

The Genetical Basis of Heterosis

In a previous communication (Jinks and Hayman 1953) a new method for the analysis of diallel crosses, based on the partitioning of D and H as described by Mather (1949), was put forward and its application to three sets of maize yield data described.

In this method dominance is measured by the ratio H_1/D . When this is zero there is no dominance, when it is equal to 1 there is complete dominance, and when it is greater than 1 there is over-dominance. In all three sets of maize data there was a high degree of apparent overdominance, i.e., H_1/D significantly greater than 1. Furthermore, all the data showed suggestions of interaction between non-allelic genes. The data of Kinman and Sprague, which was the most complete of the sets of data analysed, consisted of a 10 by 10 F_1 diallel and the F_2 progeny of these F_1 families. In these data the interaction was traced to the progeny of specific inbred lines, by the regression of array covariance on array variance. The interacting lines were mainly B_2 , and to a lesser extent Hy and Oh07.

A further test of interaction has now been applied, namely, the F_2 scaling test (Mather 1949). For this purpose the diallel crosses can be separated into the individual crosses each consisting of the two parents, an F_1 mean and an F_2 family mean. The expectations in terms of d , h and the mid parent M being

$$P_1 = M + d\Sigma \quad (\Sigma d \text{ refers to the balance of the genes in opposition})$$

$$P_2 = M - \Sigma d$$

$$F_1 = M + \Sigma h$$

$$F_2 = M + \Sigma 1/2h$$

so that for each cross of the diallel table $1/4P_1 + 1/4 P_2 + 1/2F_1 - F_2 = 0$ in the absence of non allelic interaction. One can, therefore, test for non additivity of gene action by testing this equality. For greater accuracy the modified scaling test proposed by Cavalli (1953) was used. The test consisted of estimating by weighted least squares the three parameters Σd , Σh and M , taking as weights the reciprocals of the squared standard errors of each generation mean. These parameters can then be tested for consistency over generations by a χ^2 for one degree of freedom.

Applying this test of additivity of gene action to Kinman and Sprague's data we find that the inbred lines fall into six groups, A, B, C, D, E and F, such that an A parent interacts with a B but neither of these interacts with any of the others, similarly C interacts with D, while E interacts with C and F.

A	B	C	D	E	F
Hy	R46	B2	WF9	Oh04	K159

This ties up as well as can be expected with the F_1 regression test for non-allelic gene interaction, which picked out the array B2 as the main source of interaction, since B2 interacts with four other inbred lines, i.e., groups D and E. In view of the widespread nature of the interactions it is not surprising that the F_1 method failed to detect all the interaction present since it depends to a large extent on different arrays showing different intensities of interactions.

The mean yield of the F_1 families showing genic interaction is 90.2748 compared with 77.2971 for the non interacting F_1 s, the mean of the parents giving rise to these F_1 s being 29.4905 and 27.9103 respectively. On the average, therefore, the F_1 families showing genic interaction yield 13 bushels per acre more than those showing no interaction. It would thus appear that although combining ability may be due to the operation of dominance in the F_1 families, genic interaction must be at the root of the special combining ability which leads to outstanding F_1 families. It may prove worthwhile to extend to all existing inbred maize lines this type of classification into interacting pairs, described here for those used by Kinman and Sprague.

A similar situation has been met within a diallel between *Nicotiana rustica* varieties (Jinks 1954). Here the apparent overdominance for the character height, i.e. $H_1/D > 1$, was traced to one pair of interacting groups of lines, Group A including 2 and 4, and Group B including lines 1, 3 and 6, out of 8 original lines used. In F_1 s grown over three seasons 2, 4, 1 and 6 were picked out by the F_1 regression test, while for the last two seasons all the interacting lines were picked out by the scaling test, using parents, F_1 , F_2 and backcross family means. The same genetical situation has also been found in a variety of other data (Table 1).

Table 1.

Source	Character			
	Flowering time	Height	Yield	Shape indices
N. rustica 1950-53 F_1 , F_2 and B (Jinks 1954)	$H_1 = 0.50 - 0.56$ No genic interaction	$= 2.6 - 4.0$ genic interaction		
Maize F_1 and F_2 (Kinman and Sprague 1945)			$H_1/D = 8.5 - 7.4$ genic interaction	
Galeopsis sp. 1947-50 F_1 s (Haberg.)	1. $H_1/D = 0.12 - 0.24$ No genic interaction	$= 1.64 - 2.04$ genic interaction		
	2.	$= 6.6$ genic		

3. interaction
 = 0.61
 no genic
 interaction

Rye
 F_1 s
 (Haberg.)

$H_1/D = 70.0$
 genic
 interaction

Egg Plant
 F_1
 (Sokohi 1953)

$H_1/D = 0.49$
 no genic
 interaction

$H_1/D = 0.15 -$
 0.4
 no genic
 interaction

In every one of the cases where heterosis is due to apparent over-dominance the presence of genic interaction has been proved from the data. In the one case where it has been possible to reanalyse after eliminating the interaction, viz. *N. rustica* data, only complete dominance, i.e. $H_1/D = 1$, remained. The evidence suggests that the heterosis, which is of such importance to plant breeders, results from interactions between non-allelic genes brought together in the hybrid F_1 .

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