THE ANALYSIS OF A DIALLEL CROSS OF HETEROZYGOUS OR MULTIPLE ALLELIC LINES

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1. INTRODUCTION

IN a population in which it is not possible to self the individuals and which has been under natural selection for many years, several generations of directional selection and assortative mating will not have necessarily resulted in homozygosity; indeed, natural selection will oppose such directional selection, resulting in plateauing and the maintenance of heterozygosity. Further, when selecting parental lines, the dominant homozygote and heterozygote are more likely, under assortative selection, to be used as parents than the undesirable double recessive. The situation of (homozygous, heterozygous) parental lines could also occur in a population where the frequency of the double recessive is so low that it is excluded from most small samples.

The consequences on the diallel analysis procedure, as first outlined by Jinks and Hayman (1953), of the failure of two of the basic assumptions will be considered. These are that the parents should be homozygous and that there should be no multiple allelism, the consequences of non-homozygosity being, in part, an extension of the work of Dickinson and Jinks (1956). Simultaneous failure of these assumptions will not be considered; only the failure of one of them with all the others still holding. Particular emphasis will be placed on the non homozygosity of the parents and, where relevant, it will be pointed out that the arguments applied can also be used when certain types of multiple allelism exist. It will be shown that most of the information obtained from a diallel table generated by homozygous parents can still be extracted even if the parental lines are heterozygous. There are two ways in which this can be accomplished.

The first is subject to the assumption that, in the initial population, only two genotypes exist at each locus affecting the particular trait under consideration. This can apply equally to two of the three genotypes possible from a two allele system or to two of the three homozygotes possible from a tri-allelic system. A method of analysis has been developed and will be described for combinations of loci having the two genotypes (homozygote, heterozygote). This method of analysis will be referred to as the *p*-heterozygous (partially-heterozygous) diallel analysis. Estimates will be given of the errors introduced by applying the diallel analysis techniques assuming homozygosity, to data for which the *p*-heterozygous method should be used.

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The second method is subject to no assumptions whatsoever about frequencies of genotype, but is based upon being able to recognise, in the analysis of results, that the parental lines involve all the three possible genotypes at a locus. Once such a realisation has occurred, the results can be analysed using both the *p*-heterozygous and homozygous diallel analyses or, under certain circumstances, directly. The method of recognition of full heterozygosity will be discussed, as will the errors introduced consequent upon failing to recognise the completely heterozygous nature of the parental lines. The partitioning of the heterozygous data for the application of the two diallel analysis methods will also be described and, following Dickinson and Jinks (1956), will be referred to as the "triangulation" method.

In the final section of this paper, an attempt will be made to apply the various methods and comparisons to some data.

In the homozygous diallel analysis procedure, use is made of the (V_r, W_r) graph, on which the covariance (W_r) of parents selfed on offspring, for each array r , is plotted against the corresponding variance (V_r) of offspring in each array. For the homozygous diallel, it can be shown that the points (V_r, W_r) should lie on a straight line of unit slope. The detection of the completely heterozygous situation depends upon deviations of the (V_r, W_r) graph from a unit-slope line. However, in the case of the heterozygous or multiple allelic two genotype situation, it will be shown that no such deviation occurs. The decision which method of analysis, *i.e.* *p*-heterozygous or homozygous, should be used must, therefore, be based on prior knowledge of the material.

2. *P*—HETEROZYGOUS ANALYSIS

Standard biometrical nomenclature (Mather, 1949) will be used. Hence, if there are three possible genotypes at any one locus, *AA*, *Aa* and *aa*, then the contributions made by these over and above the mid-parent value $(AA+aa)$, are taken as $+d$, h and $-d$ respectively. It will be assumed that there are no correlated gene distributions.

(i) (V_r, W_r) graph

It can be shown that, for homozygous parents, the (V_r, W_r) graph is a straight line of unit slope such that

$$W_r - V_r = \frac{1}{4}(D - H_1)$$

where $D = \Sigma 4uvd^2$, $H_1 = \Sigma 4uvh^2$, and u and v are the frequencies of *A* and *a* respectively in the parental lines. ($u+v=1$.)

Assume that the parental lines contain all possible combinations of the genotypes (AA, Aa) and (BB, Bb) and that the frequencies of these are (u_a, w_a) and (u_b, w_b) respectively. Thus, under the assumption of no correlated gene distributions the genotypes *AABB*, *AaBB*, *AABb* and *AaBb* will occur with frequencies $u_a u_b$, $w_a u_b$, $u_a w_b$ and $w_a w_b$ respectively. Consideration of a theoretical 4×4 diallel involving the

above genotypes and associated frequencies shows that, for all the resultant four arrays (assuming no non-allelic interaction)

$$W_r - V_r = \frac{1}{4}[u_a w_a d_a^2 + u_b w_b d_b^2 - u_a w_a d_a h_a - u_b w_b d_b h_b].$$

Assuming independence of genes in action it follows that, for many loci

$$W_r - V_r = \Sigma \frac{1}{4} u w d^2 - \Sigma \frac{1}{4} u w d h$$

and so the points (V_r, W_r) lie on a straight line of unit slope.

Suppose now that the parental lines consist of (AA, Aa) combined with (BB, bb) and let the relative frequencies be (u_a, w_a) and (u_b, v_b) respectively.

It can be shown that, for many loci (assuming independence of genes in action) of this type

$$W_r - V_r = \frac{1}{4}[\Sigma u w d^2 - \Sigma u w d h] + [\Sigma u w d^2 - \Sigma u w h^2]$$

summed over p -heterozygous loci.	summed over homozygous loci.
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Therefore, this situation, which is a combination of fully homozygous and p -heterozygous crosses, gives $(W_r - V_r)$ values which are combinations of the results obtained independently from the two types of cross.

The above argument is easily applied to the occurrence of combinations of pairs from the three genotypes possible from a triallelic system, assuming homozygosity.

It can be concluded that, whenever combinations of loci occur at which, in the parental lines, there are only two genotypes out of a possible three then, irrespective of what those genotypes be, the (V_r, W_r) graph is always a straight line of unit slope.

Finally, when some of the basic assumptions are not valid, the (V_r, W_r) graph for the p -heterozygous diallel can be shown theoretically to behave in a way identical to that for the homozygous diallel. Thus, in the case of non-allelic interaction for example, the central points of the graph move downwards if the interaction is complementary, upwards if duplicatory.

(ii) Method of analysis

Assume all possible combinations of (AA, Aa) , (BB, Bb) etc. occurring with frequencies (u_a, w_a) (u_b, w_b) etc.

Error variance components will be neglected. These are the same as those for the homozygous diallel with the exception that the mean variance within families does not provide an estimate of E_1 (error variance between individuals). It provides an estimate of E_1 plus a genetic component. This will not be enlarged upon here, and it will be assumed that there is sufficient block replication to obtain E_2 , and that the standard Hayman analysis has shown that, were inbred lines

being considered, it would be valid to use the homozygous diallel procedure.

The following equations can be derived for the p -heterozygous diallel, operating under the assumption of independent gene action and distribution.

$$V_{ps} = A + \frac{1}{4}B$$

$$\overline{V}_r = \frac{1}{4}A + \frac{1}{4}B - \frac{1}{4}C$$

$$\overline{W}_r = \frac{1}{2}A + \frac{1}{4}B - \frac{1}{4}C$$

$$V_r = \frac{1}{4}A + \frac{1}{4}B - \frac{1}{4}C - \frac{1}{4}G$$

where V_{ps} = variance of parents selfed

$\overline{V}_r$ = mean of variances of arrays

$\overline{W}_r$ = mean of covariance (parents on offspring) of arrays

V_r = variance of array means

$$A = \Sigma uwd^2 - \Sigma uwdh$$

$$B = \Sigma uwh^2$$

$$C = \Sigma u^2wdh - \Sigma uw^2dh + \Sigma uw^2h^2$$

$$G = \Sigma u^2w^2h^2.$$

These equations can be solved for A , B , C and G .

$$\frac{G}{B} = \frac{\Sigma u^2w^2h^2}{\Sigma uwh^2} \text{ provides an estimate of } \overline{uw}$$

and so, since $u + w = 1$ indicates the relative proportions of $\bar{u}$ and $\bar{w}$.

$$\text{Further, } \frac{A}{B} = \frac{\Sigma uwd^2 - \Sigma uwdh}{\Sigma uwh^2}.$$

If it is assumed that all the product terms dh have the same sign, *i.e.* unidirectional dominance, then A/B provides an estimate of $\frac{1-z}{z^2}$, where $z = h/d$, which can be solved for z .

It can be demonstrated that if the dh do not have the same sign, then z will be underestimated.

Having obtained $\overline{uw}$ and z , it is possible to obtain an indication as to whether $\bar{u} > \bar{w}$ or $\bar{w} > \bar{u}$ from the estimated value of C .

In conclusion, the p -heterozygous diallel method of analysis is almost as useful a tool as the homozygous one, insofar as it provides estimates of $\overline{uw}$, $\bar{u}$, $\bar{w}$ and h/d . No direct solution exists for the "mixed" case, but application of the two methods of analysis will provide upper and lower limits of the parameters.

(iii) Comparison of the two methods

It is interesting to compare the results obtained, for the mean product of genotype frequencies ($\bar{u}\bar{v}$, $\overline{uw}$) and the dominance ratio, by

applying the two methods of diallel analysis to the same data. It can be shown that the estimated mean product of frequencies is the same by both methods and, if y and z be the dominance ratios obtained by using the homozygous and p -heterozygous methods respectively

$$z = \frac{2y}{1+y}.$$

This relationship gives a measure of the error introduced by applying the wrong method of analysis to a particular set of data. For instance, if the homozygous method is applied to p -heterozygous data, then the dominance ratio will, except in the case of true overdominance, be underestimated.

Finally, it should be mentioned that the parabolic interpretations given by Hayman (1954) for the homozygous diallel are also applicable to the p -heterozygous diallel.

In conclusion to this section, it can be stated that if it is very difficult to decide which method of analysis should be used (the (V_r, W_r) straight line test and the parabolic restriction test both give identical results, and so a decision must be based on knowledge of the material), and if the wrong method of analysis is applied, the conclusions deduced will not be too erroneous.

3. COMPLETELY HETEROZYGOUS SITUATION

It is certain that in animals, and sometimes in plants, the genotypes AA , Aa and aa will exist in the population at those loci under consideration.

(i) (V_r, W_r) graph

The model given by Dickinson and Jinks (1956) is used.

Suppose that there are two loci affecting the character(s) under investigation. Then there are nine possible genotypes:

$AABB$, $AaBB$, $aaBB$, $AABb$, $AaBb$, $aaBb$, $AAbb$, $Aabb$, $aabb$.

Assume that the frequencies of A and a are u_a and v_a respectively, and those of B and b , u_b and v_b respectively. Assume also that the parental population has been obtained by random mating so that, for instance, the frequencies of $AABB$, $AaBb$ and $aabb$ are $u_a^2 u_b^2$, $4u_a u_b v_a v_b$ and $v_a^2 v_b^2$ respectively. It can then be demonstrated that the values of (V_r, W_r) obtainable from the 9×9 diallel which can be set up using the above nine genotypes lie on a triangle, with the three genotypes $AABB$, $AaBb$ and $aabb$ forming its three corners. Further, the genotypes can be grouped together as follows:—

Group 1: $AABB$, $AAbb$, $aaBB$ and $aabb$

Group 2: $AABB$, $AaBB$, $AABb$ and $AaBb$

Group 3: $AaBb$, $aaBb$, $Aabb$ and $aabb$.

The Group 1, 2 and 3 genotypes lie, one group per side, on the

three sides of the triangle, which have slopes $\tan \theta_1$, $\tan \theta_2$ and $\tan \theta_3$ respectively. If mean frequencies u and v , and a mean dominance ratio z are assumed, it can be shown that

$$\tan \theta_1 = \frac{(1-2u)}{2}z + 1$$

$$\tan \theta_2 = \frac{2(1-u)}{2-z}z + 1$$

$$\tan \theta_3 = 1 - \frac{2uz}{2+z}$$

and that, unless there is excessive overdominance

$$\tan \theta_2 > \tan \theta_1 > \tan \theta_3.$$

The values of some slopes are given in table 1.

TABLE 1

Slopes of lines forming heterozygous triangle

$h/d = 1$

u	θ_1	θ_2	θ_3
0.25	51°20'	68°12'	39°48'
0.50	45°	63°26'	33°42'
0.75	36°52'	56°19'	26°34'

$h/d = 0.5$

u	θ_1	θ_2	θ_3
0.25	48°22'	56°19'	42°
0.50	45°	53°8'	38°40'
0.75	41°11'	49°24'	35°

(ii) Method of analysis for fully heterozygous data

There are two alternative methods. The first is a direct solution of equations, as outlined by Dickinson and Jinks (1956); the second a break-down of the data following the recognition of heterozygosity from the (V_r , W_r) graph.

For a completely random mating population

$$V_{ps} = \frac{1}{2}D + \frac{1}{8}H_1 - \frac{1}{16}H_2 - \frac{1}{4}F$$

$$\bar{V}_r = \frac{1}{8}D + \frac{1}{8}H_1 - \frac{1}{16}H_2 - \frac{1}{8}F$$

$$\bar{W}_r = \frac{1}{4}D + \frac{1}{8}H_1 - \frac{1}{8}H_2 - \frac{3}{16}F$$

$$V_{\bar{r}} = \frac{1}{8}D + \frac{1}{8}H_1 - \frac{1}{8}H_2 - \frac{1}{8}F$$

where

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

$$H_1 = \Sigma 4uvh^2$$

$$H_2 = \Sigma 16u^2v^2h^2$$

$$F = \Sigma 8uv(u-v)dh.$$

The above equations, which can be derived from the equations developed by Dickinson and Jinks (1956) by substituting the conditions for random mating, can be solved directly for D , H_1 , H_2 and F . These in turn enable information to be obtained about the various genetic parameters involved *i.e.* dominance ratio, the magnitude of $\bar{u}\bar{v}$, whether or not $\bar{u} > \bar{v}$, $\bar{v} > \bar{u}$, and if there is uni- or ambi-directional dominance.

The disadvantage of this method is that there is no check on the accuracy of the estimates since these are obtained from a "full fit" set of equations.

The alternative method does not suffer this disadvantage. It is referred to as the "triangulation" method and is dependent on the recognition of triangulation on the (V_r, W_r) graph.

It will be observed in part (i) of this section that the genotypes in Group 1 form a homozygous diallel, whereas those in Groups 2 and 3 are members of p -heterozygous diallels.

Thus, if there is recognisable triangulation, three separate analyses can be performed after partitioning of the results: one homozygous analysis and two p -heterozygous analyses. These lead to three estimates of the parameters which should compensate for the fact that, following such a subdivision of the data, the number of crosses within each analysis is small.

(iii) *Consequences of failure to detect full heterozygosity*

Theoretically, it should be possible to recognise the occurrence of full heterozygosity in the parental lines, since, as has just been shown, triangulation should be obtained on the (V_r, W_r) graph. It has, however, been found difficult in practice to detect heterozygosity. In addition, it is possible to fit a significant straight line of unit slope to the "heterozygous triangle" of points, and so the situation could easily arise (and, indeed, must have already done so in the case of the homozygous method) when the diallel analysis techniques might be applied to fully heterozygous data. The effects of so applying the two techniques have been evaluated and are summarised below.

Using the homozygous diallel analysis will result in the dominance ratio being underestimated unless there is true, excessive overdominance. Similarly, if $(\bar{u}\bar{v})_{\text{actual}} > \frac{1}{6}$, $\bar{u}\bar{v}$ will be underestimated and, if $(\bar{u}\bar{v})_{\text{actual}} < \frac{1}{6}$, $\bar{u}\bar{v}$ will be overestimated.

If the p -heterozygous method is used, the conclusions with regard to the mean product of the frequencies are identical to those for the mis-application of the homozygous methods. Those for the domin-

ance ratio are more complex and are best expressed mathematically. If the true dominance ratio is x then, if u and x are such that

$$\frac{x}{u} < (x^2 - 3x + 3)$$

the dominance ratio will be overestimated. If the dh do not have the same sign then, for $0 \leq u \leq \frac{1}{2}$, dominance is more likely to be overestimated and, if $\frac{1}{2} \leq u \leq 1$, it is less likely to be so.

Figures are given in tables 2 and 3 for the amount each method, wrongly applied to fully heterozygous data, underestimates the dom-

TABLE 2
Underestimates of dominance ratio when homozygous method is applied to data from fully heterozygous material

$\begin{array}{c} x \\ \backslash \\ u \end{array}$	0.25	0.50	0.75	1.0	1.5	2.0	3.0
0.0	55.6	60.0	63.6	66.7	71.4	75.0	80.0
0.1	43.6	48.5	52.6	56.2	61.2	66.5	72.9
0.3	28.6	32.4	36.1	39.5	45.8	51.3	59.9
0.5	21.2	22.2	23.6	25.5	30.2	35.5	45.8
0.7	21.2	17.8	15.0	12.9	11.8	14.9	28.5
0.9	31.2	23.1	13.6	2.5	-21.4	-32.3	7.0
1.0	42.8	32.3	20.0	0.0	-100.0	$-\infty$	0.0

TABLE 3
Underestimates of dominance ratio when p-heterozygous method is applied to data from fully heterozygous material

$\begin{array}{c} x \\ \backslash \\ u \end{array}$	0.25	0.50	0.75	1.0	1.5	2.0	3.0
0.0	50.0	33.3	42.9	50.0	60.0	66.7	75.0
0.1	1.2	18.0	30.1	39.0	48.3	60.0	70.1
0.3	-21.2	-1.0	13.6	24.6	43.6	50.7	63.6
0.5	-31.6	-12.0	2.8	14.6	31.8	43.7	58.7
0.7	-31.6	-16.5	-3.8	6.9	24.1	37.0	54.5
0.9	-17.6	-11.1	-4.9	1.2	13.9	27.4	50.9
1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

inance ratio. In deriving these estimates, it has been assumed that all u and v are equal at all loci, as are the contributions of d and h . It has also been assumed that all dh take a positive sign. The underestimates given are

$$\left[\frac{x-y}{x} \right] \cdot 100$$

where x is the actual dominance ratio, y the apparent one. When an

entry has a negative sign, it is an overestimate. The equations used in deriving this table are:

(1) homozygous method:

$$y^2 = \frac{x^2 + 6uvx^2}{4 + (1 - 2uv)x^2 + 4(1 - 2u)x}.$$

(2) *p*-heterozygous method:

$$\frac{1-y}{y^2} = \frac{1 - 2uvx^2 + (1 - 2u)x}{x^2 + 6uvx^2}.$$

4. APPLICATION

It should be made clear at the onset that a highly flexible method of analysis is being discussed. When it is suspected that the material is fully heterozygous for instance, an attempt should be made to apply all four methods of analysis *i.e.* the fully homozygous, the *p*-heterozygous, the fully heterozygous and the triangulation technique methods. The last two mentioned should give estimates of the true values of dominance ratio and gene frequencies; the first two give estimates which can be compared with the true estimates, and the comparisons can be checked using the formulæ or tables derived previously for cases where the homozygous and *p*-heterozygous methods are erroneously applied to fully heterozygous data.

Unfortunately, little data are available to which the methods discussed can be applied. Thornber Brothers Limited set up a diallel cross in 1962 between seven strains of chickens, but the lack of complete block replication makes analysis difficult. However, for purposes of illustration, the methods discussed will be applied to one of the traits they measured, namely total egg production over a period of nine months.

The results obtained for this trait are given in table 4. The values of V_r and W_r obtained from these are:

Strain	V_r	W_r	
A	78.1	80.0	
B	24.1	28.0	$V_{ps} = 180.2$
C	45.6	63.4	$\bar{V}_r = 56.9$
D	27.6	44.3	$\bar{W}_r = 64.3$
E	11.7	24.5	$V_r = 24.7$
F	110.4	107.1	
G	100.9	103.1	

When the values of (V_r, W_r) are plotted, there is some indication of triangulation and hence of heterozygosity.

TABLE 4
Egg production over nine months (means of reciprocals)

Strain	A	B	C	D	E	F	G
A	150.6	171.6	170.3	170.8	179.6	165.5	169.0
B	171.6	166.3	170.4	176.3	176.0	164.4	176.2
C	170.3	170.4	165.9	174.7	181.4	160.3	174.2
D	170.8	176.3	174.7	164.3	179.8	169.1	168.9
E	179.6	176.0	181.4	179.8	179.7	171.5	180.1
F	165.5	164.4	160.3	169.1	171.5	139.6	162.2
G	169.0	176.2	174.2	168.9	180.1	162.2	150.1

In the following discussions and evaluations, a value of $E_2 = 9.8$ will be used. Use will be made of the notation:

$$E'_2 = \frac{E_2}{n} + \frac{n-1}{2n}E_2 = \frac{n+1}{2n}E_2.$$

(i) *Erroneous application of the homozygous method of analysis*

$$V_{ps} = 180.2 - E_2 = 170.4$$

$$\bar{V}_r = 56.9 - E'_2 = 51.3$$

$$\bar{W}_r = 64.3 - E_2/7 = 62.9$$

$$V_r = 24.7 - E'_2/7 = 23.9.$$

Application of Jinks (1954) gives, for the homozygous method of analysis

$$\frac{H_1}{D} = 0.728, \text{ and so the measure of dominance ratio} = 0.85$$

$$\bar{u}\bar{v} = 0.221, \text{ which, since } F > 0, \text{ gives } \bar{u} = 0.33, \bar{v} = 0.67.$$

(ii) *Erroneous application of p-heterozygous method of analysis*

The values of V_{ps} , $\bar{V}_r$, $\bar{W}_r$, and V_r as given in the previous paragraph hold here.

Application of the p -heterozygous equations gives

$$\bar{u}\bar{w} = 0.221; \text{ i.e. } u = 0.33, \bar{w} = 0.67$$

$$\frac{1-y}{y^2} = \frac{11.6}{124.0}, \text{ where } y = \text{apparent measure of dominance ratio.}$$

The solution of this is $y = 0.92$.

(iii) *Application of triangulation technique*

If the strains are grouped together as follows, evidence is obtained of triangulation:

Group 1: A, B, F, G.

Group 2: B, C, D, E.

Group 3: C, F.

The fact that Group 3 contains only two strains is evidence, to

some extent, of correlated gene distributions. For the purposes of illustration, this will be disregarded, and only Groups 1 and 2 will be considered.

The evidence for triangulation is that, when the two 4×4 diallels corresponding to the above groupings are considered, better straight line fits are obtained for the resulting (V_r , W_r) values than for the full 7×7 .

Group 1. This group is considered to consist of homozygous material. Analysis of the 4×4 diallel which can be extracted from the initial data gives:

$$\begin{aligned} V_{ps} &= D + E_2 = 121.1 \\ \bar{V}_r &= \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + E_2' = 97.8 \\ \bar{W}_r &= \frac{1}{2}D - \frac{1}{4}F + \frac{1}{4}E_2 = 51.6 \\ V_r &= \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + \frac{1}{4}E_2' = 22.9. \end{aligned}$$

In this instance, $E_2 = 9.8$, $E_2' = 6.1$.

Solution of the above yields

$$\begin{aligned} D &= 111.3 \\ H_1 &= 281.2 \\ H_2 &= 281.1 \\ F &= 26.0. \end{aligned}$$

The values of H_1 and H_2 indicate equal numbers of dominant and recessive homozygotes in the parental population. This is supported by the low value of F .

Further $\frac{H_1}{D} = 2.53$, giving a dominance ratio = 1.59.

Group 2. This group is assumed to consist of p -heterozygous material. Thus the following can be obtained:

$$\begin{aligned} V_{ps} &= A + \frac{1}{4}B + E_2 = 51.2 \\ \bar{V}_r &= \frac{1}{4}A + \frac{1}{4}B - \frac{1}{4}C + E_2' = 29.1 \\ \bar{W}_r &= \frac{1}{2}A + \frac{1}{4}B - \frac{1}{4}C + \frac{1}{4}E_2 = 21.5 \\ V_r &= \frac{1}{4}A + \frac{1}{4}B - \frac{1}{4}C - \frac{1}{4}G + \frac{1}{4}E_2' = 10.0. \end{aligned}$$

Again, $E_2 = 9.8$, $E_2' = 6.1$ and so

$$\begin{aligned} A &= -15.8 \\ B &= 228.7 \\ C &= 121.1 \\ G &= 58.1. \end{aligned}$$

Denoting the dominance ratio by z :

$$\frac{1-z}{z^2} = \frac{A}{B} = \frac{15.8}{228.7}, \text{ which gives } z = 1.08$$

$\frac{\bar{u}\bar{w}}{\bar{B}} = \frac{G}{B} = 0.254$ which, although $\bar{u}\bar{w}$ cannot exceed 0.250, indicates equality of $\bar{u}$ and $\bar{w}$.

This is borne out by the values of C and B since it can be shown that, for $u = w = \frac{1}{2}$, $C = \frac{1}{2}B$.

Thus, the triangulation method indicates complete dominance, tending to over-dominance, with equal frequencies of loci genotypes in the groupings considered.

(iv) *Application of theoretical heterozygous technique*

Using the values of V_{ps} , $\bar{V}_r$, $\bar{W}_r$ and V_r given in (i) of this section and the equations derived for the fully heterozygous method (which assumes random mating), the following values are obtained:

$$D = 328.8$$

$$H_1 = 334.4$$

$$H_2 = 438.4$$

$$F = 33.6$$

$$\frac{H_2}{4H_1} \text{ gives no solution for } \bar{u}\bar{v}. \quad F \text{ indicates equality of } \bar{u}, \bar{v}.$$

$$\frac{H_1}{D} \text{ indicates complete dominance.}$$

(v) *Conclusions*

Despite some of the assumptions made, evidence of complete dominance has been obtained, although little can be said about the relative values of $\bar{u}$ and $\bar{v}$ except that they lie close to 0.5. It can be shown for the "two-sided" triangle obtained here that, when equal genotype frequencies occur in the groupings considered, the overall values of $\bar{u}$ and $\bar{v}$ have limits of $\frac{5}{8}$ and $\frac{3}{8}$ respectively. Thus, in all probability,

$$\frac{1}{2} \leq \bar{u} \leq \frac{5}{8}.$$

For h/d (i.e., x) = 1, table 2 gives, for $0.5 \leq u \leq 0.7$, a value of m (the underestimate of the dominance ratio) such that $25.5 \geq m \geq 12.9$. The value of the dominance ratio obtained by applying the homozygous method is 0.85 which, for a true value of unity, is an underestimate of 15 per cent., which thus lies in the limits predicted.

Similarly, table 3 gives, for the same range of $\bar{u}$, $14.6 \geq m \geq 6.9$. The value of the dominance ratio obtained by applying the p -heterozygous method is 0.92, an underestimate of 8 per cent., which again lies within the predicted limits.

The results obtained are remarkably consistent with those predicted and indicate the probable usefulness of the methods. They would also appear reasonable insofar as, with complete dominance and only a few generations of selection, the heterozygotes would be expected to be present at high frequencies.

5. SUMMARY

A theoretical investigation of the effect of non-homozygosity and multiple allelism in the parental lines on the diallel analysis procedure has been carried out.

1. The (V_r, W_r) graph is discussed and it is shown that, provided there are only two genotypes in the parental lines, for each locus affecting the trait under consideration, the points are on a line of unit slope. The triangulation obtained in the case of full heterozygosity is also described.

2. A method of analysis is developed for evaluating genetic parameters from data from partially heterozygous lines, *i.e.* when each locus is present in the form homozygote or heterozygote.

3. A method of evaluating parameters from data from fully heterozygous parental lines (each locus present in three genotypes) is discussed.

4. Comparisons are made of the various methods, and the errors likely to be introduced by making wrong assumptions about the homozygosity or otherwise of the parental lines are evaluated.

5. The methods of analysis are applied to some chicken data. Comparisons between the numerical results obtained agree closely with expectation from theoretical comparisons.

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