HETEROSIS AND SELECTION IN BARLEY

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CURRENT theories hold that the genetic basis of heterosis is dominance and nonallelic interaction together with the distribution of genes in the parental lines. Whether defined as the difference between the mean of an F_1 family and that of its better parent, or as the difference between the F_1 mean and the two parental means, the expected difference can be expressed in terms of genetic parameters for additivity (d) and dominance (h) (MATHER 1949), and the non-allelic interaction parameters (i , j and l) of HAYMAN and MATHER (1955). If two homozygous lines, P_1 and P_2 , differ in k loci, there are $\frac{1}{2}k(k-1)$ loci pairs. Defining the interaction parameters according to the F_∞ -metric (cf. VAN DER VEEN 1959), and assuming no trigenic or higher order interaction, the parental phenotypes are

$$\frac{\bar{P}_1}{\bar{P}_2} = \pm \sum_{a=1}^k \theta_a d_a + \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [i_{ab}]_j$$

where θ is a variable which can take the values 1 and -1 . The suffixes a and b in the last term refer to loci a and b of pair j . The sign of each term will depend on the degree to which the genes are associated or dispersed and on the magnitude of the individual gene effects. The mean of F_1 becomes similarly

$$\bar{F}_1 = \sum_{a=1}^k h_a + \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [l_{ab}]_j$$

Using these expressions, the difference between F_1 and the better parent is

$$\bar{F}_1 - \bar{P}_{max} = \sum_{a=1}^k h_a + \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [l_{ab}]_j - \sum_{a=1}^k \theta_a d_a - \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [i_{ab}]_j$$

and the difference between F_1 and the midparent

$$\bar{F}_1 - \bar{P}_m = \sum_{a=1}^k h_a + \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [l_{ab}]_j - \sum_{j=1}^{\frac{1}{2}k(k-1)} [\theta_a \theta_b]_j [i_{ab}]_j$$

These expressions show clearly that the deviation of F_1 from the midparent value depends on nonadditivity of the genes involved, and the components of the difference between F_1 and the better parent is d , h , i and l (cf. JINKS and JONES 1958).

Only the d and i effects can be fixed by selection, i.e. the additive effect and the effect of homozygous-homozygous interaction. The dominance effect and the effect of heterozygous-heterozygous interaction will vanish with infinite inbreeding. How far it is possible to select homozygous lines equal to or higher in performance than the F_1 depends on the magnitude of the components and on the

linkage relations. If, for instance, the difference $\bar{F}_1 - \bar{P}_{max}$ is mainly due to over-dominance, it is clearly not possible to select lines which are equal to F_1 .

In a previous work (AASTVEIT 1961) a number of quantitative characters in barley were analysed genetically. Among the characters most thoroughly analysed, straw length, plant weight and grain yield per plant showed significant deviations from the better parent. A further investigation on the genetic variation in the progeny from one of the crosses was carried out by growing parents, F_1 , F_2 , F_3 and backcrosses simultaneously. In order to verify the conclusions drawn from the analysis of early generations, a selection experiment was started and has been continued up to F_8 . In 1962, a number of selected lines were compared with the parents and F_1 . The present paper reports the results of selection and comparisons with F_1 .

EXPERIMENTAL RESULTS

Heterosis: The parental lines [Maskin (P_1) and Opal B (P_2)] and their F_1 have been compared in five characters over five years. In the first years, reciprocal families were grown. No reciprocal differences were found; the F_1 seeds used in later years are therefore obtained from one-way crosses. A randomised block design with two to four replications was used in all experiments. Further details concerning the experimental technique are given in the paper cited above. Table 1 gives the annual means of parents and F_1 . In length of straw, plant weight and grain weight per plant the mean of F_1 was in all years higher than that of the better parent.

Tested against the pooled error (over years), the parental lines differed significantly in three characters, whereas the F_1 mean differed significantly from the mean of the parental lines in all characters (Table 2). A significant family $\times$ year interaction was found in the case of four characters. The sum of squares for this item was broken up into a component for interaction of parents with years and another component for the interaction of F_1 *vs.* parental mean $\times$ year. These items were significant for three characters each, showing that genotype-environment interaction is a component of heterosis which should not be neglected. Even when tested against the appropriate family $\times$ year interaction item, F_1 deviated significantly from the better parent in straw length and grain yield per plant (Table 1). For plant weight this difference was almost significant at the 5 percent level.

The selection experiment: The first selection was made in 1957 on the basis of F_3 family means. The selection procedure in the first generations was described in detail (AASTVEIT 1961). Among the lines selected for grain yield, two have been compared with the parents over six generations. Figure 1 gives the relative figures. The values for F_3 refer to family means. The lines 3-10-7 and 6-2-2 are both derived from one individual F_3 plant, and as far as the comparisons in Figure 1 are concerned, no reselection has been done. The plot size has been increased as more seed was available. The data from F_7 and F_8 are from ordinary variety trials.

TABLE 1
Annual means of two inbred lines and their F_1

Year	Length of straw (cm)		Heading time (days)		Number of ears per plant		Plant weight (g)		Grain weight per plant (g)	
	P_1	F_1	P_1	F_1	P_1	F_1	P_1	F_1	P_1	F_1
1955	47	54	56.0	57.0	1.2	2.7	2.6	2.3	6.0	3.5
1956	101	114	55.0	58.5	2.5	5.8	5.8	10.4	24.8	12.5
1957	88	101	57.5	60.0	3.7	5.9	7.2	18.3	29.0	21.1
1958	82	102	43.5	46.5	..	..	..	34.6	54.5	54.3
1962	64	82	61.8	65.0	3.8	6.7	9.5	18.4	27.4	23.9
Average	76.4	90.6	54.8	57.4	2.8	5.3	6.3	16.8	28.3	23.1
$F_1 - P_{max}$	14.2***						5.2		0.9**	

** $P < 0.01$. *** $P < 0.001$.

TABLE 2
Results of an analysis of variance of the data in Table 1

Item	Degrees of freedom	Length of straw	Heading time	Plant weight	Grain weight per plant	Degrees of freedom	No. of ears per plant
Between families	2	***	***	***	*	2	***
1) Between parents	1	..	***	**	.	1	*
2) F_1 vs. parental mean	1	***	**	***	*	1	***
Family $\times$ year	8	**	*	*	.	6	*
1) Parents $\times$ year	4	*	*	.	.	3	**
2) F_1 vs. parental mean $\times$ year	4	**	*	*	.	3	.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Averaged over all generations, Line 3-10-7 yielded 23 percent more than the better parent, while Line 6-2-2 yielded 27 percent less than the lowest parent.

Comparison of selected lines with the parents and F_1 : In 1962 one experiment was conducted with the two parents, F_1 and six selected F_7 and F_8 lines (Table 3). Line 6-2-2 was the same as the one for which results are presented in Figure 1. In F_5 Line 3-10-7 was reselected, and the seed used in the experiment was derived

FIGURE 1.—Means of parents and two selected lines over six generations.

TABLE 3

Comparison of parents, F_1 and six selected F_7 and F_8 lines

Family		Straw length (cm)	No. of ears per plant	Heading time (days)	Plant weight (g)	Grain weight (g)
Maskin	(P_1)	64.0	3.8	61.8	18.4	2.75
Opal B	(P_2)	65.8	9.5	68.7	23.9	4.13
	F_1	81.5	6.7	65.0	27.4	4.58
6-2-2	(F_8)	76.2	6.0	61.2	16.0	2.68
3-10-7-10	(F_8)	62.5	5.0	68.7	24.1	5.68
3-10-7-5	(F_8)	61.0	6.2	66.5	23.0	4.98
3-6-9	(F_7)	74.8	7.3	73.5	33.0	3.58
7-3-1	(F_7)	49.8	5.2	61.2	13.9	2.23
3-5-7	(F_7)	71.0	5.6	65.0	23.8	4.45
S_m		1.27	0.55	0.61	2.12	0.51

from the second generation of individual plant progenies from this reselection (Lines 3-10-7-5 and 3-10-7-10). Lines 3-6-9 and 7-3-1 were included because of their extremeness in plant weight, whereas Line 3-5-7 previously had proved to possess high yielding capacity. The experimental design was four randomised blocks. Each plot had two rows of 25 hand-sown seeds, set 15 cm apart. All character records were taken on individual plants. Table 3 shows almost the same relation between the parental lines and F_1 as in previous experiments. In grain yield, the lines 3-10-7-5 and 3-10-7-10 both exceeded F_1 , whilst Lines 6-2-2 and 7-3-1 did not reach the lowest parent. The lines 3-6-9 and 7-3-1 were most extreme in plant weight, both falling outside the range of parents and F_1 . In straw length, Line 7-3-1 was far below the lowest parent, but none of the lines was as high as the F_1 .

It is interesting to note the lack of correlation between characters. Line 3-6-9, for example, is one of the highest in straw length, number of ears per plant, heading time and plant weight, but one of the lower in grain yield per plant.

DISCUSSION

From the analysis of early generations it was concluded that dominance as well as nonallelic interaction are important components of the genetic variation of the characters in question (AASTVEIT 1961). A strong and consistent interaction was found in grain weight per plant. On the basis of various linear combinations of generation means (scaling tests), it was concluded that this interaction was mainly of the *i*-type, i.e. fixable interaction. The analysis indicated that although it was present, nonallelic interaction of genes governing the other characters must have been of minor importance. Heterosis in those characters must be due mainly to dominance and nonisodirectional distribution of genes. Breakable linkage was indicated for most of the characters studied. The relative magnitude of the heterosis components could therefore not be assessed. On account of linkage, there was little reason to believe that the apparent overdominance found in some cases was real. As a whole the data from the early generations indicated that it should be possible to select homozygous lines at least equal to the F_1 in all characters, provided that the linkages are not too close. With the exception of straw length, the present results confirm those conclusions.

SUMMARY

The genetic components of heterosis are dominance, additive gene effects and the effects of homozygous-homozygous and heterozygous-heterozygous non-allelic interactions. In a previous paper, results of analysing continuous variation in early generations of barley crosses were presented. It was concluded that heterosis in the characters studied was due to dominance and nonallelic interaction of the homozygous-homozygous type. The present paper reports results of a selection experiment for yielding capacity up to F_8 and presents the results of a comparison between parents, F_1 and selected F_7 and F_8 lines for five char-

acters. The data are in agreement with deductions from the analysis of early generations.

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