two flax genotypes, P and M, two linseed

TABLE 7

Mean family variances ($\times 10^4$) *of log plant weights of* F_2 *families in a diallel cross of genotypes and genotrophs of* Linum (*Durrant and Tyson, 1964*)

	♂ parents					
	P	M	R	D	S	L
♀ parents						
P . .	145	303	197	227	290	195
M . .	193	122	272	392	335	183
R . .	240	237	173	136	332	278
D . .	208	298	188	178	330	280
S . .	323	167	260	288	305	382
L . .	255	238	310	223	200	253

genotypes, R and D, and two genotrophs, L and S. Table 7 gives the F_2 family variances of the log. plant weights.

Hayman's (1954) analysis, table 9 (*a*), shows that the residual reciprocal differences are larger than the array reciprocal differences. The W/V graph of the reciprocal means (Durrant and Tyson) showed that there was pronounced interaction between M and D, but insertion

of each reciprocal of this cross in turn makes little difference to the graph. The $W_\female/W_\male$ graph (fig. 5) shows large deviations from a
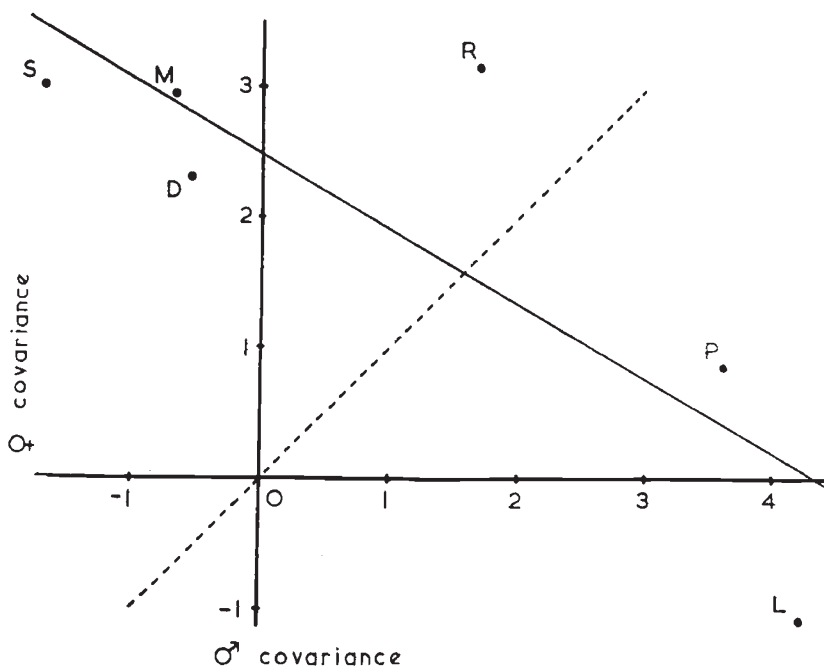
FIG. 5.—Female covariance/male covariance graph ($\times 10^5$) of *Linum* diallel.

TABLE 8

Linum diallel: estimates. Deviations of totals from zero are due to rounding off in all columns except (4) and (7). Columns (4) and (5) $\times 10^8$. Columns (2), (3), (6) and (8) $\times 10^4$

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Parent	P′	G	$(n-1)w$	$(n-1)w'$	a	b	a′	b′
P	−51	−7	−14510	−18268	−1·2	−0·034	44·9	−0·759
M	−74	132	18290	14532	22·0	0·808	−12·0	0·604
R	−23	−4	7357	3599	−0·7	0·515	−0·8	0·150
D	−18	38	14556	10798	6·3	0·793	0·8	0·449
S	109	−67	23535	19777	−11·2	−0·152	62·8	0·823
L	57	−92	−26678	−30436	−15·3	−0·970	−95·6	−1·265
Total	0	0	−22550	0	−0·1	0·960	0·1	0·002
$\bar{b}$					0·078	0·150	−0·072	

line of unit slope which are either due to large random reciprocal differences throughout the diallel table or to associated beta inheritance. Since the parents are scattered to about the same extent above and below a line of unit slope through the origin, inheritance might be judged to be approximately equal in maternal and paternal directions,

i.e. b, or $\Sigma a\mathrm{P}'$, is approximately zero. Apart from $\Sigma a\mathrm{P}'$ no information can be obtained from the graph on alpha inheritance.

If it were supposed that only alpha inheritance was present then the a values, calculated from $a_1 = \dfrac{1}{n}\, \mathrm{G}_1 = -1\cdot2$, etc., are those given in table 8, column (6), and the sum of squares is that given by Hayman's

TABLE 9

Linum diallel: analyses of variance. Sums of squares and mean squares $\times 10^8$

Item	Sum of squares	d.f.	Mean square	V.R.	P (per cent.)
Total . . .	53,678	15	...	...	...
(a) Alpha inheritance					
Alpha (c) . .	2,673	5	535	...	...
Residual (d) .	51,005	10	5,001	...	...
(b) Beta inheritance					
Beta . . .	27,553	6	4,592	1·38	...
Residual . .	26,125	9	2,903	...	...
(c) Alpha and beta inheritance					
Alpha plus beta .	44,061	9	4,896	3·05	...
a' . . .	45,770	4	11,440	7·07	< 5
b' . . .	91,479	4	22,870	14·27	< 1
$\bar{b}$ . . .	1,497	1	1,497	1·20	...
Residual . .	9,617	6	1,603	...	...
	Sum of products $\times 2$				
b'/a' . .	−88,828				
$b'/\bar{b}$ . . .	−6,244				

c item in table 9 (a) which is, as noted, relatively small. The average direction of inheritance and its magnitude is

$$-\frac{\Sigma a\mathrm{P}'}{2\Sigma\mathrm{P}'^2} = b = 0\cdot078$$

which is also small and in a paternal direction. The b values estimated assuming the presence of beta inheritance only, given in column (7) of table 8, are substantial but they are, nonetheless, not significant in table 9 (b).

Assuming the presence of alpha and beta inheritance, the a', b' and $\bar{b}$ values are given in table 8, columns (8) and (9). In table 9 (c) the alpha plus beta variance approaches significance; both the a' and the b' values are significant and negatively correlated in the reciprocal differences. $\bar{b}$ is small and not significant so that there is no evidence of any overall trend in a maternal or paternal direction.

The two genotrophs S and L have the highest b' values. S has greater dominance in the male array, *i.e.* has paternal inheritance, since it has a positive value. L has greater dominance in the female array, *i.e.* has maternal inheritance. Therefore male parents largely determine the character of the offspring in crosses with S, and female parents largely determine the character of the offspring in crosses with L. The flax varieties M and P have the next highest values of b'. Other studies have shown that parent M is similar to S in genetic, phenotypic and cytological characteristics, and parent P is similar to L. This analysis shows there is a similar pattern in their b' values.

TABLE 10

Mean F_1 flowering times in a diallel cross of Nicotiana varieties (Hayman, 1954).
Gene interaction in the 1×3 and 3×1 crosses has been removed

	♂ parents							
	1	2	3	4	5	6	7	8
♀ parents								
1	47	31	43	34	34	43	31	32
2	30	36	44	24	26	28	21	22
3	39	30	46	33	30	34	30	35
4	44	38	50	36	29	39	28	42
5	38	30	39	26	30	31	32	37
6	33	32	58	32	34	42	27	30
7	33	29	27	25	22	19	22	23
8	32	24	27	21	33	25	23	29

The genotrophs S and L have the highest a' values with M and P next while the linseed varieties, R and D, have negligible amounts. The value of a' for L is —96 which is the amount by which each cell in the male array of L is larger than its reciprocal cell in the L female array due to alpha inheritance. For S, the cells in the female array are the larger. Therefore L is more recessive, due to beta inheritance, along its female array which is also increased, relative to the male array, by alpha inheritance, or it is more dominant due to beta inheritance along its male array which is relatively decreased by alpha inheritance, and so on.

Summarising, both alpha and beta inheritance are present; the parents can be divided into three groups in respect of both alpha and beta inheritance, *i.e.* flax genotypes, linseed genotypes and flax genotrophs: the two genotrophs contrast in both forms of inheritance; there is no evidence of any overall trend in a maternal or a paternal direction.

(ii) F_1 flowering times in a diallel cross with Nicotiana

The data in table 10 were obtained by Jinks and given by Hayman (1954a) who mentions that the crosses were arranged in the greenhouse in a way that environmental effects may have inflated the

reciprocal differences. Both his c and d items were significant when tested against the error obtained from replication. In table 12 (a) the error obtained from replication is omitted and c is significantly

TABLE 11

Nicotiana *diallel: estimates. Deviations of totals from zero are due to rounding off in all columns except* (4) *and* (7)

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Parent	P′	G	$(n-1)w$	$(n-1)w'$	a	b	a'	b'
1	11	−1	152	137	−0·1	0·435	3·7	0·254
2	0	−19	255	240	−2·4	0·505	−2·3	0·446
3	10	−57	−232	−247	−7·1	0·592	−10·8	−0·459
4	0	75	115	100	9·4	0·245	9·4	0·186
5	−6	25	−52	−67	3·1	−0·234	3·3	−0·125
6	6	27	−35	−50	3·4	0·113	3·4	−0·093
7	−14	−14	4	−11	−1·8	−0·449	−2·8	−0·021
8	−7	−36	−86	−101	−4·5	−0·735	−3·8	−0·188
Total	0	0	121	1	−0·1	0·472	0·1	0
b					0·014	0·059	0·048	
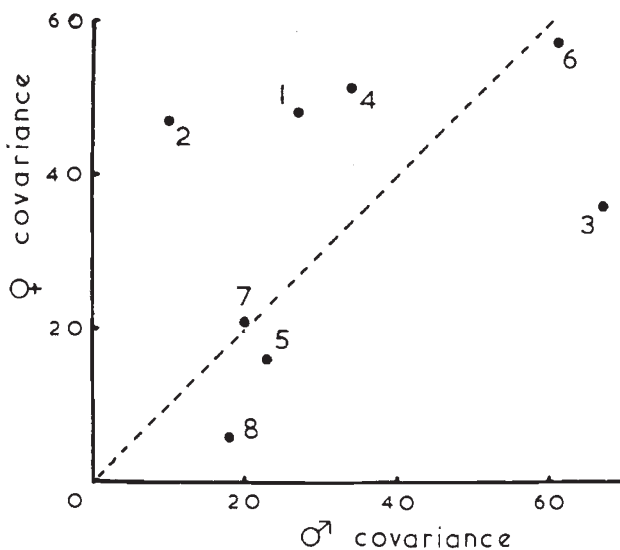
FIG. 6.—Female covariance/male covariance graph of *Nicotiana* diallel.

greater than d. This is a test assuming the presence of alpha inheritance only and table 11, column (b), shows that parents 3 and 4 have the largest a values. There is no overall tendency to maternal or paternal inheritance ($b = 0·014$) and it may be therefore that the reciprocal arrays of each of parents 3 and 4 were separated the most in the greenhouse arrangement.

TABLE 12

Nicotiana *diallel: analyses of variance*

Item	Sum of squares	d.f.	Mean square	V.R.	P (per cent.)
Total . . .	1235	28	...	...	...
(a) Alpha inheritance					
Alpha (c) . .	755	7	107·9	4·73	< 1
Residual (d) . .	480	21	22·8	...	...
(b) Beta inheritance					
Beta . . .	359	8	44·9	1·03	...
Residual . .	876	20	43·8	...	...
(c) Alpha and beta inheritance					
Alpha plus beta .	908	13	69·9	3·2	< 5
a' . . .	1073	6	178·8	8·2	< 0·1
b' . . .	279	6	46·5	2·1	...
b̄ . . .	19	1	19·0	...	...
Residual . .	327	15	21·8	...	...
	Sum of products ×2				
b'/a' . .	−436				
b'/b̄ . . .	−28				

TABLE 13

Mean weights at birth (grams × 100) and at 100 days (grams), in that order,
of F₁ families of rat diallel. (Jinks and Broadhurst, 1963)

	♂ parents					
	1	2	3	4	5	6
♀ parents						
1 . .	555 535	503 466	579 570	518 555	487 500	528 528
2 . .	548 484	473 420	542 487	528 522	501 438	536 443
3 . .	577 396	557 479	625 503	632 585	548 485	550 519
4 . .	564 389	525 479	571 493	537 456	515 438	632 475
5 . .	501 483	471 457	563 509	547 474	523 415	508 425
6 . .	539 528	553 460	539 526	523 478	522 420	515 437

The $W_\female/W_\male$ graph, fig. 6 shows that there is scatter on each side of the line, but the estimated b values given in table 11, column (7), are not significant (table 12 (b)). The estimates of a', b' and $\bar{b}$ assuming alpha and beta inheritance are present are given in table 11, columns (8) and (9). The analysis, table 12 (c), shows that only alpha inheritance is significant, confirming analyses 12 (a) and 12 (b).

(iii) F_1 weights at birth and at 100 days in a diallel cross with rats

The F_1 weights, males and females combined, at birth and at 100 days, in a diallel cross between six strains, given in table 13 have

TABLE 14

Weight at birth in rat diallel; estimates. Deviations of totals from zero are due to rounding off in all columns except (4) and (7). Columns (4) and (5) $\times 10^4$. Columns (2), (3), (6) and (8) $\times 10^2$

(1) Parent	(2) P'	(3) G	(4) $(n-1)w$	(5) $(n-1)w'$	(6) a	(7) b	(8) a'	(9) b'
1	17	−114	3608	4048	−19·0	0·387	−13·8	0·315
2	−65	46	−602	−162	7·7	0·141	9·0	−0·013
3	87	70	−1098	−658	11·7	−0·196	6·5	−0·051
4	−1	59	−6357	−5917	9·8	−0·428	10·3	−0·461
5	−15	17	3783	4223	2·8	0·382	−2·0	0·329
6	−23	−78	−1976	−1536	−13·0	−0·129	−10·1	−0·120
Total	0	0	−2642	−2	0	0·148	−0·1	−0·001
$\bar{b}$					−0·017	0·074	−0·004	

been extracted from data of Jinks and Broadhurst (1963). Taking weight at birth first, they found no genic interaction and Hayman's c and d items for reciprocal differences were not significant. The female array totals had a somewhat higher variation than the male array totals but not significantly so. Table 15 shows that neither alpha nor beta inheritance is significant, the dispersion on the $W_\female/W_\male$ graph (fig. 7) being due to error variation or erratic reciprocal differences of individual crosses, so far as can be shown by these tests.

Turning to the weights at 100 days, alpha inheritance in table 17 (a) is not significant but the $W_\female/W_\male$ graph in fig. 8 shows dispersion and beta inheritance in table 17 (b) is significant. In the simultaneous analysis in table 17 (c) highly significant values for a', b' and $\bar{b}$ are obtained, so that there is significant alpha and beta inheritance and an overall trend to maternal inheritance, *i.e.* $\bar{b}$ in columns (8), (9) of table 16 is negative. $2\bar{b}(P_s'-P_r')$ gives the estimated contribution of $\bar{b}$ to $\hat{g}_{rs}$; hence −0·6 is the estimated difference between the reciprocal crosses of any two parents per unit difference between those parents due to overall maternal inheritance, which is considerable.

The correlation between the a' and b' values is large and positive, $r_{a'b'} = 0\cdot722$, so that, in general, parents show greater dominance,

TABLE 15

Weight at birth in rat diallel; analyses of variance. All variance ratios are less than one. Sums of squares and mean squares $\times 10^4$

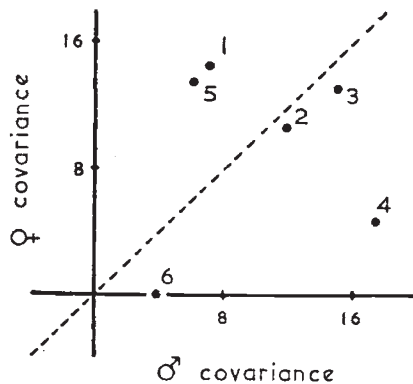| Item	Sum of squares	d.f.	Mean square
Total	11,526	15	...
(*a*) Alpha inheritance . .			
Alpha (*c*) . . .	2,489	5	498
Residual (*d*) . .	9,038	10	904
(*b*) Beta inheritance			
Beta	4,283	6	714
Residual . . .	7,243	9	805
(*c*) Alpha and beta inheritance			
Alpha plus beta . .	5,295	9	888
a'	1,576	4	389
b'	3,050	4	762
$\bar{b}$	2	1	2
Residual . . .	6,232	6	1,039
	Sum of products $\times 2$		
b'/a' . . .	650		
$b'/\bar{b}$ . . .	16		

FIG. 7.—Female covariance/male covariance graph ($\times 10^2$) of weight at birth rat diallel.

due to beta inheritance, along those arrays which are relatively decreased by alpha inheritance, and are more recessive along those arrays which are relatively increased by alpha inheritance.

The reverse relation holds in the weight at birth diallel where $r_{a'b'}$ is $-0\cdot59$. Comparing the dialleles, the two sets of a' values

2 P

have a correlation coefficient of -0.75 while the two sets of b' values
have a coefficient of 0.70, the difference between the coefficients being

TABLE 16

*Weight at 100 days in rat diallel; estimates. Deviation of totals from zero
are due to rounding off in all columns except (4) and (7)*

(1) Parent	(2) P'	(3) G	(4) $(n-1)w$	(5) $(n-1)w'$	(6) a	(7) b	(8) a'	(9) b'
1	74	339	6434	9224	56·5	$-1·553$	71·0	0·793
2	-41	33	2735	5525	5·5	1·606	10·5	0·475
3	42	-121	-11736	-8946	$-20·2$	$-1·447$	$-77·5$	$-0·769$
4	-5	-340	-12657	-9867	$-56·7$	$-0·551$	$-49·4$	$-0·848$
5	-46	67	-1329	1461	11·2	1·461	32·8	0·126
6	-24	22	-188	2602	3·7	1·364	12·6	0·224
Total	0	0	-16741	-1	0	0·880	0	0·001
$\bar{b}$					$-0·060$	0·147		$-0·299$

TABLE 17

Weight at 100 days in rat diallel; analyses of variance

Item	Sum of squares	d.f.	Mean square	V.R.	P (per cent.)
Total . . .	35,715	15	...	...	...
(a) Alpha inheritance					
Alpha (c) . .	20,935	5	4,187	2·83	...
Residual (d) .	14,780	10	1,478	...	...
(b) Beta inheritance .					
Beta . . .	28,047	6	4,674	5·49	< 5
Residual . .	7,668	9	852	...	...
(c) Alpha and beta inheritance					
Alpha plus beta .	33,912	9	3,768	12·5	< 1
a' . . .	44,538	4	11,134	37·1	< 0·1'
b' . . .	27,822	4	6,955	23·2	< 0·1
$\bar{b}$ . . .	12,452	1	12,452	41·5	< 0·1
Residual . .	1,803	6	300	...	...
	Sum of products ×2				
b'/a' . . .	$-35,992$				
b'/$\bar{b}$ . . .	$-14,922$				

significant.   Therefore it appears that beta inheritance is fairly
consistent from birth to 100 days while alpha inheritance is reversed.
It is generally appreciated with livestock that overfeeding during

early life is likely to result in poorer adult animals rather than better. Here, perhaps, a favourable prenatal life, giving a larger birth weight,
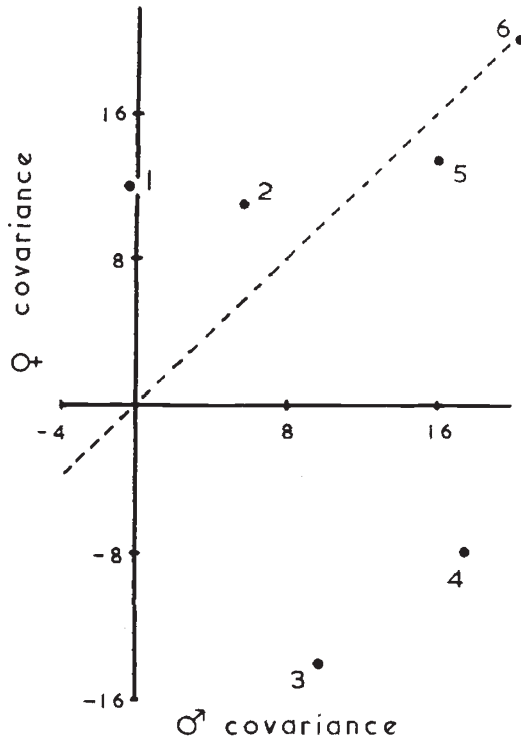

FIG. 8.—Female covariance/male covariance graph ($\times 10^{-2}$) of weight at 100 days, rat diallel.

TABLE 18

Competition diallel. This table is similar to table 1 (a), and gives a table of reciprocal differences similar to table 1 (b)

	Grown with species (columns)				Row totals $y_r.$
	1	2	3	4	
Species (rows)					
1 . .	y_{11}	y_{12}	y_{13}	y_{14}	$y_1.$
2 . .	y_{21}	y_{22}	y_{23}	y_{24}	$y_2.$
3 . .	y_{31}	y_{32}	y_{33}	y_{34}	$y_3.$
4 . .	y_{41}	y_{42}	y_{43}	y_{44}	$y_4.$
Column totals $y._r$	$y._1$	$y._2$	$y._3$	$y._4$	$y..$

may lead to a lower adult weight, but the change in dominance, measured as beta inheritance, in the prenatal, or gametic, environment, is maintained.

On the other hand, there is an overall maternal inheritance at 100 days which did not occur at birth. This could be accounted for by a maternal effect which Jinks and Broadhurst mentioned occurred at 50 days, some time after weaning, and which was probably due to the milk yields of the parents. Therefore the reciprocal differences at 100 days have three components.

It may be this pattern has appeared partly because, if alpha inheritance should be affecting the parental values it would be doing so in different directions at birth and at 100 days, since the a' values at the two times are negatively correlated. The correlation between the differences between the a' values at the two times and the differences between the P' values at the two times is 0·672, so that there is evidence that the change in alpha inheritance is partly reflected in changes in parental values. Recalculation of the a', b' and b values at 100 days using the weight at birth parental values has little effect on the a' values (79·7, −11·1, −22·7, −56·2, 8·8, 1·6) or on the b' values (1·13, 0·02, −0·26, −0·69, −0·07, −0·14), and the correlation coefficients for weight at birth and at 100 days are −0·63 for a', and 0·76 for b', almost the same as before. On the other hand, the substantial overall maternal inheritance disappears, $b = 0·11$, presumably because milk yield is related to the adult parental weights, not to the parental weights at birth. Consequently these adjustments support, rather than invalidate, the suggested occurrence here of three components determining reciprocal differences.

These methods would be particularly useful if diallels were replicated in different environments, particularly in stress environments when larger reciprocal differences are likely to occur, and measurements were made at different stages of development. The formulæ can be modified to accommodate specific genetic situations. Reciprocal differences deviating from those expected from maternally inherited characters may be analysed using formulæ similar to those given in the next section for competition studies.

6. NON-GENETIC DIALLEL TABLES

An analysis which includes the reciprocal differences as well as the reciprocal sums of a diallel table has a wider application to other sorts of data which can be arranged in the form of a diallel table. An illustration is given in table 18 of data obtained from a competition experiment where varieties, or species, are grown by themselves and in all pairs. The rows give the weights of the species when grown with each of the species at the column heads. The mixtures grown by themselves are equivalent to parents, P'; rows (R) and columns (C) are equivalent to female and male arrays respectively, and the weights of two species grown together are equivalent to the reciprocals. Analysis of the reciprocal means gives information on the behaviour of the mixtures compared with the species grown by themselves. For

example, if in the W/V graph of the reciprocal means, species which are more " dominant " have the greater values, then the mixtures tend to values which are nearer the larger species than the small.

Reciprocal differences in competition studies give information on how the species within mixtures influence one another. If the species behave in mixtures as they do when grown by themselves the columns will be identical, the W/V graph of the reciprocal means will show no " dominance ", " maternal inheritance " would be uniform and complete, and the species would be together at one point, Z, on the
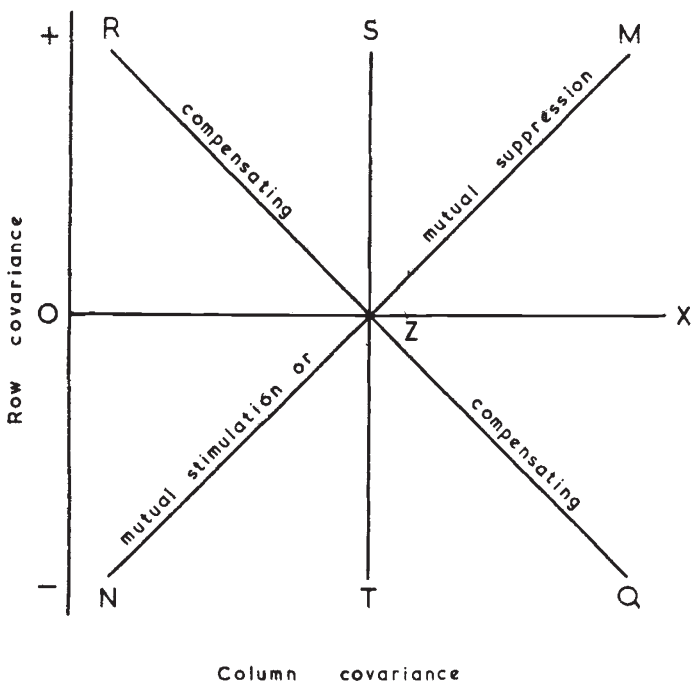
Fig. 9.—Row covariance/column covariance graph for competition diallel.

X axis of the W_R/W_C graph (fig. 9) at a distance from the origin equal to the variance of the species grown by themselves. The analysis of reciprocals in competition diallels concerns the analysis of deviations from this point, Z, in terms of alpha and beta competition, which are equivalent to associated alpha and associated beta inheritance.

Beta competition of any one parent is measured as the difference, b, between the regression coefficients of its rows and columns (R—C) respectively onto the unmixed species P'. Species with negative values of b interact in such a way that smaller species in mixtures are decreased and larger species are increased relative to one another; with positive values larger species in mixtures are decreased and smaller species are increased. In general negative values are to be expected. With beta competition, therefore, the greater the difference between two parents when grown by themselves the greater the decrease of one,

2 P 2

and/or increase of the other, when grown together in a mixture, and b is a measure of the extent to which this occurs. If species have the same values in mixtures as when they are grown by themselves then g_{12}, the difference between species P_1' and P_2' grown together in a mixture, is $P_1'-P_2'$, but the difference when beta competition occurs in the reciprocal arrays of parent P_1' only is

$$g_{12} = P_1'-P_2'+b_1(P_2'-P_1')$$

and so on.

Alpha competition occurs when a species suppresses the other species to the same extent, and/or it itself is increased to the same extent when it is grown with the other species, giving a positive value of a. Alpha competition gives a negative value of a when it is depressed to the same extent by all the other species and/or the other species are increased to the same extent when grown with it.

If only alpha competition is assumed to be present then

$$g_{12} = a_1-a_2+P_1'-P_2' \text{ etc.}$$

and the least squares estimates are

$$a_1 = \frac{1}{n} G_1-P_1' \text{ etc.}$$

The total sum of squares for the full table of reciprocal differences is

$$\tfrac{1}{4}\Sigma(g_{rs}+P_s'-P_r')^2$$

with $\frac{n}{2}(n-1)$ degrees of freedom, and the alpha sum of squares is

$$\frac{n}{2}\Sigma a^2 = \frac{1}{2n}\Sigma(G_r-nP_r')^2$$

with $n-1$ degrees of freedom.

If only beta competition is assumed to be present then

$$g_{12} = (b_1+b_2)(P_2'-P_1')+P_1'-P_2' \text{ etc.}$$

and the least squares estimates are obtained from the following set of simultaneous equations:

$$b_1(\Sigma P'^2+nP_1'^2)+b_2(P_2'-P_1')^2 \ldots +b_n(P_n'-P_1')^2$$
$$= (n-1)w_1-P_1'G_1+\Sigma P'^2+nP_1'^2$$

$$b_1(P_1'-P_2')^2+b_2(\Sigma P'^2+nP_2'^2)\ldots+b_n(P_n'-P_2')^2$$
$$= (n-1)w_2-P_2'G_2+\Sigma P'^2+nP_2'^2$$

. . . .

$$b_1(P_1'-P_n')^2+b_2(P_2'-P_n')^2 \ldots +b_n(\Sigma P'^2+nP_n'^2)$$
$$= (n-1)w_n-P_n'G_n+\Sigma P'^2+nP_n'^2.$$

The beta sum of squares is

$$\tfrac{1}{2}\Sigma b_r[(n-1)w_r-G_rP_r'+\Sigma P'^2+nP_r'^2]$$

with n degrees of freedom.

Assuming the presence of both alpha and beta competition,

$$g_{12} = a_1 - a_2 + (b_1 + b_2)(P_2' - P_1') + P_1' - P_2' \text{ etc.}$$

Using the procedure in section 4, then

$$g_{12} = a_1' - a_2' + (b_1' + b_2' + 2b)(P_2' - P_1') + P_1' - P_2' \text{ etc.}$$

and the least squares equations reduce to

$$b_1' = \frac{1}{\Sigma P'^2}(n-1)w_1' \text{ etc.,}$$

$$b = \frac{1}{2\Sigma P'^2}[(n-1)\bar{w} - \Sigma b' P'^2] + \tfrac{1}{2}$$

$$a_1' = \frac{1}{n}G_1 + P_1'(b_1' + 2b) - P_1' \text{ etc.}$$

The sums of squares formulæ for the analysis of variance, and the sums of products, are the same as those given in table 6 except the total sum of squares for reciprocal differences, given above, the alpha plus beta sum of squares which is

$$\tfrac{1}{2}\Sigma(n-1)w_r'b_r' + \frac{1}{2n}\Sigma[G_r - nP_r']^2,$$

and the residual sum of squares which is obtained by subtraction, *i.e.*

$$\tfrac{1}{4}\Sigma(g_{rs} + P_s' - P_r')^2 - \tfrac{1}{2}\Sigma(n-1)w_r'b_r' - \frac{1}{2n}\Sigma(G_r - nP_r')^2.$$

There is a difference between competition diallels and genetic diallels in that competition diallels permit an assessment of the amount each species changes in mixtures as well as the direction of the change because each species exists as an entity when grown by itself and in a mixture, whereas in a genetic diallel the reciprocal differences are expressed as deviations from the mean dominance value of each pair of reciprocal crosses. The assessment of the changes of the species in competition diallels involves the analysis of the reciprocal means as well, which is considered in another paper. The W_R/W_C graph, fig. 9, also gives information on the reciprocal means and on the reciprocal differences but the graph is of sufficient interest to give a provisional interpretation here, considering average effects over arrays.

The a', b' and b values are measures of reciprocal differences only and shift the points at right angles to the line of unit slope through Z. If the reciprocal differences are compensating, that is, species change in value by equal amounts in opposite directions in each mixture, all points will remain on the line RQ. b is the mean displacement of all points from Z, below for a negative value and above for a positive value. b' values spread the points about b, and a' values have no affect on the graph. As explained in the genetic diallel, b can also be

interpreted as alpha competition correlated with the values of the species grown by themselves.

If alpha competition only occurs, with compensating competition, the species remain together at a point on RQ, the point being raised or depressed depending upon the amount and direction of the correlation of the a values with the species grown by themselves. If it is not compensating the species are spread out on a line of unit slope through this point, individual species moving in directions outlined below for beta competition.

Where beta competition only occurs and it is not of the same magnitude and/or direction for all species, then if the species influence one another in mixtures such that the growth of one is increased by the same amount as the other is decreased in each mixture (compensating) the W/V graph of the summed reciprocals would show no " dominance ", and in the W_R/W_C graph the parents would be spread out on the line, RQ, passing through Z, with a slope of minus one. If the direction of the influence is such that large species are increased in weight and small species decreased in weight in mixtures, all the species will be below the X axis on ZQ; if the small species are increased and the large species are decreased all the species will be above the X axis on RZ. Species interacting the most will be situated further from the X axis, above or below, but if the large and small species influence each other in different directions in different mixtures they will tend to cancel out to give points near to Z.

If species influence one another in mixtures such that in each mixture both species change by the same amount in the same directions, although not necessarily the same amounts or directions for all mixtures, the W/V graph of the reciprocal means would show " dominance ", and in the W_R/W_C graph the parents would be spread out on a line of unit slope, NM, passing through Z. Then in general if the species are increased (mutual stimulation) the small species will be above the X axis on ZM, and the large species below on NZ; if the species are decreased (mutual suppression) the large species will be on ZM and the small species on NZ. Species would be expected to deviate from RQ and MN and to help in the interpretation of the deviations, another line, ST, is drawn perpendicular to the X axis through Z. Species lying to the left of ST decrease the weights of larger species with which they are grown in mixtures and increase the weights of smaller species with which they are grown. Species lying to the right of ST increase the weights of larger species with which they are grown and decrease the weights of the smaller species with which they are grown. Species above the X axis are increased in weight when grown with larger species or decreased in weight when grown with smaller species. Species below the X axis are decreased in weight when grown with larger species and increased in weight when grown with smaller species.

Taking one of the four areas defined by ST and the X axis in

more detail, say ZXTQ, species to the left of ZQ in this area are influenced more by the other species than they influence others. That is, if it is a small species it would be decreased more, or if it is a large species it would be increased more, in mixtures than larger species with which the smaller species are grown increase, or the smaller species with which the larger species are grown decrease. If the species is displaced so far as to be on ST then it does not influence the species with which it is grown although, if it is below the X axis it is itself influenced by the other species. If it moves to the left of ST it influences the other species in the opposite direction. Species displaced to the right of ZQ influence other species more than they are influenced by others. A smaller species would be decreased less, or a larger species increased less, in mixtures than the larger species with which the smaller species is grown increases, or the smaller species with which the larger species is grown decreases. If the species is on the X axis it is not influenced by the other species although if it is to the right of ST it itself influences the growth of other species. If it is above the X axis it is influenced by the other species in the other direction. If all species lie on ZT some species, proportionate to their displacement from Z, are strongly and consistently influenced by other species but none of the species individually and consistently influences the other species.

Species lying on MN show " dominance " in a genetic sense in the W/V graph of the reciprocal means yet the species are influencing each other to the same extent in mixtures. Consequently in a competition diallel " dominance " and the " influence of one species on another " have different meanings. Similarly, species may dominate one another in mixtures in an ecological sense yet they could all lie on RQ, *i.e.*, show no " dominance " in the genetic sense. Worked examples of competition diallels will be published.

7. SUMMARY

Four types of inheritance giving reciprocal differences are considered:

1. Multifactor alpha inheritance. The contributions of the homozygotes and heterozygotes of any one gene are increased, or decreased, to the same extent on the male side, or on the female side, or by unequal amounts on the male and female sides, for any number of genes.

2. Multifactor beta inheritance. Each of any number of genes has different amounts of dominance in the reciprocal crosses concerned.

3. Associated alpha inheritance. Any number of genes of each of any number of parents cooperate to add, or subtract, a constant quantity to or from the male, or female, array of the parent concerned, or constant but different quantities to, or from, the male and female arrays (*e.g.* maternal inheritance due to seed size); a constant difference between male and female arrays due to undiluted cytoplasmic inclusions.

4. *Associated beta inheritance.* Overall change in dominance of individual parents in their reciprocal arrays; *i.e.* a change in dominance due to different male and female gametic environments akin to changes in dominance due to external environmental differences.

Types 1, 2 and 3 give formulæ and graphs with similar characteristics so that they cannot be distinguished using the methods considered and are collectively referred to as alpha inheritance. Type 4 may then be simply referred to as beta inheritance.

The analytical procedure is as follows:

(i) Examine the W/V graph of the reciprocal means and determine whether any gene interaction is related to any obvious reciprocal differences of specific crosses.

(ii) Examine the $W_\female/W_\male$ graph. If all parents are on a line of unit slope alpha inheritance may be present, not beta; if the line of unit slope is displaced significantly from the origin there is overall maternal or paternal inheritance depending on the direction of displacement. If some or all parents are scattered off the line of unit slope beta inheritance may be present or there may be erratic reciprocal differences.

(iii) If alpha inheritance is suspected from the graph the parental contributions, and the average directions and magnitudes, are estimated. The test of significance is the same as comparing Hayman's *c* and *d* items.

(iv) If beta inheritance is suspected from the graph the parental contributions are estimated from a set of simultaneous equations and its significance tested.

(v) Alpha and beta inheritance are not completely separable when they are both present but they can be combined and split down into three useful items, a', b' and b which can be estimated and tested in a simultaneous analysis. b is a measure of overall maternal or paternal inheritance; a' values measure parental contributions to alpha inheritance (maternal, paternal or cytoplasmic effects), and b' values measure parental contributions to beta inheritance (change in dominance), both sets of values being expressed as deviations around b.

Four worked examples give the following results. *Linum* variation (Durrant and Tyson): significant alpha and beta inheritance in simultaneous analysis and no overall trend in male or female directions. *Nicotiana*, flowering time (Hayman and Jinks); significant alpha inheritance only and no overall trend in male or female directions. Rat weight at birth (Jinks and Broadhurst); no significance. Rat weight at 100 days (Jinks and Broadhurst); highly significant alpha and beta inheritance in simultaneous analysis with a significant overall trend in a female direction. Taking rat weight at birth and at 100 days together there are possibly three major components determining reciprocal differences, reversible alpha inheritance, constant beta inheritance, and milk yield.

The formulæ and methods may be used for non-genetic data which

can be arranged in the form of a diallel table, or they may be used after modification. Modified formulæ and graphical interpretations are given for alpha and beta competition (equivalent to alpha and beta inheritance) for competition studies on species grown by themselves and in pairs.

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