THE ANALYSIS OF GENETIC-ENVIRONMENTAL INTERACTIONS BY MEANS OF DIALLEL CROSSES

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ALTHOUGH it is a matter of importance both theoretically and practically, little is known about the constancy under different environmental conditions of the genetic components of continuous variation. This is not surprising, for study of the effects of environment upon the various genetic parameters required to specify continuous variation could not proceed until the parameters themselves were clearly defined and techniques had been developed for their detection or measurement. Recently, as a result of an expansion and generalization of the method of analysis of diallel crosses, JINKS (1952, 1955) has shown that the various statistics obtained from measurements of parents and their F_1 progeny in diallel crosses provide estimates of overall dominance, the relative dominance of parents, and the distribution of dominant and recessive alleles in the parental lines entering the diallel system. Even more important, the analysis permits the separation of certain types of non-allelic interaction from overdominance. Further extensions of the analysis and applications to a variety of experimental data (JINKS and HAYMAN 1953; HAYMAN 1954b, 1955; JINKS 1954, 1955) have demonstrated the usefulness of diallel crosses in the investigation of certain of the genetic components of continuous variation.

Diallel crosses may also be useful in the investigation of genetic-environmental interactions, and it is with this aspect of the analysis of diallel experiments that the present discussion is concerned. It will be shown that estimates of stability under different environmental conditions of certain genetic parameters can be obtained from diallel experiments replicated in time or in space.

THE ANALYSIS OF DIALLEL CROSSES

The analysis of diallel crosses has been discussed in detail elsewhere (HULL 1945; GRIFFING 1950; JINKS 1952, 1954; JINKS and HAYMAN 1953; HAYMAN 1954a, 1954b) and need only be summarized here. The analysis depends upon the estimation of the genetic parameters D , H_1 , H_2 , and F as defined by JINKS (1954), who follows the notation of MATHER (1949). Mean dominance is measured by the ratio H_1/D , i.e., the ratio of the weighted sums of h^2 and d^2 where h and d are the dominance and additive components of variation, respectively. F indicates whether dominant or recessive alleles are more frequent in the parents, being positive if dominant alleles are in excess. $H_2/4H_1$ provides an estimate of the mean value of uv , where u is the proportion of positive alleles and v the proportion of negative alleles, and $u + v = 1$. It has a maximal value of $\frac{1}{4}$ when all $u = v = \frac{1}{2}$.

The regression of W_r on V_r (the covariances and variances of parental arrays) provides a geometric representation of the degree of dominance and also permits the separation of true dominance from the spurious "dominance" caused by many types of non-allelic interaction. With no dominance, the variances and covariances

of arrays all estimate the point $(\bar{W}_r, \bar{V}_r) = (\frac{1}{2}D, \frac{1}{4}D)$ and there is, of course, no regression. With dominance, the regression line has unit slope. It intersects the W_r axis at the origin with complete dominance ($H_1 = D$), on the positive side with partial dominance ($H_1 < D$) and on the negative side with overdominance ($H_1 > D$). Most types of non-allelic interaction affect the regression line in a characteristic way, thus permitting their detection regardless of the degree of dominance. For example, complementary type of gene action increases V_r in relation to W_r , particularly for the more recessive arrays, leading to a regression line with slope less than unity.

The above relationships are not necessarily valid if (1) the inheritance is other than Mendelian and diploid, (2) the parental lines are heterozygous, (3) the genes are not independently distributed in the parents, and (4) more than two alleles exist at any one locus. The effects of non-validity of these assumptions have been considered by HAYMAN (1954b).

GENETIC-ENVIRONMENTAL INTERACTIONS

The fact that a standard error can be calculated for each of the above statistics makes possible the estimation of the significance of certain inter-environmental differences, e.g., whether mean dominance is the same in different seasons. However, a more general method of testing genetic-environmental interactions is possible from analysis of (1) the means and variances of the parents and (2) the variances and covariances of the arrays of the diallel table.

Heritable differences between the homozygous parents, in the absence of non-allelic interaction, must result from the additive effects of genes (D). Hence, parental lines differing significantly from each other must carry genes with different additive effects. Furthermore, constancy of the additive components of variation can be detected unambiguously by the parents $\times$ environments interaction item of an analysis of variance of parents. Significance provides evidence that they interact with environment, and non-significance is suggestive of the constancy of the additive effects under different environmental conditions. When non-allelic interactions are a feature of the genetic system, the situation is unambiguous if the parents $\times$ environments item is non-significant. If this item is significant, however, the conclusions cannot be clear-cut without evidence from analysis of the variances and covariances of the arrays of the diallel table because the significance could result from inconsistency of the additive effects, from inconsistency of the interactions between homozygous genes under the different environmental circumstances, or from both causes.

An analysis of variance of W_r and V_r from the diallel table provides further information about genetic-environmental interactions. But before this can be discussed, it is necessary to consider the genetic components of W_r and V_r . If a number of genes are independently distributed among several parental lines with alleles of positive and negative effect in the proportions u and v ($u + v = 1$), the covariance and variance of the r th array are

$$W_r = \Sigma 2 uvd(d \pm h)$$

$$V_r = \Sigma uv(d \pm h)^2$$

where negative signs correspond to positive alleles in the r th parent and vice versa. The difference $W_r - V_r = \sum uv(d^2 - h^2) = \frac{1}{4}(D - H_1)$, which is independent of the signs of the alleles in the parents. Asymmetry of distribution of alleles of positive and negative effects does not upset the relationship between W_r and V_r , i.e., the points on the (W_r, V_r) graph lie on a straight line regardless of the state of symmetry.

W_r is made up of terms in d^2 and dh , while V_r is made up of these same terms plus additional terms in h^2 . The relationship between W_r and V_r , therefore, varies only with the dominance components of variation. We have seen that a good test for the constancy of the additive components of variation is available from analysis of the parents. It is expedient, therefore, to minimize this component of variation in the analysis of W_r and V_r in order to improve the prospects of detecting interactions of dominance effects with environment. Dividing W_r and V_r by the variance of the parents ($V_p = D$) occurring in the same block accomplishes this result. This procedure has an additional advantage. It has been observed that basic variability fluctuates widely under different environments, tending to obscure between-environment comparisons of the genetic systems. Rescaling in the manner suggested alleviates this difficulty by placing the comparisons on similar scales.

Genetic significance of the components of variation

The genetic significance of the variances and covariances of arrays of a diallel experiment that has been replicated in time can be investigated by an analysis of variance with degrees of freedom as given in table 1. Two or more blocks of the diallel should be grown each year to permit error variance to be estimated from variation within years. The Years component of variation is calculated from the differences between the sums of $W_r + V_r$ over all arrays and blocks for each year. It therefore detects variation in $\bar{W}_r + \bar{V}_r$, i.e., $D + H_1 + F$ over years before rescaling or in $(D + H_1 + F)/D$ after rescaling. On the (W_r, V_r) graph the single points representing each year would therefore be expected to occupy the same position when environmental conditions under which the diallels were grown were identical. The Years component in the analysis of variance table should be non-significant under these circumstances. Significance of this component of variation can result from a change in response to environmental differences of one or any

TABLE 1
Components of variation and degrees of freedom for a diallel experiment replicated in time

Component of variation	Degrees of freedom
Years (environments).....	$y - 1^*$
Dominance.....	1
Years $\times$ Dominance.....	$y - 1$
Arrays.....	$a - 1$
Years $\times$ Arrays.....	$(y - 1)(a - 1)$
Dominance $\times$ Arrays.....	$a - 1$
Years $\times$ Dominance $\times$ Arrays.....	$(y - 1)(a - 1)$
Total.....	$2(y)(a) - 1$

* y and a denote the number of years (environments) and the number of arrays, respectively.

combination of D , H_1 , or F in unrescaled data. Thus, in a favorable season $D + H_1 + F$ would be expected to be larger than in an unfavorable season even though the ratio of additive effects to dominance effects remained unchanged. Rescaling by dividing W_r and V_r by the variance of the parents should, however, minimize environmental effects of this type. The most likely causes of significance of the Years component of variation (after rescaling) are differences in mean dominance.

The Dominance component of variation is calculated from the difference between the sum of W_r and the sum of V_r over all years, blocks, and arrays. From diallel theory it is clear that the magnitude of this difference is governed by the degree of dominance, the differences $\bar{W}_r - \bar{V}_r$ providing a measure of $D - H_1$ (see table 5). The Dominance component of variation can therefore be expected to be significant except when mean dominance is complete, at which point $\bar{W}_r = \bar{V}_r$ and $D = H_1$. The Years $\times$ Dominance component of variation clearly provides an estimate of the constancy of mean dominance in different years. Thus, for example, if $D = H_1$ in one year and $D = \frac{1}{2}H_1$ in another year, both the Dominance and the Years $\times$ Dominance components will be significant, the former because $\bar{W}_r \neq \bar{V}_r$ on the average and the latter because dominance is inconsistent over the two seasons.

The Arrays component of variation is calculated from the sums of $\bar{W}_r + V_r$ for each array over all years and blocks. This component of variation detects differences in rank along the regression line, i.e., in the dominance order of the parents (see table 5). With no dominance the points representing arrays all occupy the same position $(W_r, V_r) = (\frac{1}{2}D, \frac{1}{4}D)$. If dominance exists, the points scatter along the regression line at positions indicating the relative dominance of the genes of the parents. The Arrays component of variation therefore provides a test of the significance of differences in dominance among the parents entering the diallel experiment. The constancy of the dominance relationships among different parents is clearly tested by the Years $\times$ Arrays component of variation. For example, if two genes of equal additive effect govern a character and $h_a > h_b$, the dominance order will be: (1) $AABB$, (2) $AAbb$, (3) $aaBB$, (4) $aabb$. If the dominance of the Aa gene pair is reversed by a change in environment, the order will no longer be 1 2 3 4 but becomes 3 4 1 2. Under these circumstances, the Arrays item in the analysis of variance would be significant because dominance is operative. The Years $\times$ Arrays item should also be significant because the relative dominance of the parents changed with environment.

The last two components of variation, Dominance $\times$ Arrays and Years $\times$ Dominance $\times$ Arrays, provide tests for non-allelic interaction and for the constancy of such effects over environments, respectively. These items will be considered in detail later.

NUMERICAL EXAMPLE

Data with which to test this type of analysis have been kindly supplied by DR. J. L. JINKS. They consist of the flowering times from an arbitrary date of eight varieties of *Nicotiana rustica* and their $n^2 - n$ hybrids (including reciprocals), all grown in the experimental gardens of the University of Birmingham in 1951, 1952, and 1953. There were 64 plots each year. Each parent or hybrid was represented

TABLE 2

Variances and covariances of arrays for flowering time and height for 1951, 1952, and 1953 ($\times 10$)

Array	Flowering time											
	1951				1952				1953			
	Block 1		Block 2		Block 1		Block 2		Block 1		Block 2	
	W	V	W	V	W	V	W	V	W	V	W	V
1	522	376	320	276	183	245	140	254	1107	906	1089	862
2	199	70	118	49	74	56	72	66	407	221	440	225
3	904	804	591	543	232	306	179	228	1213	1220	1288	1173
4	493	415	258	164	104	75	111	102	248	186	413	220
5	212	63	103	56	44	25	57	48	128	184	319	166
6	405	165	270	109	154	141	166	184	1191	1064	1261	1074
7	410	204	394	217	37	20	48	48	281	92	254	75
8	219	57	73	26	27	38	40	83	406	172	463	180
Mean variance of parents	1207		896		203		196		1480		1519	

Array	Height											
	1951				1952				1953			
	Block 1		Block 2		Block 1		Block 2		Block 1		Block 2	
	W	V	W	V	W	V	W	V	W	V	W	V
1	414	1060	554	900	578	1143	506	907	936	1930	1039	1712
2	221	276	106	146	160	337	53	158	245	896	315	886
3	350	433	506	544	529	745	536	708	736	1029	901	1148
4	37	405	68	336	-122	261	-69	118	-101	456	20	763
5	307	457	493	606	303	306	330	345	722	1060	989	1447
6	398	715	537	586	436	569	473	602	905	1842	1245	2433
7	213	335	438	475	297	223	374	426	637	877	695	729
8	282	371	488	562	316	294	456	552	720	1075	877	1066
Mean variance of parents	329		550		461		511		560		819	

by 10 plants, grown in two plots of 5 plants, with one plot in each of two blocks. Table 2 contains the variances and covariances of arrays of the diallel table (multiplied by 10) and the mean variances of the parents (also multiplied by 10). The data for each of the three years were first analyzed in the manner described by JINKS (1952, 1954) and HAYMAN (1954a). Before analysis, each variance and covariance was rescaled by dividing by the mean variance of the parents occurring in the same block.

(W_r , V_r) graphs calculated from these data are given in figure 1. A striking anomaly of these graphs is the behavior of arrays 1 and 3 in 1952. JINKS (1954) has explained this anomalous behavior on the basis of environmental effects associated with a planting procedure peculiar to that season. When disturbances of this sort occur, or if sporadic non-allelic interaction is encountered, the offending hybrids can be eliminated from the analysis by missing plot technique as suggested by HAYMAN

FIGURE 1.—(W_r , V_r) graphs for flowering time for 1951, 1952, and 1953. Points represent the position of parental arrays in relation to the regression line of unit slope through the origin. See text for interpretation.

TABLE 3

Analysis of variance of the mean flowering times for the eight parental varieties in 1951 and 1953

Component of variation	d.f.	Sums of squares	Variance ratio	Probability
Years	1	152.25	11.46	0.01-0.001
Parents	7	12,801.37	137.60	<0.001
Years $\times$ Parents	7	1,281.20	13.77	<0.001
Error	16	212.58		

(1954b). This procedure permits the remaining entries to be analyzed and the information from them to be salvaged. Of course, no information is obtained from the hybrids that were eliminated. Rather than complicate the present discussion by an adjustment of this sort, it should be sufficient for illustrative purposes to omit completely the 1952 data and focus attention on the results of 1951 and 1953.

The (W_r , V_r) graphs of figure 1 for those years reveal that the pattern of inheritance of flowering time is one of partial dominance uncomplicated by non-allelic interaction or non-validity of any of the assumptions stated earlier.

The first step in the investigation of genetic-environmental interactions between 1951 and 1953 consisted of an analysis of the means of the parents for the two years as shown in table 3. The significance of the years item has no specific genetical interpretation, for the planting dates were not the same in the two years. Indeed, even had the planting dates been the same, any of a host of environmental factors could have caused the observed difference in the mean flowering dates for the two seasons. The significance of the parents item, however, is direct evidence that certain parents (actually 5 out of 8) flowered at different times on the average over the two seasons, and must therefore carry alleles with different additive effects (since non-allelic interaction is apparently not involved). The flowering order of the parents was 7 8 5 6 2 4 1 3 in 1951 and 7 8 5 2 4 1 6 3 in 1953. Only one shift was significant, namely, that of parent 6 relative to all other parents. It may therefore be concluded that the additive effects of the genes of all the parents except No. 6 were stable over the two seasons.

Turning to the analysis of the variances and covariances of the arrays of the diallel table, it is apparent from the Years item in table 4 that there was a real difference between $\bar{W}_r + \bar{V}_r$ in the two years. Geometrically, this indicates that the point representing the mean for 1953 lies on the regression line at a position farther from the origin than the comparable point for 1951. As we shall see below, mean dominance was similar for the two years. Hence, the significant variance ratio for years probably resulted from failure of the rescaling to equalize completely the mean additive effects of the genes governing flowering time.

The significance of the Dominance item shows that $D \approx H_1$ i.e., that mean dominance over the two years was not complete. (As we have seen, the regression lines for 1951 and 1953 each suggest partial dominance). The non-significance of the Years $\times$ Dominance item shows that the regression lines representing the two years occupy the same positions, or in other words, that the ratio of H_1/D was consistent in 1951 and 1953.

TABLE 4
Analysis of variance of W_r and V_r for flowering time for 1951 and 1953

Component of variation	d.f.	Sums of squares	Variance ratio	Probability
Years.....	1	0.2265	119.21	<0.001
Dominance.....	1	0.1846	97.16	<0.001
Years $\times$ Dominance.....	7	0.0001		
Arrays.....	7	2.8856	216.95	<0.001
Years $\times$ Arrays.....	7	0.7446	55.95	<0.001
Dominance $\times$ Arrays.....	7	0.0209	1.53	>0.20
Years $\times$ Dominance $\times$ Arrays.....	7	0.0130	0.95	>0.20
Error.....	32	0.0631		

Finally, the significance of the Arrays component of variation indicates that certain of the parents did differ from one another in dominance. In fact, 6 of the 8 parents differed significantly from each other ($P < 0.01$). Furthermore, the significance of the Years $\times$ Arrays item shows that the points representing the 8 parents moved relative to one another up or down the regression line, i.e., that the parents did not maintain the same dominance relationships. In 1951 the dominance order was 8 5 2 6 7 4 1 3, but in 1953 it had become 7 5 4 2 8 1 6 3. Of the 28 comparisons possible, all except 7 were significant ($P < 0.01$). The most stable arrays were the highly dominant ones, Nos. 2, 5, and 8, and the most recessive, No. 3. The most unstable array was No. 6, varying as it did from one of the more dominant in 1951 to recessiveness in 1953. Arrays 1, 4, and 7 were moderately unstable in their dominance relationships. The method is clearly quite sensitive in detecting changes in dominance order.

The results with the flowering-time data thus suggest that the additive effects of genes, as measured by analysis of the parental means, were quite stable in the two seasons. Dominance relationships among various parents were much affected by the play of environment. But the shifts in dominance that occurred among the individual parents balanced one another, since they did not upset the mean dominance relationships over all arrays. The non-significance of the Dominance $\times$ Arrays item provides additional evidence that non-allelic interaction is unimportant in the inheritance of flowering time.

ANALYSIS IN THE PRESENCE OF NON-ALLELIC INTERACTION

The form of the (W_r , V_r) graphs for flowering time suggests that the assumptions, enumerated above, upon which the diallel analysis is based, were fulfilled for that character in 1951 and 1953. Under those circumstances the method illustrated was capable of detecting a variety of genetic-environmental interactions. The method detects non-allelic interaction and other disturbances when they are a sporadic feature of the genetic system, and it provides procedures whereby the offending hybrids can be eliminated and the remainder analyzed. This raises the question of the interpretation of genetic-environmental interactions when epistasis is a regular feature of the genetic system. Obviously, a model based upon d and h will no longer

be adequate, but additional parameters representing interactions between loci will be required.

The development by several workers (COCKERHAM 1954; ANDERSON and KEMPTHORNE 1954; HAYMAN and MATHER 1955) of a system of notation permitting non-allelic interactions to be described in a general way provides a method of approach to this problem. In HAYMAN and MATHER'S notation the genotypes $AABB$, $AAbb$, $aaBB$, and $aabb$ have the following phenotypes:

$$\begin{array}{ll} AABB & d_a + d_b + i_{ab/} - \frac{1}{2}j_{a/b} - \frac{1}{2}j_{b/a} + \frac{1}{4}l_{/ab} \\ AAbb & d_a - d_b - i_{ab/} - \frac{1}{2}j_{a/b} + \frac{1}{2}j_{b/a} + \frac{1}{4}l_{/ab} \\ aaBB & -d_a + d_b - i_{ab/} + \frac{1}{2}j_{a/b} - \frac{1}{2}j_{b/a} + \frac{1}{4}l_{/ab} \\ aabb & -d_a - d_b + i_{ab/} + \frac{1}{2}j_{a/b} + \frac{1}{2}j_{b/a} + \frac{1}{4}l_{/ab} \end{array}$$

where d_a and d_b denote the additive effects of genes a and b , $i_{ab/}$ the interaction between d_a and d_b , $j_{a/b}$ and $j_{b/a}$ the interactions between d_a and h_b and d_b and h_a respectively, and $l_{/ab}$ the interaction between h_a and h_b . With all classical types of interaction $i_{ab/}$, $j_{a/b}$, $j_{b/a}$ and $l_{/ab}$ are equal. Using i to denote the several types of interaction, the variances and covariances of a diallel of the four genotypes given above are shown in table 5.

Generalization over many genes does not affect the additive (d) or dominance (h) components of variation in any fundamental way, but the interaction components (terms involving i) become very complex in multigenic models. A full investigation of diallel analysis of multigenic models has not been made. It is of interest, however, that the classical types of interaction give the same pattern of results for 3 and 4 gene models as with the digenic model.

The increased complexity of W_r and V_r caused by epistasis makes the genetic interpretation of the components of variation of the analysis of variance table considerably more difficult. Thus, the Years component of variation is now influenced not only by changes in dominance but also by changes in non-allelic interactions, assuming that rescaling has eliminated inter-seasonal differences in the additive effects of genes (see table 5). Non-significance of the Years item can be taken as evidence that H_1 , F , and non-allelic interactions are stable and the rescaling was effective. Significance indicates that one or more of these postulates is incorrect.

TABLE 5

Covariances and variances of arrays of a two-gene, four-line diallel experiment where $i_{ab/} = j_{a/b} = j_{b/a} = l_{/ab}$, denoted by i , and $u = v$

	W_r	V_r
$AABB$	$2d_a^2 + 2d_b^2 - 2d_a h_a - 2d_b h_b - d_a i - d_b i + h_a i + h_b i$	$d_a^2 + d_b^2 + h_a^2 + h_b^2 - 2d_a h_a - 2d_b h_b$
$AAbb$	$2d_a^2 + 2d_b^2 - i^2 - 2d_a h_a + 2d_b h_b - d_a i + d_b i + h_a i - h_b i$	$d_a^2 + d_b^2 + h_a^2 + h_b^2 + i^2 - 2d_a h_a + 2d_b h_b + 2d_b i + 2h_b i$
$aaBB$	$2d_a^2 + 2d_b^2 - i^2 + 2d_a h_a - 2d_b h_b + d_a i - d_b i - h_a i + h_b i$	$d_a^2 + d_b^2 + h_a^2 + h_b^2 + i^2 + 2d_a h_a - 2d_b h_b + 2d_a i + 2h_a i$
$aabb$	$2d_a^2 + 2d_b^2 + 6i^2 + 2d_a h_a + 2d_b h_b - 3d_a i - 3d_b i - h_a i - h_b i$	$d_a^2 + d_b^2 + h_a^2 + h_b^2 + 6i^2 + 2d_a h_a + 2d_b h_b - 2d_a i - 2d_b i - 2h_a i - 2h_b i$

The Dominance component of variation is no longer concerned exclusively with mean dominance but is also influenced by non-allelic interactions (table 5). Its significance is evidence either that dominance is not complete, or that epistasis is involved, or both. The Years $\times$ Dominance item tests the constancy of mean dominance effects and/or epistatic effects in different seasons, non-significance suggesting stability.

The Arrays component of variation can be non-significant only if all dominance and epistatic effects of the genes are zero (table 5). Significance of this component is indicative of either significant dominance and/or non-allelic interactions. The Years $\times$ Arrays item tests the stability of mean dominance and non-allelic interaction effects for each parent over seasons, non-significance again indicating stability.

The Dominance $\times$ Arrays component of variation is independent of fluctuations in the additive and dominance effects of genes with classical types of interaction systems (table 5). Since differences in $W_r - V_r$ for arrays can occur only if $i \neq 0$ in such systems, significance of the Dominance $\times$ Arrays component provides evidence that epistasis is a feature of the genetic system. The Years $\times$ Dominance $\times$ Arrays item clearly tests whether the expression of the non-allelic interaction is the same in different environments.

In a two-gene four-parent model with $d_a = d_b$ and $h_a = h_b$, the sums of squares for arrays is

$$8d^2h^2 + 6d^2i^2 - 8d^2hi + 20dhi^2 - 12di^3 + 3h^2i^2 - 9hi^3 + \frac{27}{4}i^4$$

and the Dominance $\times$ Arrays sums of squares is

$$h^2i^2 + hi^3 + \frac{1}{4}i^4.$$

If $i = 0$, it follows that the ratio of the mean square of arrays to the mean square of Dominance $\times$ Arrays will not differ significantly from unity provided that h also is zero. The ratio will, however, increase in magnitude as dominance increases. If $h = d$ and i has a positive value, as with recessive epistasis or complementary gene action (HAYMAN and MATHER 1955), the variance ratio will be small. If i has a negative value—as with duplicate type gene action, dominant epistasis, or gene action of the recessive suppressor type—the ratio will be very large. It is, of course, possible to calculate expected values for this ratio for types of non-allelic gene action other than the classical types considered above. Over-duplicate and under-complementary types, for example, give very large and very small ratios, respectively.

NUMERICAL EXAMPLE

The analysis will be illustrated using height data taken from the same plants as the flowering time data. The (W_r, V_r) graphs for height for 1951, 1952, and 1953 are given in figure 2, from which it will be noted that complementary type of gene action appears to be a constant feature of the inheritance of height. As a first step in the interpretation of the variability, an analysis of variance was performed on the

FIGURE 2.—(W_r , V_r) graphs for height for 1951, 1952, and 1953. Points represent the positions of parental arrays in relation to the regression line of unit slope through the origin. See text for interpretation.

heights of the parents (table 6). The Years item was significant, and, in fact, the mean height was different for each of the three years. It can, therefore, be concluded that the absolute values of the additive effects and/or the interactions between homozygous loci (interactions of the i_{ab} type) altered with environmental changes. The 8 parents formed 4 groups with respect to mean height over the three years, an indication of diversity with respect to the d and/or i_{ab} effects of the genes of several parents. The Parents $\times$ Years item was also significant. In fact, the only parents

TABLE 6

Analysis of variance of the mean heights for eight parental varieties in 1951, 1952, and 1953

Component of variation	d.f.	Sums of squares	Variance ratio	Probability
Years.....	2	6,168.75	224.31	<0.001
Parents.....	7	7,620.99	79.17	<0.001
Years $\times$ Parents.....	14	1,150.11	5.97	<0.001
Error.....	24	330.10		

that behaved consistently relative to one another were 1-3, 2-4, 3-8, 4-5, 4-8, 5-6, and 5-8. This provides evidence that d and/or i_{ab} type interactions were quite labile in response to environment.

The analysis of variance of W_r and V_r for the three years is given in table 7. From the significance of the Years item it can be seen that a real difference existed between $\bar{W}_r + \bar{V}_r$ over the three years. This might be interpreted as indicating that mean dominance or epistatic effects altered in each year, although other causes are possible as we have seen earlier.

The Dominance item is also highly significant. This would be expected if the degree of dominance is other than complete and/or non-allelic interaction is involved. The regression line has a slope of less than unity. That this is due to epistasis is supported by the significance of the variance ratio for the Dominance $\times$ Arrays component of variation.

The Years $\times$ Dominance item provides a measure of the stability of the mean effects of dominance and non-allelic interaction over years, its variance ratio in the present instance suggesting moderate instability. It should be noted that the Years $\times$ Dominance $\times$ Arrays item is non-significant, an indication that epistatic effects were stable over years. By thus eliminating instability of epistatic effects, shifts in mean dominance effects seem to be identified as responsible for the significance of the Years $\times$ Dominance component of variation.

The Arrays component is significant, and, in fact, comparisons between the 8 arrays showed them all to differ significantly from one another. The 8 points representing the mean values for the arrays over the three years thus occupied different positions on the regression line, i.e., were scattered along the regression line at intervals sufficiently great to be significant. It may therefore be concluded that the 8 parents are all unique with respect to the dominance and/or epistatic effects of the genes they carry.

The stability of the dominance and epistatic effects of genes of the individual parents is tested by the Years $\times$ Arrays component of variation. It is not significant, which can be interpreted geometrically as indicating that the points for arrays retained their positions relative to one another along the regression line. The genetical interpretation is one of stability of the h and i effects (recalling that i denotes general interaction) of the genes of the parents in the three environments. Thus, although changes in h and i among individual parents were not great enough to result in significance of the Years $\times$ Arrays or Years $\times$ Dominance $\times$ Arrays items, the fact that h and/or i were not completely stable is attested by the sig-

TABLE 7

Analysis of variance of W_r and V_r for height for 1951, 1952, and 1953

Component of variation	d.f.	Sums of squares	Variance ratio	Probability
Years.....	2	5.4498	25.87	<0.001
Dominance.....	1	6.7109	63.78	<0.001
Years $\times$ Dominance.....	2	0.9504	4.52	0.01-0.001
Arrays.....	7	20.6132	27.95	<0.001
Years $\times$ Arrays.....	14	2.4700	1.67	>0.20
Dominance $\times$ Arrays.....	7	2.7402	3.72	0.01-0.001
Years $\times$ Dominance $\times$ Arrays.....	14	0.7796	0.53	>0.20
Error.....	48	5.0525		

nificance of their summed effects, as measured by the Years $\times$ Dominance item. The non-significance of the Years $\times$ Dominance $\times$ Arrays item provides direct evidence that i was stable over years. The combined evidence suggests, therefore, that small changes must have occurred in h and, furthermore, that they were non-compensating or unidirectional changes such that their summed effects over all arrays were large enough to result in significance of the Years $\times$ Dominance component of variation. It can be seen from table 7 that the components of variation that are sensitive to changes in dominance effects all had small variance ratios, thereby suggesting comparative stability of dominance in the three environments under consideration, even though the variance ratios sometimes were large enough to be significant.

It has already been noted that the Dominance $\times$ Arrays and Years $\times$ Dominance $\times$ Arrays items show non-allelic interaction to be involved in the inheritance of height and that the pattern of the epistasis was nearly identical in the three seasons. The (W_r , V_r) graph suggests that the type of non-allelic interaction involved was complementary in nature. The ratio of the mean squares of Arrays and Dominance $\times$ Arrays was 7.52, a ratio of the order of magnitude expected if i had a positive value. Among the classical types of interaction, positive values of i occur with recessive epistasis or complementary type of gene action. This analysis therefore leads to the same conclusion as the (W_r , V_r) graph.

Re-examination of the flowering-time data for 1951 and 1953, where a genetic system featuring partial dominance and no epistasis was postulated from the (W_r , V_r) graph, proved to be illuminating. In those two years the Arrays/Dominance $\times$ Arrays mean square ratios were 68.0 and 141.9, ratios of the general magnitude expected with partial dominance.

SUMMARY

In the genetical description of continuous variation, the phenotypic effects of genes can be specified in many cases by three types of parameters, d , h , and i , denoting the increments due to additive effects of genes, dominance, and non-allelic interactions, respectively. An extension of the analysis of diallel crosses is presented which permits an assessment of the stability of the values assumed by d , h , and i under different environmental circumstances.

Application of the method to date of flowering and height data for intervarietal hybrids of *Nicotiana rustica* suggested that non-allelic interaction was unimportant in the genetic control of the former but a regular feature of the genetic control of the latter character. For date of flowering the additive genetic effects were comparatively stable, but the dominance effects of genes appeared to be quite unstable in different environments. In the genetic control of height non-allelic interaction of a complementary type was inferred, and it proved to be quite stable in different environments. Dominance relationships in the genetic control of height appeared to shift only moderately with environmental changes, but the additive effects of genes controlling height were altered drastically by environmental changes.

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