

# DIALLEL ANALYSIS OF THE TIME TO HEADING IN SPRING BARLEY

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Received 17.i.72

## 1. INTRODUCTION

REVIEWS of the published studies on time to heading in barley have been compiled by Smith (1951) and Nilan (1964). Early genetic studies were generally limited to single or a small number of crosses and the results indicated variously that the character was simply or polygenically determined and that dominance was present in varying degrees. Later studies, using more sophisticated statistical techniques, have also led to the conclusion that the character is quantitatively inherited and that it is partially governed by dominant genes or gene groups.

Johnson and Paul (1958) analysed data from the  $F_1$ ,  $F_2$  and  $F_3$  generations of seven crosses between spring barley varieties of different maturity periods and concluded that additive alleles at two loci were operative in the inheritance of earliness. These authors rejected the biometrical technique of analysis proposed by Mather (1949) in favour of Mendelian analysis. Eunos (1964) re-analysed the data from five of the seven crosses by biometrical techniques and concluded that two to five effective factors were operating. He also detected overdominance in three of the five crosses. Aksel and Johnson (1961) studied "sowing-to-heading period" in 10-parent (six-rowed and two-rowed varieties) and 6-parent (six-rowed varieties) diallels at  $F_2$ . Biometrical analyses described by Hayman (1954*b*) were used and the 6-parent crosses were also analysed by a single array technique (Jinks, 1956). They found that dominance acted in the direction of short sowing-to-heading period and that the two-rowed varieties fell in the most recessive group. Of the six-rowed varieties, O.A.C. 21 was one of those showing an excess of recessive genes.

The results of Paroda and Hayes (1971) confirmed previous findings, that the character was quantitatively inherited and that both additive and dominance components were present. They found a considerable shift in the position of relative dominance of different arrays in different environments and stressed the need to carry out genetic studies in environments similar to those in which the information is to be applied.

The results to be described here were obtained for two seasons from a 13-parent diallel in which parents,  $F_1$  and  $F_1$  were grown in the same experiment.

## 2. MATERIALS AND METHODS

The experiment\* was conducted in order to study a number of quantitatively inherited agronomic characters including yield and its components and

\* After the completion of this experiment the original Deba Abed stock was found to be heterogeneous for rachilla hair length. No obvious morphological heterogeneity was apparent during the course of the crossing programme.

TABLE 1

*List of parents, pedigree and source of origin of parents used in the diallel*

Variety	Origin	
1. Olli*	Selection from a Finnish variety	Ottawa, Canada
2. Pirkka*	(Maskin × Finnish variety) × (Olli × Manchurian variety)	Tammisto, Finland
3. Cambrinus	Balder × Strengs Franken III	Groningen, Holland
4. Ymer	Maja × (Seger × Opal)	Svalov, Sweden
5. Deba Abed	Abed Denso × Wihenstephaner II	Abed P.B.S., Denmark
6. Scotch Bere*	Old Scottish land race	Scotland
7. O.A.C. 21*	Selection from Mandscheuri barley	Ontario, Canada
8. Golden Promise	Gamma-ray mutant from Maythorpe	D. Miln & Co., Chester, England
9. Maris Baldric	Spratt Archer × Freja	P.B.I., Cambridge, England
10. Midas	((Proctor × Wong) × Mildew resistant "A") × Gamma-ray mutant from Maythorpe	D. Miln & Co., Chester, England
11. Mosane	Balder × Piroline	Gembloux, Belgium
12. Sultan	((((Kenia × Arabian) × Kenia) × F <sub>1</sub> Agio) × Kenia) × Balder	CEBECO, Holland
13. Boreham Warrior	Plumage Archer × Freja	Guinness, Warminster, England

\* Six-rowed varieties.

the production of diastatic enzymes. The 13 spring barley varieties used in the study are listed in table 1. Most of the two-rowed varieties are currently of some commercial interest, whilst the six-rowed varieties, with the exception of Scotch Bere, were chosen for their high diastatic enzyme activity during germination. Scotch Bere was included as an adapted six-rowed variety which had not been subjected to selection for diastatic power.

Data are presented here for time to heading in the material grown, though the varieties were not chosen primarily for the study of this character. They do, however, represent a fairly wide range (table 2).

TABLE 2

*Mean number of days to heading for parents relative to Boreham Warrior*

Variety	1970		1971	
	I	II	I	II
1	-17.3	-16.4	-14.2	-17.7
2	-12.7	-10.6	-9.7	-9.9
3	-6.4	-6.3	-4.6	-7.2
4	-6.3	-5.1	-4.5	-4.3
5	-6.9	-5.3	-4.6	-7.6
6	-6.5	-4.8	-5.0	-6.2
7	-12.1	-10.5	-6.5	-11.1
8	-6.0	-1.7	-4.8	-4.1
9	-8.7	-5.2	-1.9	-4.9
10	-4.0	-2.5	+2.0	-2.3
11	-6.5	-5.4	-4.8	-6.2
12	-3.4	-1.6	-2.6	-3.1
13	0.0	0.0	0.0	0.0

Hybrid material was produced by hand-pollination in the greenhouse during 1968 and 1969. Whenever possible, 30 grains of each  $F_1$  hybrid were produced. Seed of the  $F_2$  generation was obtained by selfing four  $F_1$  plants of each cross in the greenhouse.

The experiment consisted of genotypes 1 to 9 (table 1) crossed in a full diallel (including parents and reciprocals) of five sibs per cross per replicate; a  $13 \times 13$  half diallel (not including reciprocals and comprised partly of the pooled reciprocal crosses from the  $9 \times 9$  full-diallel set), with ten sibs per cross, and a  $13 \times 13$   $F_2$  half diallel, again with ten sibs per cross. Ten plants of each parent were also included and, in the case of the  $F_1$  full diallel, five plants were sampled from ten to represent the parents. Two replicate blocks were sown in each of two years and plants were individually randomised within each replicate.

Seeds were sown in paper pots ("Japanese Plant Pots") which were 2 cm. diameter by 12.5 cm. long. Sowing was done according to the field plan and dry soil was used so that the whole experiment could be watered at the same time on completion of sowing. In addition to the experimental material, five spare grains of each genotype were sown to replace losses.

Seedlings approximately 10 cm. tall were transplanted into dibbed holes in rows set 15 cm. apart, with 7.5 cm. between plants within rows. Each replicate consisted of two sub-blocks, of four rows each, surrounded by two guard-rows.

Time to heading was recorded for each plant as the number of days from an arbitrary date to the day when 2-3 cm. of awn were visible above the auricle of the flag leaf on the main tiller.

Computer programs were written to perform the analyses of Jinks and Hayman (1953), Hayman (1954*a, b*), Jinks (1954) and Jones (1965), and for the least squares estimation of genetic components. The programs were used on the IBM 360/50 and ICL System 4/75 computers of the Edinburgh Regional Computing Centre.

### 3. RESULTS

Variances were calculated for each cross and tested for homogeneity using Bartlett's Test. Significant heterogeneity was detected in the 1970 data which was only partly accounted for by correlations between means and variances. Logarithm and square-root transformations did not appreciably reduce this heterogeneity and all subsequent analysis was conducted on the untransformed data. Heterogeneity of variance was also detected in the 1971 data and no correlation was found between means and variances. Again, all analyses were conducted on untransformed data.

Table 2 shows the range, represented by the parents, of the character under consideration. Boreham Warrior was the latest parent except in replicate block I in 1971, where Midas was 2.0 days later. The four sets of comparative times of heading, with this exception, show considerable consistency.

Analyses of variance using the model proposed by Hayman (1954*a*) are shown in table 3 (*a*) for the full-diallel sets and in table 3 (*b*) for the half-diallel sets. The method for the analysis of half-diallel tables is described by Jones (1965). Additive and non-additive effects were evident in all the analyses but there was no indication of significant reciprocal effects in the

TABLE 3 (a)  
*Analysis of data for time to heading in each of two seasons*

Item	d.f.	9 × 9 F <sub>1</sub> 1970	9 × 9 F <sub>1</sub> 1971
		M.S.	M.S.
<i>a</i>	8	1188.66***	1090.17***
<i>b</i> <sub>1</sub>	1	21.16	15.36
<i>b</i> <sub>2</sub>	8	27.85*	16.51
<i>b</i> <sub>3</sub>	27	38.46***	26.30***
<i>b</i>	36	35.62***	23.82***
<i>c</i>	8	19.31	20.69
<i>d</i>	28	18.09	9.64
Blocks	1	4.71	108.53**
<i>Ba</i>	8	25.22*	12.88
<i>Bb</i> <sub>1</sub>	1	0.98	5.54
<i>Bb</i> <sub>2</sub>	8	2.39	15.56
<i>Bb</i> <sub>3</sub>	27	16.25	11.50
<i>Bb</i>	36	12.74	12.24
<i>Bc</i>	8	13.82	11.95
<i>Bd</i>	28	13.22	16.64
<i>Bt</i>	80	14.27	13.81
Within-family variance		12.47 (645 d.f.)	11.36 (646 d.f.)

TABLE 3 (b)  
*Analysis of data for time to heading in each of two seasons*

Item	d.f.	13 × 13 F <sub>1</sub> 1970	13 × 13 F <sub>1</sub> 1971	13 × 13 F <sub>2</sub> 1970	13 × 13 F <sub>2</sub> 1971
		M.S.	M.S.	M.S.	M.S.
<i>a</i>	12	2226.28***	2037.97***	2754.96***	1630.29***
<i>b</i> <sub>1</sub>	1	26.07	100.28**	795.85***	1032.14***
<i>b</i> <sub>2</sub>	12	86.12***	44.42***	116.04***	26.77**
<i>b</i> <sub>3</sub>	65	45.35***	34.32***	35.90***	24.18***
<i>b</i>	78	51.38***	36.72***	57.97***	37.50***
Blocks	1	5.12	217.92***	498.32***	732.70***
<i>Ba</i>	12	21.33	15.26	11.09	16.08
<i>Bb</i> <sub>1</sub>	1	0.21	12.88	74.73*	2.06
<i>Bb</i> <sub>2</sub>	12	5.56	11.47	9.75	8.62
<i>Bb</i> <sub>3</sub>	65	12.84	11.25	30.49***	16.72**
<i>Bb</i>	78	11.56	11.30	27.86***	15.29*
<i>Bt</i>	90	12.86	11.83	25.63***	15.39*
Within-family variance (F <sub>1</sub> + Parents)		13.14 (1631 d.f.)	11.46 (1635 d.f.)		

\*\*\* Probability < 0.001 \*\* Probability 0.01–0.01 \* Probability 0.01–0.05

analyses of the full-diallel sets (table 3 (a)). In all cases the main effects were tested against the within-family variance as being the best measure of environment. In most cases this item was close in value to the block × genotype interaction item, *Bt*.

Additive gene effects are clearly involved in the inheritance of this character, but non-additive effects are also important.

For each diallel table the variance (*V<sub>r</sub>*) and parent-offspring covariance (*W<sub>r</sub>*) of members of the same array were calculated and the regression of *W<sub>r</sub>* on *V<sub>r</sub>* was performed. Since the analyses of table 3 (a) gave no evidence of reciprocal effects, attention was confined mainly to the 13 × 13 half-diallel sets.

*1970 Data*

Analysis of the form described by Mather and Jinks (1971) was performed in which the differences in the magnitude of  $Wr - Vr$  and  $Wr + Vr$  over arrays were tested with the differences over replicate blocks. Highly significant differences in  $Wr + Vr$  values over arrays were revealed in the  $F_1$ , indicating non-additive genetic variation. Significant differences between  $Wr - Vr$  values indicated that the simple model was inadequate. Examination of the  $Wr - Vr$  values revealed clear and consistent deviations, over replicate blocks, associated with arrays 4, 7 and 10. When the C-scaling test (Mather, 1949) was applied, interaction was evident for 13 crosses common to both replicate blocks. However, when the regression of  $Wr$  on  $Vr$  was plotted for means over blocks, the rather poor linear fit ( $b = 0.4924 \pm 0.1032$ ) appeared to be due mainly to the point representing the Midas array (10) and re-analysis, with data for Midas omitted, gave  $b = 0.7748 \pm 0.0513$  with no significant heterogeneity for values of  $Wr - Vr$ . Omission of both the Midas (10) and O.A.C. 21 (7) arrays from the analysis gave a regression  $b = 0.8329 \pm 0.0441$ .

After omitting only the Midas array the regression coefficients  $b$ ,  $Wr/Vr$  for each block were compared in a joint regression analysis. The joint regression was highly significant and the replicate blocks were in agreement. Fig. 1*a* shows the  $Wr$ ,  $Vr$  graph for the diallel table of means over replicate blocks. The graph indicated partial dominance with array 1 (Olli) containing most of the dominant genes and array 7 (O.A.C. 21) containing most of the recessive genes. The regression coefficient differed significantly from 1, indicating non-allelic interaction or correlated gene distributions. No correlation was found between  $y_r$ , the mean of the common parent, and  $Wr + Vr$ , indicating that dominance was not unidirectional. The  $Wr$ ,  $Vr$  graph for the  $F_2$  data is shown in fig. 1*b*. The slopes of the regression lines were similar in both graphs and the Olli array clearly contains far more dominance than any of the other arrays.

Regression of  $Wr$  on  $Vr$  for the  $4 \times 4$  six-rowed diallel gave coefficients for both blocks not significantly different from 1, and the joint regression coefficient was  $0.9762 \pm 0.0733$ . The  $Wr$ ,  $Vr$  graph for mean values over blocks is shown in fig. 2*a*. The intercept of the regression line on the  $Wr$  axis indicated partial dominance and the Olli array again occupied a position nearest the origin but the locally adapted variety, Scotch Bere, now occupied the extreme recessive position. A high correlation ( $r = 0.9308$ ) was found for  $Wr + Vr$  and  $y_r$ , indicating that dominance was acting in the direction of earliness. Analysis of variance for the half-diallel table confirmed both additive and non-additive effects.

Considering now the two-rowed population, analysis of variance for  $Wr + Vr$  and for  $Wr - Vr$  over arrays and blocks revealed no significant differences and although the joint regression analysis for  $b$   $Wr/Vr$  failed to indicate heterogeneity of regression between the two blocks, the regression for block I was not significantly different from zero whilst that for block II was just significant ( $P < 0.05$ ). The  $Wr$ ,  $Vr$  graph for mean values over blocks showed apparent over-dominance which was no doubt a spurious result of interaction. Again, removal of the Midas array resulted in a regression line with a slope not differing from unity and passing through the origin of the  $Wr$  and  $Vr$  axes (fig. 3*a*). Complete dominance was thus

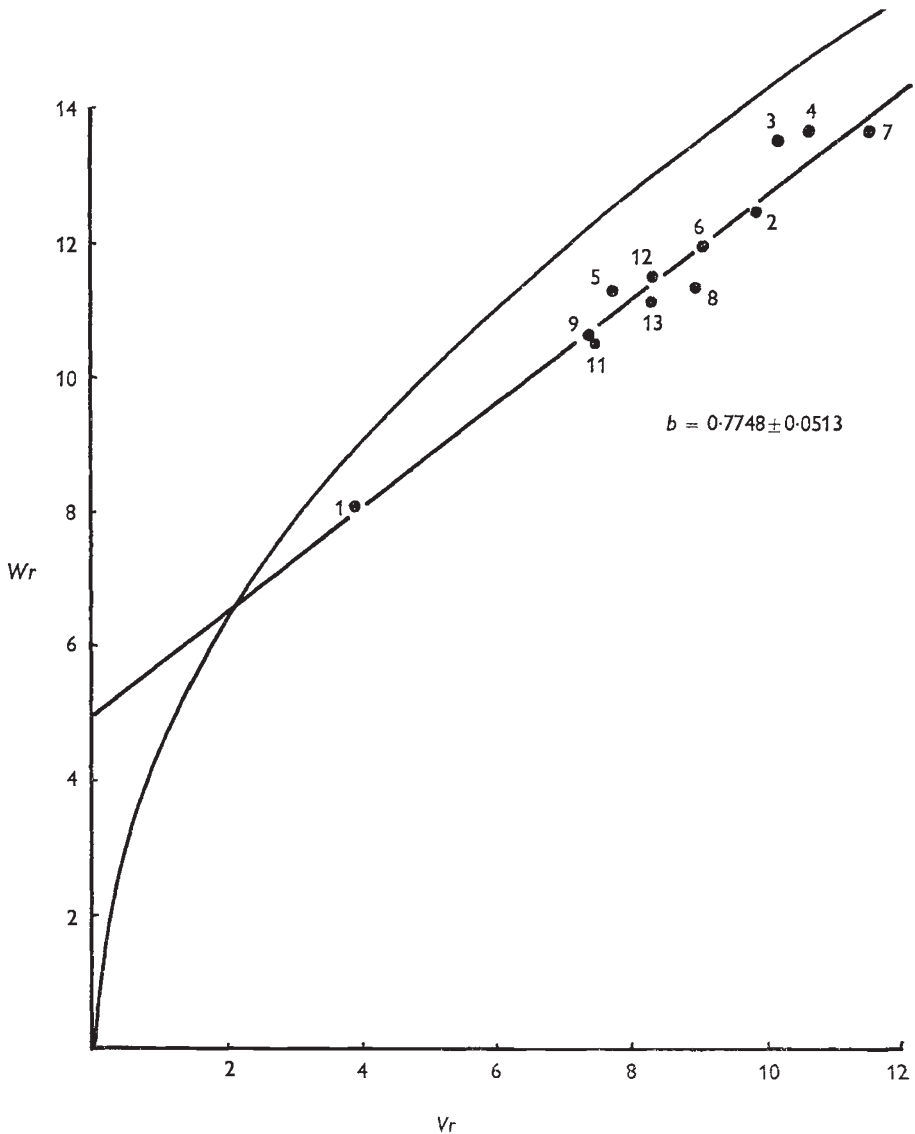


FIG. 1a.— $W_r$ ,  $V_r$  graph for the  $13 \times 13$   $F_1$  half-diallel set, means over blocks, 1970 data omitting data for array 10.

indicated with the Deba Abed array (5) containing the most dominant genes, a position, relative to the other two-rowed varieties, which was not apparent when data from the six-rowed population was included in the analysis (fig. 1a). No simple relationship was found between position on the regression line and parental phenotype performance. The correlation coefficient for  $W_r + V_r$  and  $y_r$  was  $r = 0.2183$ , which did not reach significance.

The orders of dominance for arrays in both the six-rowed and two-rowed populations were confirmed when  $W'r$  was plotted against  $W_r$ . The dotted lines in figs. 2b and 3b represent slopes of  $\frac{1}{2}$  passing through the origin. In

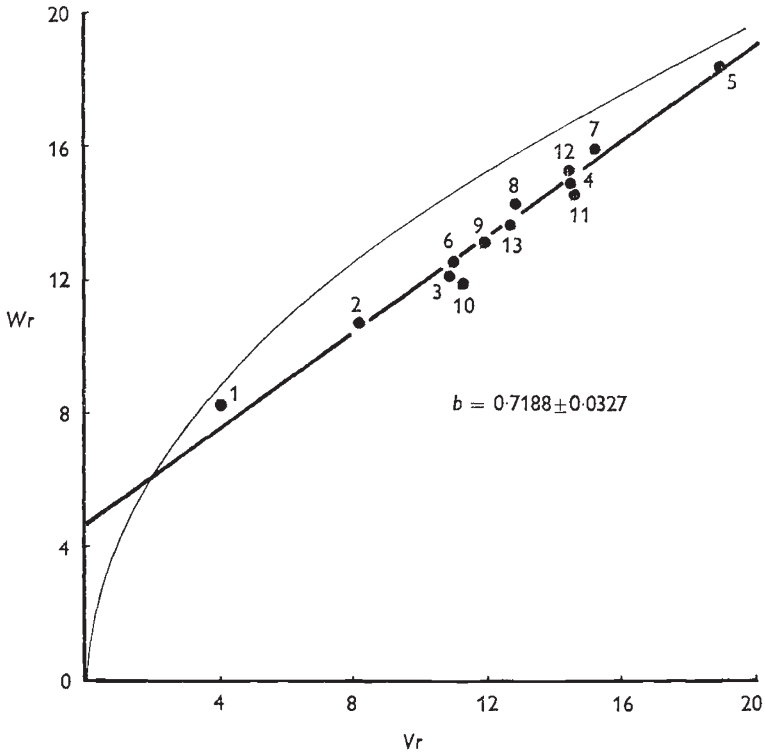


FIG. 1b.— $W_r$ ,  $V_r$  graph for the  $13 \times 13$   $F_2$  half-diallel set, means over blocks, 1970 data.

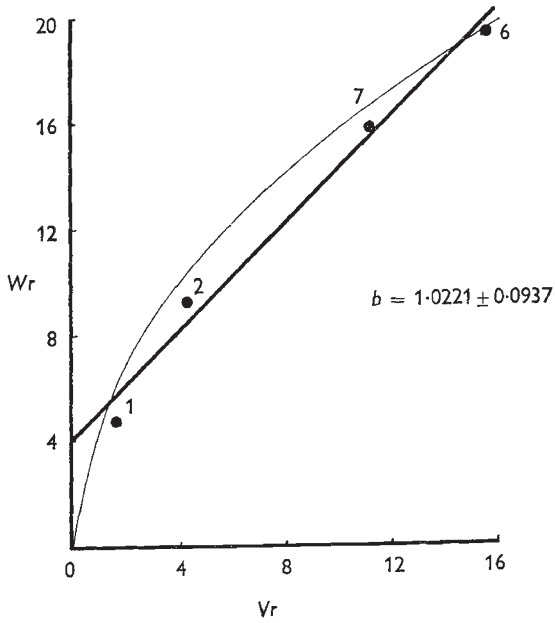


FIG. 2a.— $W_r$ ,  $V_r$  graph for the  $4 \times 4$   $F_1$  diallel subset, comprising only six-rowed genotypes and their crosses, means over blocks, 1970 data.

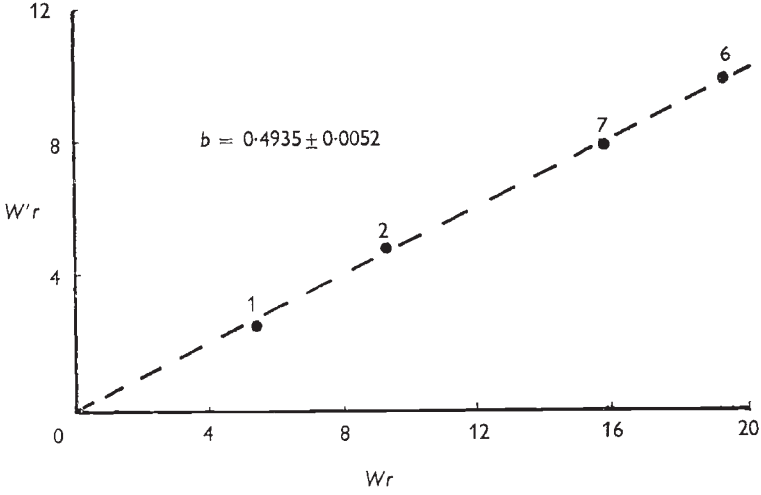


FIG. 2b.— $W'r$ ,  $Wr$  graph for the  $4 \times 4$   $F_1$  diallel subset comprising only six-rowed genotypes and their crosses, means over blocks, 1970 data.

the case of the six-rowed population all the points fell on the line, indicating gene symmetry. In the two-rowed population all the points fell above the line, suggesting some gene asymmetry and no unusual parental genotypes.

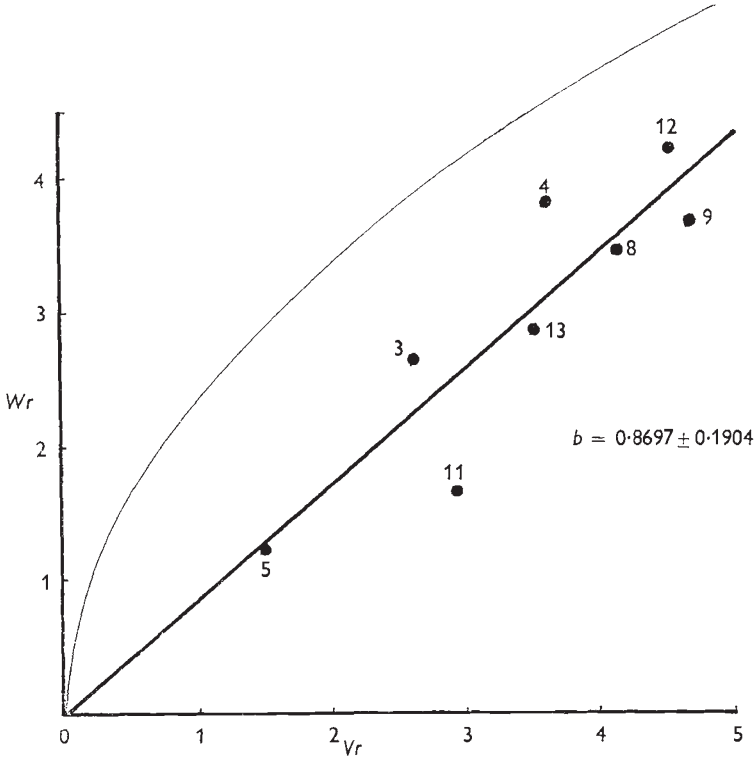


FIG. 3a.— $Wr$ ,  $Vr$  graph for the  $8 \times 8$   $F_1$  diallel subset, comprising only two-rowed genotypes and their crosses and omitting the interacting Midas array, means over blocks, 1970 data.



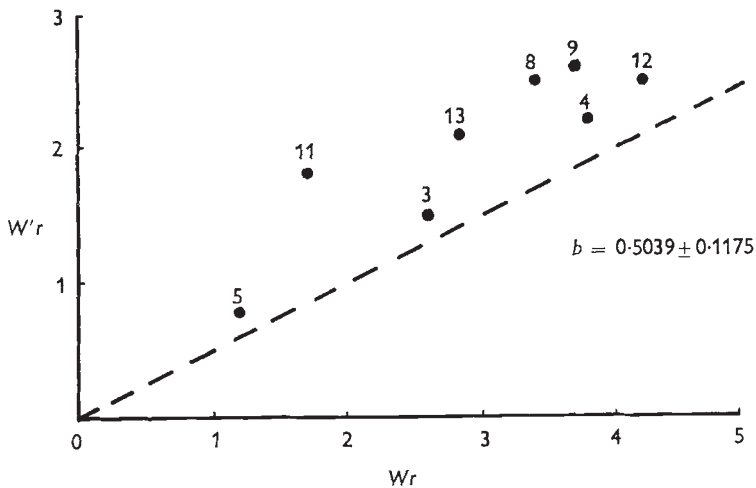


FIG. 3*b*.— $W'r$ ,  $W'r$  graph for the  $8 \times 8$   $F_1$  diallel subset, comprising only two-rowed genotypes and their crosses and omitting the interacting Midas array, means over blocks, 1970 data.

#### 1971 Data

$W_r$ ,  $V_r$  graphs for the  $13 \times 13$   $F_1$  and  $F_2$  diallel sets are shown in figs. 4*a* and 4*b*. In the  $F_1$  generation the Olli array again occupied the position of the most dominance, and partial dominance was indicated for the population as a whole. In both replicate blocks the Midas array occupied a position of high variance and covariance, but the value of  $W_{10} - V_{10}$  was large and negative when all other values were positive. Apparently the Midas array was again showing interaction and depressing the slope of the regression. The C-scaling test showed interaction in four crosses with Midas in replicate block 2 but no Midas crosses showed interaction in block 1.

When the  $F_1$  data, after omitting the Midas array, were re-analysed, a slope not differing from 1 was obtained. A correlation was found between  $y_r$  and  $W_r + V_r$  ( $r = 0.8036$ ,  $P < 0.01$ ) showing that dominance was acting in the direction of earliness.

When the six-rowed and two-rowed populations were analysed separately, the six-rowed population again showed a very good fit to a regression of unit slope (joint regression coefficient  $b = 0.9481 \pm 0.0556$ ). The Olli and Pirkka arrays showed more dominance than the O.A.C. 21 and Scotch Bere arrays which alternated in the two blocks for the extreme position for recessive genes. The two-rowed population gave regression coefficients which differed markedly between replicate blocks ( $b = 0.7916 \pm 0.2042$  and  $b = 0.1879 \pm 0.0557$ ) and removal of the Midas array resulted in a non-significant regression for block 1 and a slope significantly less than 1 in block 2.

For the estimation of the six components of variation, *viz.*  $D$ ,  $H_1$ ,  $H_2$ ,  $F$ ,  $E_0$ ,  $E_1$  (or  $E_2$  for  $F_2$  generation) six statistics were available in  $F_1$  and  $F_2$ . These were the variances of the parents ( $V_p$ ), mean variances of arrays ( $\bar{V}_r$ ), variances of array means ( $V\bar{r}$ ), mean covariances of arrays ( $\bar{W}r$ ) and the direct estimates of environmental variances  $E_0$ ,  $E_1$  and  $E_2$  for the parental,  $F_1$  and  $F_2$  generations respectively.

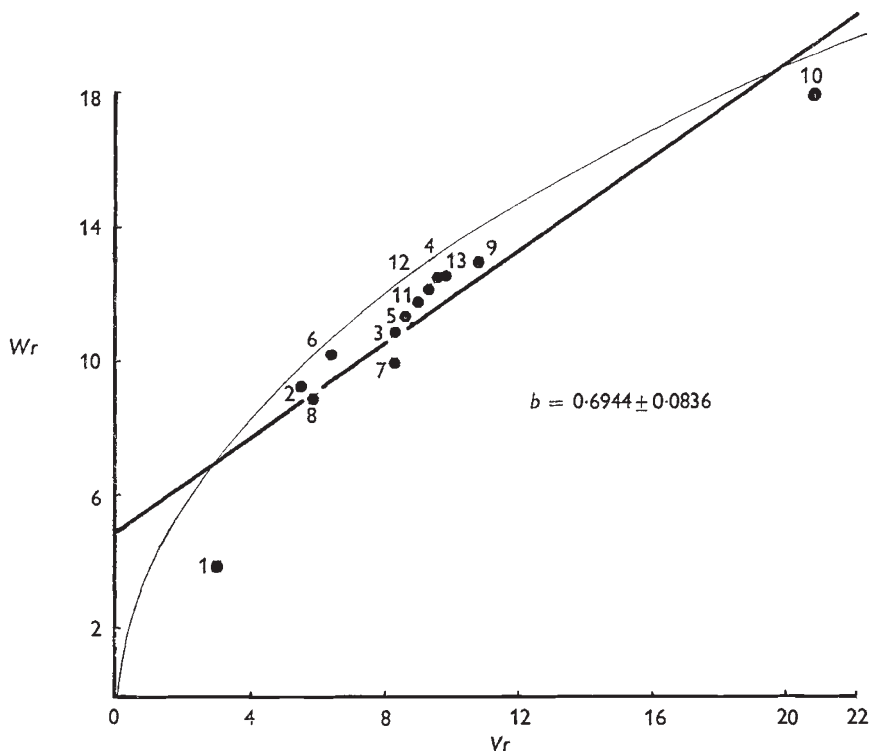


FIG. 4a.— $W_r$ ,  $V_r$  graph for the  $13 \times 13$   $F_1$  half-diallel set, means over blocks, 1971 data.

The six equations were solved by an unweighted least squares technique (Mather, 1949; Mather and Vines, 1952; Mather and Jinks, 1971). The estimation of six parameters from six statistics in each generation resulted in a perfect solution and no standard errors could be attached to the values obtained. Values for the components and ratios between them are given in table 4 for  $F_1$  and  $F_2$  in each season.

The existence of partial dominance is confirmed by  $\sqrt{(H_1/D)} < 1$  in almost all cases, though the very high estimates obtained for  $H_1$  and  $H_2$  in  $F_2$  for both replicate blocks in 1970 and one replicate block in 1971 resulted in  $\sqrt{(H_1/D)} > 1$ , indicating over-dominance, which was not suggested by the  $W_r$ ,  $V_r$  graphs.

The negative value of  $F$  suggests that there was an excess of recessive alleles present in the inbred lines irrespective of whether these were increasing or decreasing in their effect on time to heading. The values for  $H_2/4H_1 < 0.25$  indicate unequal frequencies of negative and positive alleles among the parents.

The values for  $\frac{1}{2}F/\sqrt{[D(H_1 - H_2)]}$  were variable between the diallel sets and in two cases exceeded the theoretical maximum of 1. This expression measures the consistency of the ratio of  $h$  to  $d$  over all loci.

The quantity  $(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$  was approximately 0.5 in most cases, indicating that the proportion of dominant and recessive allelomorphs

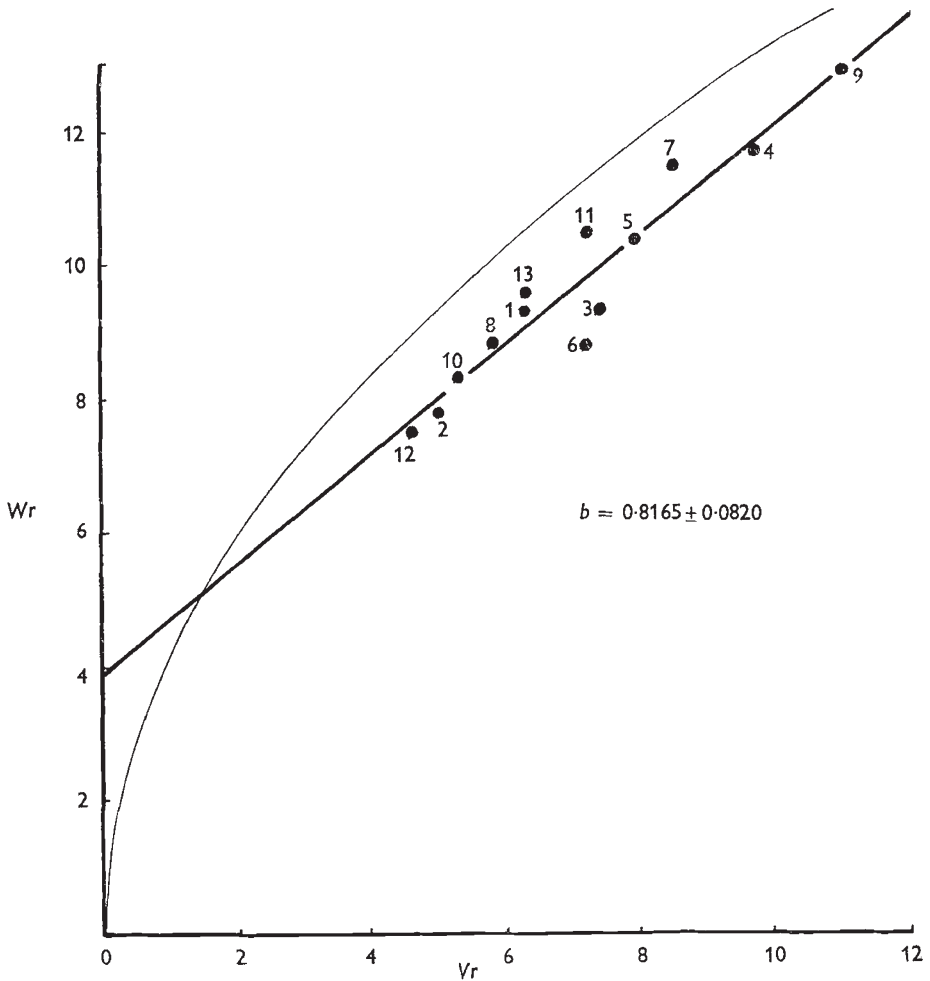


FIG. 4*b*.— $W_r$ ,  $V_r$  graph for the  $13 \times 13$   $F_2$  half-diallel set, means over blocks, 1971 data.

in the parents was unequal and that there were approximately two recessive genes or effective factors for each dominant gene or gene group involved in the control of this character.

More accurate estimates of the genetic components should be obtainable by using more statistics, and 12 are available when  $F_1$  and  $F_2$  data are combined (see Hayman, 1958, tables 1, 1*b*). Seven parameters were estimated (table 5), leaving five degrees of freedom to calculate the variance of the deviations of observed from expected for the 12 statistics. The standard errors in the 1970 results, particularly those associated with  $H_1$  and  $H_2$ , were large, but more precise estimates for the components were obtained for the 1971 data. The conclusions drawn from table 4 were largely substantiated.

The values for the seven components derived from the 12 statistics of  $F_1$  and  $F_2$  data pooled were used to reconstruct expected values for the statistics, and the overall deviation of observed from expected was tested against heterogeneity between blocks (Mather and Jinks, 1971). The overall

TABLE 4  
Components of variation for time to heading in two seasons

Component	1970				1971			
	13 × 13 F <sub>1</sub> Blocks		13 × 13 F <sub>2</sub> Blocks		13 × 13 F <sub>1</sub> Blocks		13 × 13 F <sub>2</sub> Blocks	
	I	II	I	II	I	II	I	II
<i>D</i>	19.06	18.76	19.06	18.76	15.38	19.32	15.38	19.32
<i>H</i> <sub>1</sub>	10.76	8.77	42.02	46.39	5.34	6.85	17.20	4.61
<i>H</i> <sub>2</sub>	7.39	5.34	21.34	28.55	3.58	5.36	15.96	2.31
<i>F</i>	-9.34	-9.51	-27.79	-36.05	-11.27	-8.37	-11.61	-6.11
<i>E</i> <sub>0</sub>	0.79	1.15	0.79	1.15	1.11	1.05	1.11	1.05
<i>E</i> <sub>1</sub>	1.18	1.57	—	—	1.09	1.22	—	—
<i>E</i> <sub>2</sub>	—	—	2.57	2.09	—	—	1.96	1.70
$\sqrt{(H_1/D)}$	0.751	0.684	1.485	1.573	0.589	0.595	1.057	0.488
$H_2/4H_1$	0.172	0.152	0.127	0.154	0.168	0.196	0.232	0.125
$\frac{1}{2}F\sqrt{[D(H_1-H_2)]}$	-0.583	-0.593	-0.700	-0.985	-1.083	-0.780	-1.329	-0.458
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	0.5081	0.4590	0.3413	0.2414	0.2332	0.4665	0.4739	0.5109

deviation item was found to be significant, indicating a failure of the model due to epistasis.

In order to determine the relative sizes of *D* and *H*<sub>1</sub> the relationship,

$$\bar{W}r - \bar{V}r = \frac{1}{2}D - \frac{1}{4}H_1$$

was used after correcting  $\bar{W}r$  and  $\bar{V}r$  for their environmental components (Mather and Jinks, 1971). *D* was found to be significantly larger than *H*<sub>1</sub> in the F<sub>1</sub> data from both seasons and this was taken as further evidence that dominance was incomplete.

An analysis was conducted on the F<sub>1</sub> data for 1970 to estimate general and specific combining abilities. The Method 4, Model I analysis of Griffing (1956) was used and highly significant effects for both g.c.a. and s.c.a. were obtained (table 6). The parents Olli (1) and Pirkka (2) showed high general

TABLE 5  
Components of variation for time to heading calculated from statistics derived from the L<sub>1</sub> and L<sub>2</sub> generations (Hayman, 1958)

Component	1970 Blocks		1971 Blocks	
	I	II	I	II
<i>D</i>	19.6022 ± 2.6438	19.4131 ± 3.4781	15.4484 ± 1.1422	19.3113 ± 0.9383
<i>H</i> <sub>1</sub>	11.0664 ± 10.6567	9.7873 ± 14.0197	7.4419 ± 4.6041	8.4106 ± 3.7823
<i>H</i> <sub>2</sub>	8.6660 ± 10.4307	9.2192 ± 13.7224	2.7526 ± 4.5065	4.0984 ± 3.7021
<i>F</i>	-13.1666 ± 7.1466	-16.0443 ± 9.4019	-8.5715 ± 3.0877	-5.5229 ± 2.5365
<i>E</i> <sub>0</sub>	0.5358 ± 1.8738	0.8559 ± 2.4651	1.0823 ± 0.8096	1.0472 ± 0.6651
<i>E</i> <sub>1</sub>	0.5805 ± 1.7284	0.5218 ± 2.2739	1.1490 ± 0.7468	1.3866 ± 0.6135
<i>E</i> <sub>2</sub>	4.4808 ± 1.4115	4.5170 ± 1.8570	2.4455 ± 0.6098	1.6229 ± 0.5010
$\sqrt{(H_1/D)}$	0.7514	0.7100	0.5459	0.6599
$H_2/4H_1$	0.1958	0.2355	0.0925	0.1218
$\frac{1}{2}F\sqrt{[D(H_1-H_2)]}$	-0.9597	-2.4156	-0.5035	-0.3029
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	0.3822	0.2642	0.4289	0.6438

TABLE 6  
 General and specific combining ability effects for time to heading,  $F_1$  data SCA 1970 and 1971 (below) estimates

	GCA													
	1970	1971	13	12	11	10	9	8	7	6	5	4	3	
1	-6.896	-7.190	0.056	0.638	0.665	-1.898	0.747	-0.744	-1.262	-0.153	1.165	-0.598	-0.426	1.811
2	-3.178	-2.980	-0.024	-0.070	0.839	-6.142	0.130	0.939	0.703	0.348	0.703	-0.179	1.030	1.721
3	0.059	0.211	3.038	1.020	-0.553	-0.317	0.529	1.438	-2.080	0.029	-0.853	-2.917	-1.144	-1.144
4	1.932	1.420	-0.367	0.921	-1.170	0.552	0.321	0.230	0.094	0.239	-1.006	-1.188	0.021	0.021
5	-0.532	0.638	-1.298	1.483	-0.189	0.347	-1.808	0.702	-1.317	2.093	2.311	-0.753	-0.753	-0.753
6	-2.005	-2.162	-0.776	0.930	-0.961	-0.642	-1.170	-0.161	-1.397	-0.752	2.203	0.121	0.121	0.121
7	1.977	1.701	0.629	0.211	1.038	2.274	0.020	-0.171	0.411	0.920	-1.062	-1.062	-1.062	-1.062
8	-0.414	1.111	-0.408	-0.426	0.630	1.849	0.083	-2.108	-1.926	-0.061	-0.306	-0.306	-0.306	-0.306
9	4.532	3.683	-0.549	-1.497	-1.188	0.330	1.003	-1.488	0.076	1.883	0.621	0.621	0.621	0.621
10	0.468	-0.199	0.374	-1.344	0.183	-3.680	0.665	-1.026	0.056	0.621	0.621	0.621	0.621	0.621
11	0.795	1.111	-0.706	-0.152	0.358	-0.724	1.049	-1.342	1.121	0.621	0.621	0.621	0.621	0.621
12	0.265	1.111	-1.835	1.347	-0.326	4.511	0.656	1.765	1.121	0.621	0.621	0.621	0.621	0.621
13	3.677	2.765	-0.652	-1.197	-0.288	0.330	-1.797	3.112	1.121	0.621	0.621	0.621	0.621	0.621
	$\pm 0.35$	$\pm 0.32$												

S.E. ( $\hat{g}_i - \hat{g}_k$ )

1970 population mean ( $\hat{\mu}$ ) = 56.7  $\pm$  0.09  
 S.E. ( $\hat{S}_{ij}$ ) = 0.74

1971  $\hat{\mu}$  = 60.3  $\pm$  0.09  
 S.E. ( $\hat{S}_{ij}$ ) = 0.69

combining ability for earliness and the largest specific combining ability effect was for Midas  $\times$  O.A.C. 21 ( $10 \times 7$ ). In order to obtain unbiased estimates the parents were not included in the analysis.

When the analysis was conducted on the 1971 data a very similar result was obtained with regard to general combining ability estimates. Specific combining ability effects were, however, small with the exception of that for the cross Olli  $\times$  Midas which was as early as the Olli parent.

#### 4. DISCUSSION

The experiment was a large one in terms of the number of genotypes included and the design differs from those of most previously reported experiments on cereals. In these previous experiments, genotypes were grown in plots of several plants within each replication, often with plants widely spaced (Whitehouse *et al.*, 1958; Lupton, 1961; Crumpacker and Allard, 1962; Paroda and Hayes, 1971). In the experiments reported here, plants were grown as closely as possible, commensurate with field recording, so that characters were measured under growing conditions approaching those of agricultural practice. The randomisation of plants within a single block ensured a wide sampling of environmental variability while possible effects of interplant competition were also distributed at random. Replicate blocks constituted statistically independent experiments. The incorporation of parents  $F_1$  and  $F_2$  together in both years permitted comparisons to be made between generations without confounding seasonal effects and the extra statistics obtainable by consideration of the  $L_1$  and  $L_2$  tables together (Hayman 1958, table 1*b*) allowed standard errors to be attached to the estimates of genetic components.

The analysis of variance clearly demonstrated that the genetic variation was largely additive ( $a$ ), and smaller, but nevertheless significant, effects due to non-additive variance were also detected. In the  $9 \times 9$  full diallels in both seasons this non-additive variance fell mostly into the ( $b_3$ ) category with only a suggestion of gene asymmetry ( $b_2$ ). In the half diallels significant non-additive effects could be associated with all three ( $b$ ) items. An important assumption in the theory of diallel analysis, namely that of no reciprocal differences, was also tested by Hayman's ( $c$ ) and ( $d$ ) in full diallels. No significant effects were found.

Heterogeneity of  $Wr - Vr$  in the graphical analysis was detected in several cases and the regression of  $Wr$  on  $Vr$  was, in a number of cases, significantly less than unity. In addition, regressions of  $W'r$  on  $Wr$  indicated asymmetry of gene distribution, associated particularly with the two-rowed genotypes. Whenever possible, interactions were removed and the analysis continued.

In the six-rowed genotypes subgroup, interpretation was relatively straightforward. Dominance was in the direction of earliness, with the point representing the array of Olli, the earliest variety, taking up a position on the regression slope signifying an excess of dominant genes, while in the array of O.A.C. 21 an excess of recessive genes was indicated. This latter result agrees with the findings of Aksel and Johnson (1961). However, when two-rowed and six-rowed genotypes were considered together, O.A.C. 21 was revealed to be relatively early so that the direction of dominance was no longer clear. In addition, when the two-rowed genotype subgroup and the complete diallels were considered, the model was clearly inadequate in

several cases, with regression coefficients significantly less than unity. Ambidirectional dominance was suggested. Three of the four six-rowed parents are adapted to American growing conditions and strong selection may have been practised for time of heading. This may have resulted in the fixation of dominant genes acting in the direction of earliness. In European genotypes, on the other hand, selection has tended towards intermediate or late types, a situation in which different genes, with dominance working in either direction, could survive in the population.

The data for Midas appeared to be largely responsible for failure of the  $Wr/Vr$  test, particularly in the 1970 season, although the C-scaling test did not indicate consistent interaction in this array. Nevertheless, considerable improvement in the fit to the model was found when these data were omitted from the analysis. There would thus appear to be evidence for non-independence of gene distribution and the scatter of points in fig. 4a, where the point for the Midas array occupies an extreme position, shows curvature which is concave downwards suggesting gene association (Coughtry and Mather, 1970).

An indication of seasonal effects in the expression of dominance was the clear unidirectional dominance found in the  $12 \times 12$  diallel (Midas omitted) in the 1971 data. Unidirectional dominance could not be shown in the 1970 data except for the six-rowed subgroup. Paroda and Hayes (1971) also noted changes in the expression of dominance in different environments, and indeed, between two of the eight environments they studied, a complete reversal in the direction of dominance was detected.

The graphical analyses confirmed that in addition to additive effects, partial dominance was operating in the determination of heading time.

Estimation of the components of genetic variation confirmed that  $D$  was large relative to  $H_1$  and  $H_2$  in most cases and that  $F$  was large and negative, showing an excess of recessive alleles. The precision of the estimates of  $H_1$  and  $H_2$  was low and it is a feature of the set of statistics used that the C-matrix derived from the matrix of coefficients contains relatively large values for the  $CH_1H_1$  and  $CH_2H_2$  elements. In the population as a whole it was estimated that an approximately 2 : 1 ratio existed between recessive and dominant genes for this character. The ratio  $\frac{1}{2}F/\sqrt{[D(H_1 - H_2)]}$  twice exceeded the theoretical maximum of 1 and in these data was not a useful measure of the consistency of the ratio  $h$  to  $d$  effects.

The combining ability analyses are perhaps most helpful when making parental choices. High g.c.a. would be desirable if the additive effect of a single genotype was all that was required. On the other hand, if other factors were important in the choice of parents, high s.c.a. for the character analysed, between parents satisfactory in other respects, would be looked for.

The g.c.a. effects in the 1970 and 1971 seasons were highly correlated ( $r = 0.9692$ ,  $P < 0.001$ ), showing that the additive genetic effects did not interact with seasonal effects. Large negative g.c.a. effects were exhibited by Olli, Pirkka and O.A.C. 21, while Midas and Boreham Warrior showed large positive g.c.a. effects. Estimates for s.c.a. effects in the 1971 season were low, as was the correlation between seasons ( $r = 0.4005$ ,  $P < 0.01$ ), suggesting that non-additive effects are influenced by environment. The s.c.a. values contain effects due to non-additive variation which may include non-allelic interaction. The variability of s.c.a. effects in the Midas array for the 1970 season is perhaps a confirmation of the disturbances indicated

by other tests. The Boreham Warrior array, on the other hand, showed a much smaller range of values indicating mainly additive effects for lateness in this genotype.

### 5. SUMMARY

1. Diallel analysis was applied to untransformed data from two seasons for time to heading in spring barley.

2. Analysis of variance of data from  $9 \times 9$  full diallels at  $F_1$  for two seasons indicated no significant differences between reciprocal crosses. Large additive effects were detected, but non-additive variation was also significant in the control of this character.

3. Analysis of data from  $13 \times 13$  half diallels at  $F_1$  and  $F_2$  for two seasons also detected significant additive and non-additive effects. Graphical analysis revealed considerable departures from the model which in some cases could be removed by omitting the Midas array from the analysis.

4. No interaction was evident when a subgroup, consisting of a  $4 \times 4$  diallel between six-rowed parental genotypes, was analysed, and graphical analysis revealed partial dominance with dominance acting in the direction of earliness.

5. Considerable interaction was present when a subgroup, consisting of a  $9 \times 9$  diallel between two-rowed parental genotypes, was analysed and results were inconsistent over both blocks and seasons.

6. Estimation of genetic components confirmed that additive genetic variance was high and that partial dominance was operating in the inheritance of this character. Gene asymmetry was detected and there was an excess of recessive genes.

7. The expression and direction of dominance was in some cases found to be different between seasons.

8. Large effects for general and specific combining ability both for early and late heading were detected.

*Acknowledgments.*—We would like to thank Mrs M. Sinclair, Mrs E. J. C. Pearce, Mr M. I. Chapman, Mr R. B. W. Williamson and Mr R. W. Hutchison for technical assistance. We also thank Mr J. L. Fyfe and Dr R. J. Killick for advice during the course of the work and for helpful criticism during the preparation of the manuscript.

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