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Title ESTIMATES OF GENE ACTION FOR HEADING DATE AND YIELD IN BARLEY

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The purposes of this study were to determine the amount of heterosis present for heading date and grain yield and to estimate the type of gene action for these traits in a diallel cross of seven spring barley varieties.

Seven varieties were crossed in all possible combinations in the spring of 1963. The following year, the 21 F_1's and the seven parental varieties were planted in a greenhouse groundbed on the campus of Oregon State University. Gene action estimates for heading date and grain yield were obtained from the F_1 population by the following: general and specific combining ability estimates, and narrow- and broad-sense heritability estimates. The magnitude of heterosis was measured by the deviation of the F_1 means from the parental midpoint or from the high parent's mean.

The analysis for the combining ability effects indicated that both general and specific combining ability effects were significant for date of heading and for yield. This would indicate that additive as well as non-additive gene action was present for both traits. A comparison of the broad- and narrow-sense heritability estimates obtained for heading date and grain yield also confirms the presence of both additive and non-additive gene action for these traits.

The amount of heterosis present in the F_1 crosses for grain yield and heading date was quite small. None of the 21 different single crosses yielded significantly more than its high parent.

The association of heading date and plant yield appeared to be negligible when both two-rowed and six-rowed plants were correlated. When the crosses and parents were separated according to row number, it was found that heading date was positively associated with yield for six-rowed barleys but negatively associated for two-rowed barleys. The differences in these two associations could be due to the different manner that high yields are obtained by these two groups.

ESTIMATES OF GENE ACTION FOR HEADING DATE AND YIELD IN BARLEY

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INTRODUCTION

There are two general categories of plant characters based on the nature of their inheritance. These are commonly referred to as simple and complex characters. The usual method of studying the simply inherited traits is by determining the ratio of one character to another in the segregating generations following a cross. The traits that have a more complex inheritance are often evaluated by determining various gene action estimates. Heading date of barley has generally been considered to be an example of a simply inherited trait, while the inheritance of yield is considered to be a complex trait.

Barley breeders in their attempts to develop improved varieties have in the past largely selected the parents for their crosses based on the parental characteristics or performance. This method has been highly successful, particularly when the breeders were working with the predominantly simply inherited characters. Their success with the complex traits has not often been as spectacular. A better understanding of the predominant type of gene action that controls a particular complex trait would then allow the barley breeder the opportunity to select those parents that when crossed would produce more productive offspring.

The possibility of widescale utilization of hybrid barley makes it even more imperative for barley breeders to determine better methods of evaluating the type of gene action controlling the important plant characters. Determining better ways of selecting those barley varieties as parents which have the most opportunity of giving maximum heterosis or hybrid vigor also becomes necessary.

It was the purpose of this study to determine estimates of the type of gene action present in seven widely divergent barley varieties for heading date and grain yield. Three different methods of estimating gene action were used. These were combining ability estimates as measured by the diallel cross analysis, heritability estimates in the F_1 generation and the expression of heterosis in the F_1 generation. A second objective was to determine the extent of heterosis present in the hybrid combinations and thus attempt to identify the best parents. The evaluation of the superior hybrid combinations was determined by estimates of general and specific combining ability effects associated with each of the respective parents.

REVIEW OF LITERATURE

The inheritance of heading date and yield in barley has been the subject of many investigations. Conflicting results on the number of genes and type of gene action controlling heading date have evolved from these studies. As a result, heading date has been considered both a qualitative and a quantitative trait. Yield has been regarded by most workers as strictly a quantitative trait. A recent comprehensive review of the genetics of barley by Nilan (21, p. 1-278) gives a detailed summary of the findings on the inheritance of both heading date and yield in barley.

In an early paper on the inheritance of heading date in barley, Wilson (27, p. 68) reported that F_2 plants resulting from crosses involving one barley variety used as the female parent and four different varieties as the male parent segregated for maturity in such a manner as to suggest that earliness was recessive and lateness was dominant. Similarly, Frey (8, p. 227), in a different cross, found earliness of heading to be recessive and determined by a single gene. In two additional crosses, the segregation of late to early was 9:7. Frey concluded that date of heading in barley was controlled by relatively few genes and the character was easily fixed in later generations.

Griffee (12, p. 935) found earliness of heading in barley to be dominant and controlled by a single factor in a cross between an early six-rowed variety and a late two-rowed variety. This appeared to be linked with the factor for row number. Similarly, in five crosses involving seven different parents, Chin (4, p. 269) found earliness was dominant and appeared to be controlled by at least two genes. He concluded from his results that earliness might depend upon the number of dominant genes present.

Yasuda, as cited by Nilan (21, p. 149), found two factor pairs responsible for maturity in barley. He postulated that those varieties which were homozygous dominant for these factors were 60 days earlier than the varieties which were homozygous recessive. Each allele appeared to be additive, and no interaction between genes was present in the F_1 hybrids.

The F_1 and F_2 generations in four out of five barley crosses studied by David (6, p. 295) flowered earlier than either of their parents, indicating dominance for earliness. A ratio of 9 early to 7 late plants was obtained in the F_2 generation. The F_2 data, together with the F_3 progeny tests, indicated the presence of two important complementary factors for earliness. No evidence for the segregation of genetic factors for yield in any of the five crosses was reported. Correlation coefficients between days to flowering and yield were all negative, and some were statistically significant.

From a large number of barley crosses, Harlan and Martini (15, p. 558) noted that hybrids headed quite uniformly when compared with their respective parents. The average awn emergence or heading date of the hybrids had a tendency to be intermediate between the two parents. The average awn emergence date of the hybrids was more than two days earlier than the average of the parents. The earliness of many hybrid combinations from crosses among late varieties indicated that there were many factors for earliness.

Johnson and Paul (18, p. 223) reported that earliness in barley was controlled by "increaser alleles" at two loci. They hypothesized that the parents in each late x early cross differed in these two alleles and assumed that they were also homozygous lines. Observed frequencies in the F_2 progeny were in good agreement with the expected 1:2:1:4:4:4 ratio.

The effect of the date of sowing on heading date of barley was studied by Bell (3, p. 185). He concluded that heading date was greatly influenced by date of sowing and that earliness tended to be dominant in early generations, but a considerable amount of transgressive segregation was present in later generations.

Heading date in barley was treated as a quantitative character in a study by Aksel and Johnson (2, p. 242). Through the use of diallel analysis, these workers conluded that a short sowing-to-heading period was dominant over a long sowing-to-heading period. These workers also found a positive association between a long first period and high yield when only the six-rowed parents of the diallel cross were considered. A similar study on heading date in wheat was conducted by Crumpacker and Allard (5, p. 275).

Since yield has almost always been considered as a quantitatively inherited trait, there has been only a few attempts to study segregation for yield. Nelson, as cited by Smith (23, p. 178), studied F_2 barley plants from intercrosses of four varieties with twenty different varieties and concluded that there was a heritable factor which contributed to the differences in yield between the parents.

Heritability

Heritability may be considered as a measure of the phenotypic variation in a population that is genetic in nature. Lush (20, p. 356) first discussed heritability and developed the parent-progeny method of estimating heritability, which became widely used by animal breeders long before it was used by plant breeders. From these early studies there are now two general types of heritability estimates recognized. These are: broad-sense heritability estimates, which include both the additive and the non-additive genetic variances and narrow-sense heritability estimates which are composed of only the additive genetic variance.

Warner (26, p. 427) summarized the different techniques for estimating heritability in plants. The two most commonly used are the parent-progeny regression and variance components obtained from the analysis of variance.

The limited value of broad-sense heritability estimates when computed for self-pollinated crops such as barley, was clearly demonstrated by Grafius, Nelson and Dirks (10, p. 258). A broad-sense heritability estimate of 26 percent for yield was obtained from F_3 barley lines. Selection based on this heritability value was made, but no gains were observed in the next generation. Grafius concluded the reason for this lack of success was that the broad-sense heritability estimate overestimated the genetic potential present. This was because the broad-sense heritability estimate contains both additive and non-additive genetic effects and the non-additive effects can be lost upon selfing and thus are of limited value in estimating performance of later generations in self-pollinated crops. A narrow-sense heritability estimate of 4 percent was obtained from the same F_3 lines, thus confirming the conclusion that little gain in yield could be expected by selection in this generation.

A mean heritability estimate of 76 percent for seven barley crosses based on regression of F_3 plants upon F_2 parents for date of heading was reported by Frey (8, p. 228), while Jogi (17, p. 294), using the variance method, obtained narrow-sense heritability estimates for date of heading in barley crosses in F_4 lines grown at two locations of 90 and 96 percent respectively. Fiuzat and Atkins (7, p. 417) reported broad-sense heritability estimates for date of heading in two crosses of 92 and 91 percent respectively. These same crosses had broad-sense heritability estimates for yield of 51 and 44 percent respectively. All heritability estimates were computed by the variance method on F_2 data.

Combining Ability

Sprague and Tatum (34, p. 931) in 1942 defined and discussed the terms general and specific combining ability. They defined general combining ability as the average performance of a line in hybrid combinations and specific combining ability as those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved. The authors concluded that general combining ability estimates provide an indication of the importance of genes which are largely additive in their effects, while specific combining ability estimates depend upon genes with dominant or epistetic effects.

Carnahan, as cited by Gowen (9, p. 52), reported on crosses of four flax varieties which had been selected as desirable parent lines with each of four other lines of different genetic origin. For an average of all crosses, the F_1's yielded 40 percent more than the average of the parents. The lowest yielding cross, however, resulted from a cross of the highest variety with the second highest variety. There appeared to be a good relationship between the performance of the parents and the average performance of their F_1 crosses. The yield of the parents was as good as or better an indicator of the combining ability in the four crosses.

Powers (22, p. 268) concluded from a study of tomato hybrids that, in general, the inbred lines having superior combining ability as determined by the behavior of the F_1 hybrids, are themselves superior, but exceptions are sufficiently important so that they cannot be ignored.

Kronstad and Foote (19) classify parental lines of winter wheat for general and specific combining ability effects for grain yield and its components. Narrow-sense heritability estimates for the same characters were also computed by the parent-progeny regression method. Information on the contribution of each parent with regard to additive or non-additive gene action to its F_1's was obtained. Certain varieties were found to contribute favorably in most crosses, while others contributed favorably only in specific crosses. Good agreement between heritability and combining ability estimates was found. It was concluded by these workers that combining ability analysis can be beneficially employed in screening potential parents to determine those that are most likely to produce the highest number of high yielding progeny in later generations.

Heterosis

The phenomenon of a hybrid exceeding its parental midpoint in performance has been designated as heterosis. In cross-pollinated crops, this type of heterosis can be of direct value. Such is the case with hybrid corn. However, in self-pollinated crops, such as barley, this type of heterosis is of limited practical value. Before hybrid vigor can be of practical value in self-pollinated crops, the hybrid must exceed the best parent since this parent is already homozygous and thus will maintain its level of performance. Generally, the expression of heterosis is also much less in self-pollinated crops than in cross-pollinated crops, regardless of the way that it is measured.

One of the first papers on barley where heterosis was measured using both methods was published by Immer (16, p. 203). He found that the average increase in yield of the F_1 crosses over the mean of the two parents was 27 percent. Four of the six F_1's exceeded the high parent in yield.

The possible genetic situations which might account for the expression of heterosis in barley crosses were discussed by Aastivit (1, p. 159). According to Aastivit, overdominance and non-allelic interaction are two of the most common theories used to explain heterosis. Aastivit reported that whether heterosis is defined as the difference between the F_1 and the midpoint of the two parents or defined as the amount that the F_1 exceeds the high parent, the expected difference can be expressed in terms of genetic parameters for additivity, dominance and the non-allelic interaction. If the difference between the F_1 mean and the high parents mean is mainly due to overdominance, it is clearly not possible to select lines which are equal to the F_1. Thus, the type of gene action controlling the expression of heterosis would be important in self-pollinated crops. Aastivit also reported that the mean of the F_1 for date of heading in a cross involving two six-rowed barley varieties was almost equal to the midpoint of the parents. Heterosis for yield was observed, and it was concluded that the type of gene action controlling the expression of this heterosis was not overdominance alone, and thus, selection of lines equal to the F_1 performance was possible.

Grafius (11, p. 553) presented a slightly different view of heterosis in barley. Dominance and epistasis were both recognized as mechanisms capable of producing heterosis, but of the two, epistasis would seem to be most prominent in barley. In crosses involving all possible combinations of six barley varieties, all F_1 values exceeded the parental means for yield.

Heterosis in barley was extensively studied by Hagberg (14, p. 345). When 17 different F_1's were compared to their respective parents, he found as a rule the F_1's were intermediate or as early as the earliest parent in their heading date. Most of the F_1's were intermediate or equal to the best parent in tillering, length of ear, weight of 1,000 seeds and yield of grain per plant. In some combinations, the F_1 was superior to the best parent, but the differences were not significant.

Suneson and Riddle (25, p. 60), using male-sterile barley for the production of large quantities of hybrid seeds, found the F_1's had an average yield advantage over both parents of more than 20 percent. A difference in the combining ability of the seven varieties used was also noted.

MATERIALS AND METHODS

Seven spring barley varieties of diverse origin were selected as parental lines for the crosses used in this study. These varieties consisted of four two-rowed barleys, Hannchen, Piroline, Domen and Abed Denso, and three six-rowed barleys, Trebi, Atlas 46 and Traill. A detailed description of each variety is given in Appendix Table 1.

In the spring of 1963, these seven varieties were crossed in all possible combinations. No attempt was made to keep the reciprocals of each cross separate. Crosses were made by hand pollination, and only plump, well-filled seeds were chosen for use. The 21 F_1 crosses and the seven parental varieties were planted in a ground bed in a greenhouse on the campus of Oregon State University, Corvallis. The planting was made on March 26, 1964 and the plants harvested in mid-August. The experimental design was a randomized block with four replications.

The greenhouse site was chosen for this study to obtain a better control of the aphids that attack barley and transmit Barley Yellow Dwarf Virus. Another reason this site was chosen was to provide a uniform environment for the growth of the plants.

Before planting, a 20-4-6 fertilizer was applied at the rate of 500 pounds per acre. The experimental material was located in the center of the ground bed to eliminate as much as possible water seepage near the walls of the greenhouse. The experiment was surrounded by oat plants to minimize border effects on the outside plants. To insure a uniform stand and to standardize emergence, all seeds were germinated in petri dishes until the coleoptiles were about one inch long, then the seedlings were transplanted into the soil bed. Four seedlings were planted per entry in each plot. The plants within the plots were space planted 18 inches apart. The rows were also 18 inches apart. To provide sufficient moisture for the plants, the experiment was flood irrigated four times during the growing season.

Heading dates were obtained for each plant by recording the date when the first head was 50 percent exposed. The heading date for each plant was recorded as days after June 15.

Yields were obtained on the individual plants by removing the heads from each plant as each head matured. This procedure prevented loss due to shattering. The heads were then threshed by hand, and yield was recorded as grams of grain per plant.

Functional analyses of variance using plot means for heading date and yield per plant were computed.

Combining ability estimates were computed by procedures outlined by Griffing (13, p. 465). Model I and Method 4 were selected as the best suited procedures for this experiment. In Model I, the assumption is that the experimental data are to be regarded as the entire population about which inferences are to be made. Method 4 was selected because it requires only one set of F_1's and does not require reciprocal F_1's or parents. Estimates of general and specific combining ability variances associated with each parent were also determined.

Narrow-sense heritability estimates were computed by the parent-progeny method, in which the F_1 means are regressed upon the parental averages. In addition, both broad and narrow-sense heritability estimates were computed by the variance component methods. The following formulae derived from Grafius _et al_. (10, p. 254) were used:

$$Hbs = \frac{\text{among cross MS - Error MS}_1}{\text{among cross MS}} = \frac{Vh + Va}{Vh+Va+Ve}$$

$$Hns = \frac{\text{among parent MS - Error MS}_2}{\text{among cross MS}} = \frac{Va}{Vh+Va+Ve}$$

where:

Hbs = Heritability in the broad-sense
Hns = Heritability in the narrow-sense
Error MS_1 = Environmental variance for crosses
Error MS_2 = Environmental variance for parents
Vh = Non-additive genetic variance
Va = Additive genetic variance
Ve = Environmental variance

Heterosis observed for yield was measured both as the amount that the F_1 exceeded the parental average and also as the amount the F_1 exceeded the high parent. In the case of heading date, heterosis for both earliness and lateness was expressed as the deviation of the F_1 from the parental average or from the early or late parent.

The relationship between heading date and yield was determined by computations of simple correlation coefficients. The mean yield per entry was correlated with the mean date of heading for parents and F_1's. Also, the population was separated into two groups according to row number and the association of these two traits was determined for each group.

RESULTS

The mean heading date recorded as days after June 15 and the mean grain yield in grams for the seven parents and 21 single crosses are given in Table 1.

Analysis of Variance

A functional analysis of variance for date of heading is given in Table 2. For this analysis, the F_1's and parents were considered as a single group, as well as separate groups. The results indicated that there were significant differences between the entries at the one percent level. Significant differences at the one percent level were present between the parents and between the F_1's when they were considered as separate groups. There was no significant difference present for among groups. A least significant difference of 2.0 days was found for the parents when they were analyzed as a separate group. The six-rowed parents, Traill, Atlas 46 and Trebi, had mean heading dates of 11.2, 11.4 and 12.5 days respectively. The heading dates of the six-rowed parents were not significantly different from one another. The heading dates for the two-rowed parents, Domen, Piroline, Hannchen and Abed Denso, were 16.4, 12.2, 15.2 and 16.2 respectively. Three out of the four two-rowed parents were not significantly different from one another,

Table 1. Mean heading date and yield in grams of the seven parental varieties and the 21 single crosses, 1964.

Entries	Heading date[1]	Yield[2]
Traill	11.2	60.2
Atlas 46	11.4	54.7
Trebi	12.5	64.8
Domen	16.4	46.9
Piroline	12.2	51.6
Hannchen	15.2	55.3
Abed Denso	16.2	50.0
Traill x Atlas 46	8.5	63.7
Traill x Trebi	11.5	57.3
Trebi x Atlas 46	15.1	63.9
Domen x Piroline	14.4	59.5
Domen x Abed Denso	15.9	55.5
Domen x Hannchen	15.4	51.2
Piroline x Abed Denso	14.9	53.0
Piroline x Hannchen	14.6	62.1
Abed Denso x Hannchen	14.9	53.6
Traill x Domen	13.2	59.1
Traill x Abed Denso	13.1	65.1
Traill x Piroline	10.8	61.0
Traill x Hannchen	14.4	68.0
Trebi x Domen	11.5	61.5
Trebi x Abed Denso	12.2	53.1
Trebi x Piroline	9.7	52.5
Trebi x Hannchen	9.7	44.9
Atlas 46 x Domen	11.1	44.2
Atlas 46 x Abed Denso	8.5	54.5
Atlas 46 x Piroline	10.5	50.2
Atlas 46 x Hannchen	8.5	55.0

LSD at .05 level = 1.7 days
LSD at .05 level = 10.0 grams

1. Number of days after June 15
2. Mean plant yield in grams

Table 2. Functional analysis of variance for date of heading.

Source	d.f.	Sum of squares	Mean squares
Replications	3	16.02	5.340*
Entries	27	666.09	24.670**
Among groups	1	39.50	39.500 N.S.
[1]Within groups	26	626.59	24.099**
Within parents	6	124.11	20.685**
Within F_1's	20	502.49	25.124**
[2]Reps x Entries	81	123.07	1.519
[3]Reps x among groups	3	2.20	.733
[4]Reps x w/in parents	18	31.89	1.772
[5]Reps x w/in F_1's	60	90.96	1.516
Total	111	805.18	

N.S. = Non-significant at the five percent level
* = Significant at the five percent level
** = Significant at the one percent level
1 = Error term for among groups
2 = Error term for replications and entries
3 = Error term within groups
4 = Error term for within parents
5 = Error term for within F_1's

LSD and C.V. for parents = 2.0 days and 9.8 percent
LSD and C.V. for F_1's = 1.7 days and 10.0 percent
LSD and C.V. for combined F_1's and parents = 1.7 days and 9.8 percent

but the three were significantly later than all of the six-rowed varieties. Piroline was significantly earlier than the other three two-rowed parents, but not different from the six-rowed parents. A least significant difference of 1.7 days was found for the F_1's when they were analyzed alone. Using this LSD, many significant differences were present among the 21 single crosses. The F_1's mean heading dates ranged from 8.5 days to 15.9 days after June 15. The coefficient of variation was 9.8 percent, while the coefficients of variation of 9.8 and 10.0 percent were found for the parents and F_1's when they were considered as separate groups. The similarity of these two C.V.'s for the two groups indicated that the same variation was present in both groups.

A functional analysis of variance for yield is presented in Table 3. Significant differences in yield were present at the one percent level when all entries were analyzed together. The two groups, the parents and the F_1's, were not significantly different in their yield. When the parents were analyzed as a separate group, no significant differences were found among the parents in their mean yields. However, significant differences were present among the F_1's when they were considered separately. Least significant differences of 9.9 and 10.0 grams were found for the F_1's alone and for the combined groups respectively. The coefficients of variation ranged from 14.8 percent for the parents to 12.2 percent for the F_1's and 12.7 percent for the

Table 3. Functional analysis of variance for plant grain yield.

Source	d.f.	Sum of squares	Mean squares
Replications	3	79.14	26.380 N.S.
Entries	27	4,238.06	156.965**
Among groups	1	114.33	114.330 N.S.
[1]Within groups	26	4,123.73	158.605**
Within parents	6	903.60	150.600 N.S.
Within F_1's	20	3,220.13	161.007**
[2]Reps x Entries	81	4,144.52	51.167
[3]Reps x among groups	3	36.52	12.173
[4]Reps x w/in parents	18	1,185.44	65.858
[5]Reps x w/in F_1's	60	2,922.56	48.709
Total	111	8,461.72	

N.S. = Non-significant at the five percent level
** = Significant at the one percent level
1 = Error term for among groups
2 = Error term for replications and entries
3 = Error term for within groups
4 = Error term for within parents
5 = Error term for within F_1's

C.V. for parents = 14.8 percent
LSD and C.V. for F_1's = 9.9 grams and 12.2 percent
LSD and C.V. for combined F_1's and parents = 10.0 grams and 12.7 percent

two combined.

Heritability

Heritability estimates computed by the parent-progeny regression and the variance method for both traits are shown in Table 4. The narrow-sense heritability estimate found by the parent-progeny regression for heading date was extremely high, while the estimate for yield was low. When both broad- and narrow-sense estimates were calculated by the variance method, the broad-sense estimates were higher than the narrow-sense estimates for both traits. Regardless of the method used, heading date had a higher heritability value than yield.

Heterosis

The mean date of heading for the 21 single crosses, the deviations from the midpoint of the parents, and also the deviations from either the late or early parents, are given in Table 5. Heterosis for both earliness and lateness was observed. The LSD from the combined groups was used as a value to determine which deviations could be considered significant. There were five crosses significantly earlier than the earliest parent. Only one cross, Trebi x Atlas 46, was significantly later than its latest parent. No heterosis was observed between any of the two-rowed x two-rowed crosses. Two of the four Trebi x two-rowed crosses

Table 4. Heritability estimates for date of heading and yield computed by regression and variance methods

Character	Method	Broad sense	Narrow sense
Date of heading	Parent-progeny regression	--	.98
	Variance components	.94	.71
Yield	Parent-progeny regression	--	.26
	Variance components	.70	.52

were significantly earlier than the early parent. Two out of the four two-rowed x Atlas 46 crosses were significantly earlier than the earliest parent. The three six-rowed parents, when intercrossed, produced one F_1 significantly earlier than the earliest parent, one F_1 not significantly different from either parent and one F_1 significantly later than the latest parent.

The mean yield of the 21 single crosses and their deviation from the midpoint of the parents and from the high yielding parent are found in Table 6. The LSD of ten grams from the combined analysis was used to determine significant deviations of the F_1's means from their high yielding parent. None of these crosses was significantly different from the high yielding parent. Over one-half of the crosses had mean yields which were less than the high parent's yield. The cross between Piroline and Hannchen exhibited the most heterosis for yield when heterosis was determined as the amount that the F_1 exceeds the high

Table 5. Mean heading dates of the 21 single crosses and the amount of heterosis of each expressed as the deviation from the parental average and from the latest or earliest parent.

Cross	Heading dates					Deviations	
	F_1	Late parent	Early parent	Parental average	Parental average - F_1	Early parent[1] - F_1	Late parent[2] - F_1
Traill x Atlas 46	8.5	11.4	11.2	11.3	2.8	2.7*	---
Traill x Trebi	11.3	12.5	11.2	11.9	0.6	---	---
Trebi x Atlas 46	15.1	12.5	11.4	11.9	-3.2	---	-2.6*
Domen x Piroline	14.4	16.4	12.2	14.3	-0.1	---	---
Domen x Abed Denso	15.9	16.4	16.2	16.3	0.4	---	---
Piroline x Abed Denso	14.9	16.2	12.2	14.2	-0.7	---	---
Piroline x Hannchen	14.6	15.2	12.2	13.7	-0.9	---	---
Abed Denso x Hannchen	14.9	16.2	15.2	15.7	0.8	---	---
Traill x Domen	13.2	16.4	11.2	13.8	0.5	---	---
Traill x Abed Denso	13.1	16.2	11.2	13.7	0.6	---	---
Traill x Piroline	10.8	12.2	11.2	11.7	0.9	0.4	---
Traill x Hannchen	14.4	15.2	11.2	13.2	1.2	---	---
Trebi x Domen	11.5	16.4	12.5	14.5	3.0	1.0	---
Trebi x Abed Denso	12.2	16.2	12.5	14.4	2.2	0.3	---
Trebi x Piroline	9.7	12.5	12.2	12.4	2.7	2.5*	---
Trebi x Hannchen	9.7	15.2	12.5	13.9	4.2	2.8*	---
Atlas 46 x Domen	11.1	16.4	11.4	13.9	2.8	0.3	---
Atlas 46 x Abed Denso	8.5	16.2	11.4	13.8	5.3	2.9*	---
Atlas 46 x Piroline	10.5	12.2	11.4	11.8	1.3	0.9	---
Atlas 46 x Hannchen	8.5	15.2	11.4	13.3	4.8	2.9*	---
Domen x Hannchen	15.4	16.4	15.2	15.8	0.4	---	---

LSD = 1.7 days

* LSD from the analysis of the combined groups was used to determine significance

1 Only those F_1's which are earlier than the earliest parent are considered

2 Only those F_1's which are later than the latest parent are considered

Table 6. The mean yield in grams of 21 different single crosses and the deviations of these from the midpoint of their parents and from the high parent

	Yield per entry				Deviations	
Cross	F_1	High parent	Low parent	Parental average	F_1 $\bar{x}$-parental $\bar{x}$	F_1 $\bar{x}$-high parent $\bar{x}$
Traill x Atlas	63.7	60.2	54.7	57.5	6.2	3.5
Traill x Trebi	57.3	64.8	60.2	62.5	-5.2	-7.5
Trebi x Atlas	63.9	64.8	54.7	59.8	4.1	-0.9
Domen x Piroline	59.5	51.6	46.9	49.3	10.2*	7.9
Domen x Abed Denso	55.5	50.0	46.9	48.5	7.0	5.5
Domen x Hannchen	51.2	55.3	46.9	51.1	10.1*	5.9
Piroline x Abed Denso	53.0	51.6	50.0	50.8	2.2	1.4
Piroline x Hannchen	62.1	55.3	51.6	53.5	8.6	8.2
Abed Denso x Hannchen	53.6	55.3	50.0	52.7	0.9	-1.7
Traill x Domen	59.1	60.2	46.9	53.6	5.5	-1.1
Traill x Abed Denso	65.1	60.2	50.0	55.1	10.0*	4.9
Traill x Piroline	61.0	60.2	51.6	55.9	5.1	0.8
Traill x Hannchen	68.0	60.2	55.3	57.8	10.2*	7.8
Trebi x Domen	61.5	64.8	46.9	55.9	5.6	-3.3
Trebi x Abed Denso	53.1	64.8	50.0	57.4	-4.3	-11.7
Trebi x Piroline	52.5	64.8	51.6	58.2	-5.7	-12.3
Trebi x Hannchen	44.9	64.8	55.3	60.1	-15.2	-19.9
Atlas x Domen	44.2	54.7	46.9	50.8	-6.6	-10.5
Atlas x Abed Denso	54.5	54.7	50.0	52.4	2.1	- 0.2
Atlas x Piroline	50.2	54.7	51.6	53.2	-3.0	- 4.5
Atlas x Hannchen	55.0	55.3	54.7	55.0	0.0	- 0.3

*LSD from combined analysis of variance was used to determine significance = 10.0 grams parent. The Traill x Hannchen cross exhibited the most heterosis for yield when heterosis was determined as the deviation of the F_1's mean from the parental average.

The extent of heterosis for yield measured by deviations and percent increase in yield of the F_1's means over the parental means when the F_1's and parents were grouped according to row number is found in Table 7. The amount of heterosis exhibited by the three groups of F_1's varied. Two-rowed x two-rowed crosses showed the most heterosis, and the two-rowed x six-rowed crosses showed the least. When the mean yield of the seven parental varieties was compared to the mean yield of the 21 single crosses, the F_1's showed an average increase in yield of 3.96 percent.

Table 7. A comparison of the mean yields in grams of the F_1's and parents when they are grouped according to row number

Crosses	Parental mean	F_1 mean	Deviations $F_1 \bar{x} - P\bar{x}$	% Increase over parental $\bar{x}$
Six-rowed x six-rowed	59.9	61.6	1.7	2.83%
Two-rowed x two-rowed	51.0	55.8	4.8	9.41%
Six-rowed x two-rowed	55.5	55.8	0.3	.54%
All crosses	55.5	57.7	2.2	3.96%

Correlation

A correlation value of r = .024 was obtained when the mean heading date and the mean yield of all 21 crosses and parents were correlated. When the mean heading date and the mean yield of the six-rowed parents and their intercrosses were correlated, a value of r = .569 was obtained. A correlation value of r = -.257 was obtained for the mean heading date and yield of the two-rowed parents and their intercrosses. None of the correlation coefficients was significant.

Combining Ability

The observed general and specific combining ability mean squares for heading date and yield are listed in Table 8. Both general and specific combining ability effects were significant for date of heading and yield. The observed mean squares for general combining ability for both date of heading and plant yield were larger than the observed mean squares for specific combining ability. Estimates of general combining ability effects associated with each parent for both traits are presented in Table 9. Positive general combining ability effects associated with a parent indicates that the parent produced F_1's which required more days to head or produced more grain than a parent which has a negative general combining ability effect.

Table 8. Observed mean squares of the general and specific combining ability analysis for date of heading and yield for the 21 single crosses.

Source of variation	d.f.	Mean squares	
		Date of heading	Yield
Between crosses	20	25.1230**	161.0070**
General combining ability	6	35.4667**	172.9133**
Specific combining ability	14	20.4886**	154.9229**
Error	60	1.5160	48.7093

**Significant at the one percent level

Table 9. Estimates of general combining ability effects associated with each parent.

Parent	Date of heading	Yield
Traill	- .49	6.33
Atlas 46	-2.31	-2.21
Trebi	- .85	-1.81
Domen	1.55	- .31
Piroline	.23	- .85
Hannchen	.75	.45
Abed Denso	-1.15	1.55

Only two parents, Traill and Hannchen, had positive general combining ability effects for yield. The three six-rowed parents had negative general combining ability effects for date of heading. The four two-rowed parents had positive general combining ability effects for date of heading.

Estimates of specific combining ability effects associated with each parent for both traits are presented in Table 10. When yield is considered, the greatest effect was found in the cross of Atlas 46 x Trebi. Large negative values were found in the crosses of Hannchen x Trebi and Atlas 46 x Domen. The specific combining ability effects for date of heading were small, with the exception of the cross between Atlas 46 and Trebi.

Table 10. Estimates of specific combining ability effects associated with each parent.

Parents	Trait	Abed Denso	Hannchen	Piroline	Domen	Trebi	Atlas	Traill
Traill	x_1	3.22	4.12	-1.58	-4.02	-4.26	2.48	---
	x_2	.15	1.85	-1.23	- .15	.35	- .99	
Atlas	x_1	1.16	- .34	-3.84	-10.38	10.88	----	
	x_2	-2.63	-2.23	.29	- .43	5.97		
Trebi	x_1	- .58	-10.78	-1.86	6.58	----		
	x_2	- .59	-2.49	-1.97	-1.49			
Domen	x_1	.26	3.91	3.56	----			
	x_2	.91	.81	.33				
Piroline	x_1	-1.70	5.40	----				
	x_2	1.23	1.33					
Hannchen	x_1	-2.40	----					
	x_2	.71						
Abed Denso	x_1	----						
	x_2							

x_1 Yield
x_2 Date of heading

DISCUSSION

The commercial use of hybrid barley may be the next step in the development of higher producing barley varieties. Before it will be feasible to produce hybrid barley on a commercial scale, additional research is needed on the actual mechanics of producing hybrid seed. Studies to determine the amount of heterosis present in barley would also be desirable. One of the current methods of developing higher yielding barley varieties is through the process of hybridization of selected parents followed by selection in later generations of desirable segregates. The success of the hybrid program or by the selection method will be determined to a large extent by the choice of appropriate parents. It is apparent that a variety which would make a good parent for the production of hybrids might not necessarily be a suitable parent for the hybridization and selection method, since the maximum expression of high yield in these two methods is the result of different types of gene action. The hybrid program capitalizes mainly upon non-additive genes, while the hybridization and selection depends entirely on the additive gene action.

Regardless of the method, the problem of screening prospective parents to identify those that will contribute the most to the breeding program must be resolved. A possible technique whereby the breeder can determine the breeding potential of prospective parents is through a diallel crossing system. This system provides for the examination of F_1 populations obtained from crossing of a series of parents in all possible combinations and allows the breeder to observe large numbers of different hybrid combinations. It was the purpose of this study to examine heading date and yield in seven different barley varieties crossed in a diallel combination.

Heading date

Heading date in barley is often used as a measure of maturity. Maturity under certain conditions can be a very important character. Some varieties of barley may be able to produce well under seasonal changes in moisture due to their early or late maturity. Some disease epidemics can be avoided by growing early or late maturing varieties. An early or late maturing variety may fit into a particular cropping program better than another variety. For these reasons, heading date has received considerable attention by barley breeders.

The type of gene action controlling heading date and the number of genes involved has not been completely resolved in barley. From the results of this study, based on F_1 data, it appears that for the seven widely diverse varieties investigated, heading date was controlled by relatively few genes, but both additive and non-additive genes may be present.

An indication of the number of genes which controlled heading date in these barley crosses can be obtained by observing the behavior of the different parental combinations. There was similarity between the F_1's of two-rowed parents when they were intercrossed. This would indicate that the two-rowed varieties must have similar genes in common which control heading date. Although the six-rowed parents were all early, they appeared to have different factors for earliness since they behaved quite differently when they were crossed to each other and to the four two-rowed parents. One could conclude from these observations that the number of genes conditioning earliness was not large, but that there would have to be more than one major gene present to account for the differences in the three six-rowed parents.

Estimates of the type of gene action controlling heading date can be obtained by studying heritability estimates and combining ability estimates. The amount of heterosis present for a trait also may serve as an indication of the type of gene action controlling that trait.

The magnitude of the narrow-sense heritability estimate indicated the portion of additive genetic variance for heading date which was present in the total phenotypic variation. The magnitude of the broad-sense heritability estimate indicated that portion of the total variation which is genetic in nature.

This estimate would include both the additive and the non-additive variances. Theoretically, the broad-sense heritability estimates would equal the narrow-sense heritability estimates if the total genetic variance was due entirely to additive genes or genes which behave in an additive manner. This would be true because of the assumptions involving the type of genetic variation present in parental lines and the hybrids. Genetic differences between homozygous parents can be considered to be the result of additive genes. Genetic differences between hybrids may be either the result of additive, non-additive or a combination of these types of gene action. The extremely high narrow-sense heritability estimate of 98 and 71 percent obtained for heading date in this study by both the regression and variance methods, would support the conclusion that additive gene action was responsible for the majority of the genetic variation present for heading date.

The difference in magnitude between the regression method and the variance method in estimating narrow-sense heritability for heading date in this study, might be accounted for by a bias present in this population. Although the parental lines were selected from widely divergent areas of the world, they can be separated into two groups according to their heading date. The six-rowed parents constitute an early heading population and the two-rowed parents a late heading population. Since heading date appears to be controlled by relatively few genes, crosses within these two populations generally result in progeny which are similar to the parents, thus leading to a high parent-progeny regression value.

The broad-sense heritability estimates for heading date determined by the variance method exceeds the narrow-sense heritability estimates also computed by the variance method. The amount that the broad-sense estimate exceeded the narrow-sense was sufficiently large to make it evident that non-additive gene action also conditioned heading date.

An indication of the importance of the additive gene action for heading date can also be observed in the significant mean square for general combining ability. Another type of gene action which might contribute to the general combining ability estimate is additive x additive interactions.

An indication of the importance of the non-additive type of gene action can be observed in the significant mean square for specific combining ability. High specific combining ability for a trait is brought about by genes which exhibit dominance and epistasis.

The expression of heterosis for a trait can be used as an indication of the extent of non-additive gene action present. When a trait such as heading date is considered, it must be realized that heterosis can occur for either earliness or lateness. Thus, heterosis for both earliness and lateness should be considered as a measure of the same phenomenon of non-additive gene action. Approximately one-third of the crosses studied in this experiment exhibited heterosis for heading date. This incidence of heterosis among the crosses and more particularly among crosses involving certain parents, is an indication that some of the parents studied were carrying genes with the ability to produce heterotic effects.

Yield

Yield in barley, as in other small grains, is a complex trait controlled by many genes, some of which may have additive effects and some non-additive effects, as well as the various complicated interactions. The type of gene action influencing yield in this population can be determined at least in part, by computing heritability estimates and combining ability estimates. The expression of heterosis can also be used as an indication of the type of gene action present for this character.

From the results obtained in this study, yield was found to be controlled by both additive and non-additive genes. When the narrow-sense heritability estimate is compared with the magnitude of the broad-sense heritability estimate for yield, it is evident that both additive and non-additive genes are present in controlling the expression of yield. A comparison of the mean squares for general and specific combining ability estimates also supports this general conclusion. The amount of heterosis as expressed in the number of crosses which exceed the parental average in yield was less than for heading date. Since some crosses did exhibit heterosis, some non-additive genes for yield must be present in this population.

Selection of parents

The screening of varieties to be used as prospective parents for either of the two breeding methods previously mentioned should be based on the breeding potential of each parent. Estimates of the type of possible genetic contribution by each parent to its progeny can be obtained by general and specific combining ability effects associated with each parent. The best measurement of the breeding potential of each parent for the hybrid program can be obtained by direct examination of the hybrid means obtained in the diallel analysis.

The selection of prospective parents for the hybrid breeding programs can be best accomplished by observing the F_1 combinations of these parents. This may not even be necessary for a simply inherited trait like heading date that has an extremely high narrow-sense heritability. The parental mean for heading date in this study would serve equally well as the information obtained from diallel analysis for selection of parents. Since specific combining ability effects are based upon F_1 data, information found in this manner would be expected to be quite similar to that which can be obtained by the simple observation of the hybrid means. If this is true, as it is suggested by this study, then there is little need to compute combining ability effects for the parental lines for the hybrid program. Selection, thus, should be based, depending upon the trait, on parental means or hybrid means.

The best parental combination for the development of a high yielding two-rowed hybrid among the varieties studied here based upon their hybrid means, would be a cross between Piroline and Hannchen. This same parental combination would be selected if selection was based on estimates of specific combining ability effects associated with each parent. Atlas 46 and Trebi would be selected by both methods as the best parental combination to produce a high yielding six-rowed hybrid. It is interesting to note that if the parental combinations were selected on the basis of their parental means, the same parents would have been selected for the two-rowed hybrid, but Traill would be one of the six-rowed parents for the six-rowed hybrid.

In self-pollinated crops, to obtain high yielding new varieties, it has been the general practice to select and cross the two highest yielding parents which between them possess the desired characters and which are well adapted to the location.

This has been done mainly because breeders considered this the best method of improving barley varieties. Thus, crossing of parents with the best breeding potential has not always been done. By selecting the highest yielding parents, valuable genetic material which might lead to superior yielding progeny may be overlooked.

The selection of parents which possess the best breeding potential for the development of high yielding segregates following hybridization and selfing should be based upon estimates of the different genetic contributions possible by each parent. It becomes clear that the expression of heterosis is of little value in determining the breeding potential of parents for the hybridization and resulting selection program. Heterosis exhibited in the F_1 generations will decrease steadily with each self-pollinated generation. This is because the expression of heterosis is brought about by genes which are non-additive in nature and non-additive gene action is lost during increased homozygousity due to self-pollination. Additive gene action is not affected by the selfing process, thus parents which contain a large proportion of additive genes for yield will be able to produce the highest portion of high yielding segregates. Selection of parents based upon their general combining ability effects and not on parental means or specific combining ability effects, might provide a more efficient way of accumulating favorable additive genes for yield.

There have been many attempts to combine the high yield of six-rowed barley with the desirable characters of two-rowed barleys. The main limitation to these crosses has been the segregation for row number and kernel size which occurs in later generations of such crosses. The evaluation of the F_1's resulting from two-rowed x six-rowed barley crosses is often confounded by the lack of uniformity of row number.

In this population, the two highest yielding parents, which include a six-rowed and a two-rowed parent, were Trebi and Hannchen. It is of particular interest to note that Trebi had a negative general combining ability effect. It is also of interest that the specific combining ability effect for the Trebi x Hannchen cross was negative. According to the combining ability analysis, the use of Trebi as the six-rowed parent in combination with Hannchen would be less desirable than the Traill x Hannchen combination. For a trait such as yield, the parental yielding ability determined by a variety's mean yield may not be a good indication of a variety's breeding potential. Additional generations are needed to check these predictions.

The selection of parents for hybridization and later selection for heading date could also be based upon combining ability analysis. Since heading date is controlled by fewer genes than yield and under the control of primarily additive gene action, it would not be necessary to base selection of possible parents upon combining ability analysis. Heading date would be readily fixed as suggested by Frey (8, p. 227) and only limited segregation in later generations would take place.

The association of heading date and yield was extremely low when the 21 crosses and the seven parents were correlated. This low correlation coefficient indicates that for the population studied here, these two traits are not associated and that selection for a particular heading date would have little effect on yield. However, when the population was separated into two groups according to row number, heading date and yield appeared to be associated. These two traits were positively associated when only the six-rowed parents and their intercrosses were considered which is in agreement with Askel and Johnson (2, p. 254). A negative association was found for these two traits when the two-rowed parents and their intercrosses were considered. Breaking the population correlation coefficient into meaningful units, shows that there is some association between these two traits which should be considered.

The explanation for the positive association of heading date and yield among the six-rowed parents and the negative association among the two-rowed parents lies in the manner that these two barley types attain their maximum yield. In general, six-rowed varieties are characterized by having relatively few heads per plant but each head has a large number of seeds. Two-rowed varieties have a larger number of heads per plant than six-rowed varieties, but each head has a small number of seeds. Thus, six-rowed varieties obtain high yields through large numbers of seeds per head while two-rowed varieties obtain high yields through a large number of heads per plant.

Seed number per head is determined partly by the formation of the perianth which provides space for the kernel to develop. The period of sowing-to-heading is when formation of the perianth takes place, while actual seed development takes place after heading. A longer sowing-to-heading period, as related by a later heading date, allows for maximum perianth formation. Thus, those six-rowed varieties with a late heading date are generally the most productive as the positive association points out. A long sowing-to-heading period also provides for maximum perianth formation in two-rowed varieties. Since high yields are generally obtained through larger numbers of heads per plant instead of large numbers of kernels per head, a positive association would not be expected. A longer sowing-to-heading period for a two-rowed plant generally means that the plant will have a shorter period in which tillering can take place. This reduces the number of heads per plant which is the main component of yield for two-rowed varieties and could account for the negative association of heading date and yield.

SUMMARY AND CONCLUSIONS

The first objective of this study was to determine the type of gene action present for heading date and yield. A further objective was to identify those parental genotypes which would be expected to perform the best in a hybrid program or a program of hybridization followed by selection of desirable segregates.

To accomplish these objectives, seven widely divergent barley varieties were crossed in all possible combinations in the spring of 1963. The 21 F_1's and seven parents were space-planted in greenhouse beds in 1964, and heading date and yield were recorded on an individual plant basis. Estimates of gene action were obtained by combining ability and heritability estimates, as well as by the expression of heterosis. Parental varieties were studied on the basis of varietal means, hybrid means and combining ability estimates.

From the results of this study, the following conclusions were made:

1. Both heading date and yield in this population appeared to be conditioned by both additive and non-additive gene action.
2. The extremely high narrow-sense heritability estimates obtained for heading date in this study indicated that the parental mean heading date would serve as a good

criterion for selection for desired heading dates.

3. The low to medium narrow-sense heritability estimates obtained for yield in this study indicated that additional information other than the parental mean yield is needed before selection of the most desirable parents could be made.
4. The failure of any hybrid combination to produce significantly more grain than the high parent of that combination demonstrates that none of the parental combinations observed in this study could be used in the commercial production of hybrid barley.
5. From the general and specific combining ability effects associated with each parent in this study, it could be concluded that the highest yielding parents might not have the most breeding potential for the plant breeding procedure of hybridization followed by selection. It appears that good genetic material may be lost when only superior appearing varieties are selected as parents.
6. In this study, yield and heading date were not significantly correlated. There was a positive association present between heading date and yield for the six-rowed parents and their intercrosses. When the two-rowed parents and their intercrosses were considered, a negative association was found. The difference in these

two associations was concluded to be due to the different manner that high yields are obtained by these two groups.

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APPENDIX TABLE 1

A DESCRIPTION OF THE VARIETIES IN THIS STUDY

Variety name	C.I. No.	Origin	No. rows	Utilization
Atlas 46	7323	A bulk seed lot from a cross between Hanna x Atlas[7] and Turk x Atlas [8] made in California.	6	Malting
Trebi	936	A plant selection from a bulk seed lot from Asiatic Turkey.	6	Feed
Traill	9538	A selection from a cross between Titan and Kindred made in North Dakota	6	Malting
Piroline	9558	A selection from a cross of Weihenstephaner MPI x Margensot made in Holland.	2	Malting
Hannchen	531	A pure line selection from Hanna made at Svalof Plant Breeding Station, Sweden.	2	Malting
Abed Denso	----	Field mutant from Abed Plant Breeding Station, Denmark	2	Not released
Domen	9562	A selection from a cross of Opal B and Maskin made in Norway.	2	Malting