

AN ABSTRACT OF THE THESIS OF

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AREA AND MALTING QUALITY IN 21 SPRING BARLEY CROSSES

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The purpose of this study was to determine the amount of heterosis in three complex traits in barley and to investigate the concept of component interaction as a means of producing heterosis. The complex traits were grain yield, total leaf area, and malting quality.

Seven varieties of spring barley were crossed in all possible combinations in the spring of 1963. The following year, the 21 F_1 's and seven parental varieties were space planted in a replicated, randomized block design in a greenhouse groundbed on the campus of Oregon State University. Since three of the seven parents were six-rowed barleys (Hordeum vulgare L., emend. Lam) and four were two-rowed barleys (Hordeum distichum L., emend. Lam), crosses within and between six-rowed and two-rowed barleys were included in this study. The 21 crosses were separated according to their respective parental row numbers throughout this study.

The evaluation of heterosis for the complex traits was made by

the component approach. The amounts of heterosis for the complex traits were related to the expression of heterosis of their components. The association between components and the complex traits and between the different components, were determined by computing simple correlation coefficients. The direct and indirect relationships of the components to the complex traits were further analyzed by path coefficient analyses. Estimates of the type of gene action present for the complex traits, as well as for their respective components, were made by computing general and specific combining ability estimates and narrow-sense heritability estimates.

Heterosis may occur in a complex trait even though none of the components of the complex trait exhibit heterosis. This situation has been called component interaction. When parental varieties do not differ in the complex trait but possess large differences in the components of the complex trait, component interaction may occur in the hybrid to produce heterosis in the complex trait. Additive expressions for the components in the hybrids of such parental varieties may result in the hybrids exceeding both parents in the complex trait.

Large differences in the components of the three complex traits were found to exist among the parental varieties in this study while the parental varieties were not greatly different in the complex traits. These findings would suggest that component interactions were likely to occur in the hybrids produced by crossing the parental varieties. However, in this study, the expression of heterosis for the three complex traits was limited, with

only a few crosses expressing a substantial amount of heterosis. The lack of heterosis, particularly in those crosses where the largest differences in the components existed between the parental varieties, could be ascribed to the failure to obtain an additive expression in the hybrid for the most important components. The relationships between the components of the complex traits also indicated that the components were not completely independent. The lack of independence of the components could also prevent component interactions. There were several crosses which did exhibit component interaction in the expression of heterosis for the complex trait but these were relatively few in comparison to those which did not exhibit component interaction.

Estimates of gene action, in general, were in agreement with the observations of heterosis. Those traits which exhibited the most heterosis were found to be controlled mainly by non-additive gene action while those traits exhibiting a slight amount of heterosis were found to have large additive gene action estimates associated with them.

THE EVALUATION OF HETEROSIS FOR GRAIN YIELD,
TOTAL LEAF AREA AND MALTING QUALITY
IN 21 SPRING BARLEY CROSSES

by

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THE EVALUATION OF HETEROSIS FOR GRAIN YIELD,
TOTAL LEAF AREA AND MALTING QUALITY
IN 21 SPRING BARLEY CROSSES

INTRODUCTION

Plant breeders have been interested for many years in ways and means by which gains from heterosis might be utilized in self-pollinated crops such as barley. Recent discoveries of methods to produce large quantities of hybrid seed in barley have enhanced the possibility of widespread commercial use of barley hybrids. Male sterile balanced tertiary trisomics and male sterile-phytocide linkages or a combination of both, are two recent genetic procedures conceived for the production of hybrid barley. The success of commercial hybrid barley will partly be dependent upon the ability to identify parental varieties which, when crossed, will give a maximum expression of heterosis. Likewise, information on the extent to which heterosis can be obtained in hybrid barley is also needed.

The occurrence of heterosis has been observed and measured by many workers in many different plants and animals. There have been genetical, physiological and morphological hypotheses presented to explain the occurrence of heterosis but as yet no single hypothesis has been found to be completely acceptable. The amount of heterosis present in hybrids has been measured by several different methods. Heterosis has been deemed to be present when the mean value for the particular trait in the hybrid has exceeded the parental midpoint or when the hybrid value exceeded the better

parental value. In the self-pollinated species, the latter method is considered to be more important, since the hybrid must exceed the better parent before the hybrid would possess economic importance or advantage.

The two major cultivated species of barley are Hordeum vulgare L., emend Lam., the well known six-rowed barley, and Hordeum distichum L., emend Lam., the two-rowed barley. These two species are separated primarily on the basis of a single genetic factor controlling the fertility of the lateral florets, but they likewise differ in several well recognized morphological and physiological characters. Varieties of these two species are often crossed freely in conventional barley breeding programs and similarly, crosses between varieties within these species would possibly be used in hybrid breeding.

It is often difficult to analyze, interpret and predict the genetic behavior of complex plant traits. To provide a basis for a better understanding of complex traits, the "component approach" or subdividing the complex trait into its logical components has been undertaken. Three such complex traits in barley are grain yield, total leaf area, and malting quality.

Heterosis may be exhibited for the complex trait itself as well as for the individual components. For this reason, knowledge of the behavior and genetic control of the individual components that together constitute a complex trait may be important before a full understanding of this trait can be obtained.

The main objective of this study was to measure and analyze the occurrence of heterosis for three complex traits through examination of their respective components. Towards this objective, the following specific studies were directed: (1) to demonstrate the existence of reciprocal differences in the components of the three complex traits in crosses between H. vulgare and H. distichum; (2) to determine the relationship between the components and the complex traits; and (3) to relate gene action estimates for the complex traits and their respective components to the occurrence of heterosis.

LITERATURE REVIEW

A comprehensive and thorough review of the literature on the cytology and genetics of barley was published by Smith (1951). Nilan (1964) extended this review and included the more recent literature. These two publications provide a complete survey of the literature on the broad topics of the cytology and genetics of barley and also provide more specific references on the important characteristics of the barley plant.

For the purpose of this review, the pertinent literature has been grouped into sections for each of the major plant traits covered in this study. These traits were as follows: yield and components of yield; total leaf area and components of total leaf area; and malting quality.

Yield and Components of Yield

One of the first studies on grain yield of barley where emphasis was placed on the behavior of the components of yield was conducted by Immer (1941). The amounts of heterosis for grain yield, heads per plant, kernels per head and weight per seed were determined for six different barley crosses between six-rowed parents. The average amounts that the F_1 's exceeded the parental averages for heads per plant, kernels per head, weight per seed and yield per plant were 8.3, 11.1, 4.9, and 27.3 percent respectively. Immer stated, "Average heterosis for yield per plant of all crosses must be greater than any one of the three components into which it

was separated since the F_1 exceeded the average of the parents for each of the components."

The expression of heterosis for grain yield per plant, weight of 1,000 seeds, length of ear and tillers per plant was determined for 17 F_1 barley crosses by Hagberg (1953). In general, the F_1 's were intermediate or equal to the best parent; however, in a few combinations, the F_1 's were superior to the best parent but the differences were not significant. In crosses between two-rowed and six-rowed barleys, the weight of 1,000 seeds was about 20 percent higher than the two-rowed parents which had heavier seeds than the six-rowed parents. It was concluded that heterosis in barley was found mainly in those characteristics which have not been the object of man's selection pressures. There appeared to be no relation between the degree of heterosis and the geographical location of the parents.

A recent paper on forage and grain production of four six-rowed barley hybrids and their parents was published by Pawlisch and Van Dijk (1965). These authors observed heterosis for forage yield in all hybrids when heterosis was measured over the high parent. The percentage increase of the F_1 's in forage yield over the high parents ranged from 8 to 31 percent. Two of the hybrids had more forage yield than the best commercial variety in the area. The grain yields of the four hybrids were 37, 25, 8 and 25 percent over the better parent. When the components of grain yield were compared, it was found that no single component was consistently better in the hybrids than in the parents.

The expression of heterosis for grain yield was measured by Suneson and Riddle (1944) in an experiment where large quantities of hybrid seed were used in solid seedings. The average yields of the F_1 's were more than 20 percent better than the parents. The F_1 's from the two-rowed and six-rowed parents had lower tiller number and bushel weights, but they had higher weight per seed and grain yield per plant than did the better parent.

Another study was conducted by Suneson (1962) on the evaluation of hybrid vigor in three six-rowed barley crosses. The F_1 's and parents were seeded in various planting designs and densities. The crosses were found to be 30 to 50 percent more productive than the parents. Maximum differences between the F_1 hybrids and their parents were found when the hybrids were competing with their parents in mixed stands. Smaller differences were found between parents and hybrids at thinner spacings. Suneson (1962) concluded that with a long growing season, tillering and head size can be maximized from thin stands. Tillers per plant appeared to be the principle component which caused increased yields in the hybrids. None of the hybrids exceeded the best parent in number of seed per head or weight per seed.

A modern and mathematical interpretation of yield in barley was presented by Grafius (1959). In this work, yield was discussed on the basis of a geometrical model where yield was pictured as the volume of a rectangular parallelepiped with heads per plant, seeds per head, and average seed weight as the edges. A slight increase in the component with the shortest edge of this

parallelipiped would result in the greatest increase in volume. In an actual experiment, Grafius (1959) found that all of the F_1 values exceeded the parental means for yield. The average F_1 values exceeded the parental means for heads per plant, seeds per plant and weight per seed. The associations between the components were either small or zero and from these results it was suggested that there are no genes for yield per se but only genes for the components of yield. From these results, Grafius also concluded that epistasis was the most prominent cause of heterosis in barley.

The type of gene action controlling heterosis in barley was investigated by Aastveit (1964). It was stated by Aastveit "that if heterosis is due to over-dominance, then it would not be possible to select segregating lines which are equal to the F_1 ." In this study, the author found a slight amount of heterosis for yield in the barley hybrids, while no heterosis was found for tillers per plant. A significant interaction was found for the F_1 means versus the parental means x years for the three characters. This indicated that the genotype-environmental interaction is a component of heterosis which should not be neglected. Selection of F_8 generation lines which were equal to the F_1 's in grain yield, indicated that heterosis was not due to over-dominance.

Heterosis in complex characters was investigated by Williams (1959) who stated, "when two parents differ reciprocally for two interacting components, and if the F_1 levels compensate one another in such a way that their product is greater than in the parent, heterosis is inevitable." Therefore, it follows that

reciprocal inequalities in the levels of component characters in the parents and intermediate levels in the hybrids must lead to heterosis in the complex characters. It was shown from data with wheat and tomatoes that essentially additive genetic systems for the components may lead to an erroneous interpretation of the existence of non-additive gene action for the complex trait.

The expression of heterosis for grain yield and its components (weight per kernel, kernels per spikelet, spikelets per spike, and spikes per plant) in wheat has received considerable attention. Whitehouse, Thompson and Do Valle Ribeiro (1958) found no heterosis for the components of grain yield in wheat. The means for the components in the 16 hybrids were, on the average, slightly in excess of the midparent. However, heterosis was found for grain yield. It was concluded by these workers that gene interactions were responsible for the expression of heterosis for grain yield. Kronstad and Foote (1964) used estimates of general and specific combining ability to determine the type of gene action present for grain yield in diallel crosses. No significant specific combining ability was found for any of the components but significant specific combining ability was found for grain yield. The mean values for the components were generally intermediate between the two parental varieties.

Johnson and Aksel (1959) studied the inheritance of yielding capacity in a fifteen parent diallel cross of barley. Yield was considered to be a complex trait with heads per plant, kernels per head, and weight of seed as the components of yield. The crosses

involved five two-rowed and ten six-rowed barleys. The two-rowed and six-rowed parents and crosses were separated when it became apparent that they did not behave in a similar manner. Over-dominance for yield was found in the subsequent nine parent diallel. The associations, as measured by the correlation coefficients between the components for the six-rowed F_3 plants were -0.440, 0.390, and 0.110 for number of kernels per head versus average kernel weight, number of kernels per head versus grain yield, and weight per kernel versus grain yield, respectively. The associations for the same traits for the two-rowed F_3 plants were -0.100, 0.710, and -0.310, respectively.

Trebi was used as a male parent in five barley crosses which were studied by David (1931) and grown in a greenhouse under uniform environmental conditions. David concluded that the parents which had been used in this study did not differ significantly in genetic factors for yield. A high simple correlation coefficient between stems and plant yield was observed. There was little evidence for the inheritance of stem number.

The major differences and similarities between six-rowed and two-rowed barleys were studied by Wiklund (1954). The correlations between tiller number and grain yield for two-rowed and six-rowed groups were +0.700 and +0.250, respectively. The kernels on two-rowed segregates from two-rowed x six-rowed crosses were larger than those usually found on two-rowed plants. The number of kernels per head on these segregates was fewer than on the normal two-rowed varieties. The author concluded that this was due to the

inheritance of the low rachis node number from the six-rowed barleys. The six-rowed x two-rowed hybrids were not able to compete with the best varieties for that area.

Kump (1953) studied tillering, number of internodes per rachis, percent of fertile spikelets on the ear, weight per kernels, and total yield per main ear in three six-rowed x two-rowed crosses. He concluded that hybridization of Hordeum vulgare and Hordeum distichum can produce six-rowed barley varieties of better quality and more reliable yields. This was based on the facts that the six-rowed segregates had more internodes per head and larger seeds per head. The yields of two-rowed segregates were also increased as the result of larger seeds per head. The associations between yield and its components and among the components have been the object of several studies. Lambert and Liang (1952), in a study with six-rowed segregates from crosses between two-rowed barleys, found simple correlation coefficients for yield and tiller number, yield and seeds per head and for yield and weight per 1,000 kernels of 0.606, 0.095, and 0.131, respectively. The associations between the components were -0.363, -0.135, and -0.305 for tiller number and kernel number, tiller number and weight per 1,000 kernels, and kernel number and weight per 1,000 kernels, respectively. Similarly, Fluzat and Atkins (1953) determined the association between the components of yield and yield in a segregating barley population. They found that the correlation coefficients between tiller number and yield, tiller number and weight per seed, and weight per seed and yield were 0.880, -0.240, and -0.040, respectively. No

heterosis in the F_1 's was observed for tillers per plant or grain yield, while a slight amount was observed for kernel weight.

Broad-sense heritability estimates for tiller number per plant, yield per plant, and kernel weight were 26.5, 47.3, and 29.9 percent, respectively.

Heritability estimates for grain yield in barley have been determined by several workers. Grafius, Nelson and Dirks (1952) obtained broad-sense heritability estimates from F_3 lines of 26 percent. The narrow-sense estimate for these F_3 lines was only four percent. Jogi (1956) found narrow-sense heritability estimates for grain yield in F_6 lines of 61, 64, and 60 percent for three experiments. Frey (1954) used the regression of F_5 lines on F_4 lines to obtain a narrow-sense heritability estimate for yield of 30 percent.

The inheritance of genes controlling the fertility of lateral florets in barley and their effect on yield has also received considerable attention. An extensive summary of the literature of fertility was published by Nilan (1964). Powers (1936) described the appearances of plants with VV, Vv and vv genes. Plants with VV genes did not have kernels developed in the rudimentary lateral florets. The heterozygote Vv approached the Hordeum deficiens parent (vv) in that no lateral grains were produced, but it was distinguishable from the VV homozygote in that the lateral florets, although rudimentary, were noticeably developed. In a cross between VV and vv barleys, a slight amount of heterosis was found for grain yield. In a recent study, Swasup and Sharma (1965) presented data from a study of the segregates from crosses between

Hordeum vulgare, H. distichum, and H. irregulare that indicated that the inheritance of fertility of lateral florets was more complicated than a single gene pair.

Total Leaf Area and Components of Total Leaf Area

A search of the literature revealed that only a limited amount of work has been reported on leaf area traits in barley. There have been a few studies demonstrating the importance of leaf area in barley and a few studies on the genetic control of leaf length and width. These studies, along with a few pertinent findings in other crops, will be reviewed.

Gardener, et al. (1964) found in barley that total leaf area, leaf size, and orientation were important factors in determining grain yield. Measurements of leaf area, dry weight, and light interception were taken every three days on six barley varieties. The higher yielding varieties had narrow upright leaves, while those of lower yield had wider and drooping leaves. It was concluded by Gardener (1964) that the higher yielding varieties had optimum leaf area indexes which were reached later in the year, nearer the grain filling period. Total leaf area and net assimilation rates were measured periodically for three barley varieties by Watson, Thorne and French (1958). The three varieties differed in grain yield, but no differences in total leaf area or net assimilation rates were found. It was concluded that the higher yields obtained by two of the varieties were not due to greater production of dry matter by the leaves. There was a strong indication that

the differences in yields were due to the ears being exposed for a longer time. It was found in a greenhouse experiment that 26 percent of the dry matter in grain came from the ears, 59 percent came from the flag leaf lamina and sheath, and 15 percent from parts of the shoot below the flag leaf.

Meyazawa, as cited by Smith (1951), found width of leaf was intermediate in hybrids between narrow and broadleaved types. The F_2 plants tended to segregate on a 1:2:1 ratio. Longer leaves tended to be dominant over shorter leaves. The classification of the F_2 plants suggested that there was only one gene controlling leaf length. Ramage and Day (1960) found a 10:3:3 ratio for leaf width in the F_2 generation of a cross between a mutant with two-thirds normal width and a mutant with one and three-fourths normal width. Jain (1961) found leaf shape to be linked with the earliness factor on chromosome V.

The expression of heterosis for total leaf area in beans was studied by Adams and Duarte (1961, 1963). Heterosis in the hybrid was interpreted by the component interaction model. A variety with few large leaves was crossed to a parent with many small leaves. There was a non-significant negative correlation between leaf size and leaf number which suggested that the components were under different gene controls. The genes for leaf size behaved in an additive manner with the F_1 having intermediate sized leaves. The genes controlling leaf number were dominant with many leaves being dominant over few leaves. There was a large amount of heterosis for total leaf area in the F_1 , since the parents complemented

each other. It was concluded that this type of heterosis could be fixed, since it is not dependent upon heterozygosity.

Kheiralla and Whittington (1962) conducted a diallel analysis for leaf area, log fruit weight, and number and dry weight in tomatoes. The diallel analysis showed that the genetic control of log fruit weight and number was largely additive. Similar analyses of dry weight and leaf area data showed considerable variation with time. It was concluded that extreme caution is necessary in generalizing types of gene action from a genetic analysis made at only one point of time. Most of the crosses in this study were intermediate for fruit yield and total leaf area.

Malting Quality

The determination of malting quality of barley requires extensive physical and chemical measurements. For this reason, most papers on the subject of malting quality are concerned with only a small group of the characteristics which constitute malting quality. A noteworthy exception is the recent book edited by Cook (1962), Barley and Malt. This book provides a historical, as well as modern, review of the studies on malting quality. The anatomy and genetics of the barley plant and an explanation of the various chemical and physical tests of malting quality are discussed. Nitrogen content, diastatic power, and extract are three of the more common tests performed on barleys to determine malting quality.

The relation between grain yield and protein content on wheat

and barley was studied by Neatby and McCalla (1938). A negative relationship was found for ten barley varieties between yield and protein content. The differences in the yield between the high and low protein varieties were remarkably consistent from location to location in this study. It was suggested that this negative relationship between yield and protein would simplify the breeding of low protein malting barleys.

Canadian workers have carried out many studies on the relationship among quality factors and between quality factors and other agronomic traits. A summary of their findings was reported by Anderson, Sallans and Meredith (1941). The results were obtained on nine six-rowed and three two-rowed barleys grown at 12 locations. Simple and partial correlations were computed for the various traits. The intervarietal correlations revealed that as nitrogen content increased, the nitrogen factors of the malt also increased; however, the carbohydrate factors decreased. The intravarietal relations showed no evidence for regularities in composition between nitrogen fractions or between nitrogen fractions and carbohydrates. The partial correlation coefficients indicated that the genes controlling salt-soluble nitrogen may also control other malting properties.

The associations between protein, extract, and diastatic power were studied by Hsi and Lambert (1954). Data were obtained from F_5 and F_6 lines from six-rowed x six-rowed crosses. Negative correlations were found between protein and extract and also between diastatic power and extract. Protein and diastatic power were

positively associated in both F_5 and F_6 lines. The associations of malting quality traits with other agronomic traits were also studied. Significant positive correlation coefficients were found for average kernel weight and extract. There was a good association between diastatic power of F_5 lines with that of F_6 lines, which suggested a high heritability for diastatic power.

Den Hartog and Lambert (1953) studied the relationship between agronomic and malting quality characters of barley. The correlation coefficients for diastatic power with protein, yield, kernel weight, and extract were 0.640, -0.280, -0.280, -0.160, and -0.400, respectively. The correlation coefficients for extract with kernel weight, yield, and protein were 0.540, 0.540, and 0.520, respectively. It was concluded that it would be possible to select lines good for yield and malting quality.

Heritability for four quality characters in barley were determined in early generations of barley crosses by Rasmusson and Glass (1965). Narrow-sense heritabilities were high for diastatic power, intermediate for kernel plumpness, and low for extract and protein. Protein was positively associated with diastatic power but was negatively associated with extract. It was suggested that the gain in simultaneous selections for extract, protein, and diastatic power would be reduced by this association.

Diastatic power was studied by Day, Down and Frey (1955). It was found that diastatic power was associated with the two-rowed versus six-rowed characteristic. The two-rowed barleys in this study had the highest mean diastatic power. The authors reported

that the broad-sense heritability estimate for diastatic power in F_3 progenies for three crosses was 32.4 percent.

Selection for malting quality in early generations of barley hybrids was reported by Sisler and Banasik (1951). Quality determinations consisting of extract, kernel weight, and diastatic power were made on 136 F_3 lines from a cross of Titan x Kindred. These lines were generally higher in extract and kernel weight, but lower in diastatic power than Kindred. About 27 percent of these lines were judged to have desirable quality. The data obtained on F_3 lines were useful in selecting lines whose progeny were likely to have good quality. About 75 percent of the lines derived from these selected lines had good malting quality.

MATERIALS AND METHODS

Three six-rowed and four two-rowed spring barley varieties were used in these studies. The seven varieties were chosen to represent rather wide geographic areas of origin for the express purpose of obtaining genetic diversity. A description of each variety is given in Appendix Table 1. The seven parental varieties were crossed with each other in a diallel system. The crosses were made by means of hand emasculation and pollination, and only well developed seeds were chosen for later use. Reciprocal crosses between the parents were not kept separate, thus there was a total of 21 different crosses. These 21 F_1 crosses and the seven parental varieties were planted in a greenhouse groundbed on the campus of Oregon State University, Corvallis, Oregon, on March 26, 1964. The experiment was designed as a randomized block with four replications. The greenhouse groundbed was chosen for this study to obtain a better control of the aphids that attack barley and transmit barley yellow dwarf virus (BYDV) disease, and the greenhouse also offered a means of controlling possible environmental variation.

Before planting, a 20-4-6 fertilizer was applied at the rate of 500 pounds per acre and worked into the soil. The experimental plants were located in the center of the groundbed to eliminate as much water seepage as possible 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,

and when the coleoptiles were about one inch long, the seedlings were then transplanted into the soil bed. Each F_1 cross and the parents were represented by four seedlings in each plot. The plants were spaced 18 inches apart within the rows, and 18 inches between rows. The experiment was flood-irrigated four times during the growing season to provide adequate soil moisture. Aphids were controlled by two fumigations during the growing season with Tetraethyl Dithiopyrophosphate.

Yield and Components of Yield

Total grain yield per plant was determined by weighing all of the grain from each plant. The heads of each plant were removed as they ripened. This procedure prevented possible losses due to shattering of over-ripe heads. The heads from each plant were threshed by hand-rubbing and the yield was recorded as grams of grain per plant. The mean grain yield of the plants of each plot was computed and these plot means were used throughout the study.

The components of grain yield are recognized in barley as the number of kernels per head, weight per kernel, and the number of heads per plant. In this study, the number of kernels per head and weight per kernel for each plot were determined from a random five head sample taken from each plant within the plot. The number of kernels on each head was counted and weighed and mean weight per kernel was determined. Again, a single plot mean for number of kernels per head and weight per kernel was obtained. The number of heads per plant was determined by counting all of the tillers

with well developed heads on each of the four plants within a plot. A single mean tiller number per plot was determined and used in subsequent calculations.

Total Leaf Area

The total leaf area (TLA) in square centimeters was determined for one randomly selected plant in each plot. Total leaf area was computed by the following formulae:

$$(L \times W) \text{ per tiller} \times b = \text{Area per tiller; area per tiller} \times \text{number of tillers per plant} = \text{TLA per plant}$$

Where:

$(L \times W)$ = The length x maximum width product

b = The mean coefficient of the leaf area for each leaf divided by the $(L \times W)$ product of that same leaf

Four tillers were selected at random and marked on each plant. The length and maximum width of all of the leaves present on each of these tillers were measured to the nearest millimeter. The sum of the length x weight $(L \times W)$ products of all the leaves on the four tillers was divided by four and this quotient was multiplied by b giving the mean TLA per tiller. A mean b coefficient of 0.686 was determined from a preliminary study by Carleton and Foote (1965). This b coefficient was used for all TLA estimates. The mean TLA per tiller was multiplied by the number of tillers per plant to obtain an estimate of the plant's TLA.

The components of TLA per plant are leaf size and leaf number. In this study, leaf size was divided into leaf width and leaf

length. Since the number of leaves per plant was not determined, the number of tillers per plant was used as an indication of the number of leaves per plant. Tiller number was used as an estimate of total leaf number by making the assumption that all tillers have the same number of leaves. Thus, in this study, the components of TLA per plant were leaf width, leaf length, and tiller number per plant.

The mean leaf width and mean leaf length of all the leaves of the four tillers used to estimate TLA were taken as the components of TLA. The number of tillers on each of the selected plants was counted at the time that the measurements for estimating TLA were taken.

Estimates of TLA per plant were made at two stages of growth. The first estimate was made on May 13, 1964, when the majority of the plants were in the boot stage, just prior to the time of heading. The second estimate, including the same four tillers of the same plants, was made on May 28, 1964. Most of the plants had reached heading at the time of the second measurements.

Estimating TLA at these two stages of growth provided an opportunity to compare the changes in TLA during this period of growth. It also provided an opportunity to measure changes in the contributions of the components to TLA.

Malting Quality

Seed from the four plants of each plot was combined together and a 300-gram sample sent to the U.S.D.A. Barley and Malt

Laboratory, Madison, Wisconsin, for malting quality tests. The first quality measurements were the "Prediction Test" as outlined by Meredith and co-workers (1942), which consisted of determining the barley nitrogen, barley extract, and barley diastatic power. After the preliminary quality tests, the seed from each replication was bulked to give one sample for each of the 21 F_1 crosses and parents. These samples were then experimentally malted according to the standard procedures used at the Barley and Malt Laboratory. From the several physical and chemical determinations obtained on the malt produced from each sample, the three chosen for study were the malt nitrogen, malt extract, and malt diastatic power. To determine the relationship between the predictive test values and the malting values, simple correlations between the two were computed.

Malting quality in barley is not easy to define or reduce to simple chemical or physical terms. For this reason, no university acceptable definition of malting quality can be widely applied. Likewise, it is difficult to single out one or a small number of the chemical tests and interpret the malting value of the barley from these results. However, for the purpose of this study, the three important quality criteria of malting barley, malt nitrogen, malt diastatic power, and malt extract, were chosen.

In order to obtain a single value which would represent the malting quality value of the barley samples, a quality index was designed and computed. For the purpose of constructing this quality index, Hannchen, one of the parents used in this study, was chosen as the standard. Hannchen barley has been widely grown

in the Willamette Valley and Klamath Basin areas of Oregon for many years and the barley is recognized as possessing many of the desirable quality factors associated with two-rowed malting barleys. Barley varieties with wide deviations from the Hannchen quality would not be considered as satisfactory malting varieties in this index.

The formula for the quality index was as follows:

$$Q_1 = - \left| r_{11}u_1 \right| - \left| r_{22}u_2 \right| + r_{33}u_3$$

Where:

Q_1 = Quality index value

r_{11} = Simple correlation coefficient of barley nitrogen and malt nitrogen

u_1 = $\frac{\text{Entry } \bar{x} \text{ nitrogen} - \text{Hannchen } \bar{x} \text{ nitrogen}}{\text{Standard deviation for nitrogen}}$

r_{22} = Simple correlation coefficient of barley diastatic power and malt diastatic power

u_2 = $\frac{\text{Entry } \bar{x} \text{ diastatic power} - \text{Hannchen } \bar{x} \text{ diastatic power}}{\text{Standard deviation for diastatic power}}$

r_{33} = Simple correlation coefficient of barley extract and malt extract

u_3 = $\frac{\text{Entry } \bar{x} \text{ extract} - \text{Hannchen } \bar{x} \text{ extract}}{\text{Standard deviation for extract}}$

The index was constructed in such a way that any deviation from Hannchen in barley nitrogen and diastatic power would reduce the index value while those entries having higher extract values than Hannchen were favored. The use of the correlations between the predictive barley tests and the actual malting values allows for the adjustment of error in the predictive tests. The

deviations of the entry means from the Hannchen mean for the three quality tests were divided by their respective standard deviation so that they could be summed. The deviations from Hannchen divided by the standard deviation places the values on the same relative magnitude.

A numerical example of the computation of the quality index for the variety, Trebi, is given in Appendix Table 2.

Analysis of Data

A functional analysis of variance was computed for yield, total leaf area, and their respective components, as well as for barley nitrogen, diastatic power, and extract. The 21 F_1 's and seven parents were first treated as one group and then divided into four subgroups. These four subgroups were the six-rowed x six-rowed (6 x 6) crosses, six-rowed x two-rowed (6 x 2) crosses, two-rowed x two-rowed (2 x 2) crosses and the parents. A functional analysis of variance was used so that between group comparisons could be made to determine if there were significant differences in the expression of a particular trait among these four groups.

The simple correlations for yield and TLA and their individual components were analyzed by pathway coefficient analysis as described by Wright (1921). A comparison of the direct and indirect effects of the various components on the complex trait is possible through the use of this method. The direct and indirect effects of the components on the complex trait for one group were compared to those of another group to determine if any differences existed

between groups.

The associations between yield and its components with total leaf area and its components were determined by computation of simple correlation coefficients. Grain yield and its components were correlated with the leaf area measurements at both stages of growth. The crosses and parents were separated according to row number, thus giving associations for two-rowed, six-rowed, and two-rowed x six-rowed barleys.

Simple correlations were used to determine the associations between the quality traits and the two complex traits in this study. The inter-associations between diastatic power, barley nitrogen, and extract were also determined by simple correlation coefficients. All correlations were obtained for the six-rowed barleys, two-rowed barleys, and six-rowed x two-rowed (6 x 2) crosses separately.

The amount of heterosis present for each trait was measured by two methods: first, heterosis was measured as the amount that the F_1 mean exceeded the parental average, and second, as the amount the F_1 exceeded the high parent. Duncan's new multiple range test was used to determine if the amounts that the F_1 means exceeded their respective high parent were significant.

An interpretation of the presence or absence of heterosis for the three complex traits was made by an examination of the amounts of heterosis for their components. The relative importance of the individual components was also determined and considered in this interpretation of the expression of heterosis for a complex trait. The existence of complementing components within the parents of the

different crosses was also determined.

Estimates of gene action controlling the expression of the traits in this study were obtained by combining ability analysis. Sprague and Tatum (1942) postulated that general combining ability estimates provide an indication of the presence of additive genes while specific combining ability estimates depend upon genes with dominant and epistatic effects. General and specific combining ability estimates were computed for all traits in two separate groups of crosses. Estimates were made for the (2 x 2) crosses and for the (6 x 2) crosses. It was not possible to estimate general and specific combining ability for the six-rowed x six-rowed (6 x 6) crosses since there were only three six-rowed parents and there are no degrees of freedom for the specific combining ability effect in a 3 x 3 diallel.

Combining ability estimates for the (2 x 2) crosses were computed by a procedure outlined by Griffing (1956). Method 4 of Model I was selected as the best suited procedure for this experiment. Estimates of general (GCA) and specific combining ability (SCA) were obtained for this group by the following formulae:

$$r \text{ SS(GCA)} = \frac{1}{P-2} \sum (X_{i.})^2 - \frac{4}{P(P-2)} \sum X_{..}^2$$

$$r \text{ SS(SCA)} = \sum (X_{ij})^2 - \frac{1}{P-2} \sum (X_{i.})^2 + \frac{2}{(P-1)(P-2)} \sum X_{..}^2$$

Where:

r = Number of replications

P = Number of parents

$\sum (X_{i.})^2$ = Sum of each parental array squared (averaged over replications)

$\sum X_{..}^2$ = Sum of all parental arrays squared (averaged over replications)

$\sum (X_{ij})^2$ = Sum of each hybrid combination squared (averaged over replications)

Combining ability estimates for the (6 x 2) crosses were computed by a procedure outlined as Experiment II of Comstock and Robinson (1952). The following formulae were used to estimate general and specific combining ability in this group:

$$r \text{ SS(GCA 6)} = \frac{\sum (X_{i.})^2}{n_1} - \frac{\sum X_{..}^2}{n_1 n_2}$$

$$r \text{ SS(GCA 2)} = \frac{\sum (X_{.j})^2}{n_2} - \frac{\sum X_{..}^2}{n_1 n_2}$$

$$r \text{ SS(SCA)} = \sum (X_{ij})^2 - \frac{\sum X_{..}^2}{n_1 n_2} - \text{SS(GCA 6)} - \text{SS(GCA 2)}$$

Where:

SS(GCA 6) = Sum of squares of general combining ability for six-rowed parents (averaged over replications)

SS(GCA 2) = Sum of squares of general combining ability for two-rowed parents (averaged over replications)

SS(SCA) = Sum of squares for specific combining ability (averaged over replications)

$\sum (X_{i.})^2$ = Sum of each six-rowed parental array squared (averaged over replications)

$\sum (X_{.j})^2$ = Sum of each two-rowed parental array squared (averaged over replications)

$\sum (X_{ij})^2$ = Sum of each hybrid combination squared (averaged over replications)

$\sum X_{..}^2$ = Sum of all parental arrays squared (averaged over replications)

n_1 = Number of two-rowed parents

n_2 = Number of six-rowed parents

r = Number of replications

Once the estimates of general and specific combining ability were obtained, the variance components for these estimates were determined. The expected mean squares for general and specific combining ability for the (2 x 2) crosses and the (6 x 2) crosses are given in Tables 1 and 2 respectively.

From Table 1, the components of general and specific combining ability and a narrow-sense heritability estimate were computed as follows:

Table 1. Expectations of mean squares for general and specific combining ability estimates for (2 x 2) crosses

m.s.		Expectation of m.s.
General combining ability	A	$\sigma^2_e + r\sigma^2_{SCA} + r(P-2)\sigma^2_{GCA}$
Specific combining ability	B	$\sigma^2_e + r\sigma^2_{SCA}$
Error	C	σ^2_e
$r = \# \text{ reps}$		$P = \# \text{ parents}$

Table 2. Expectations of mean squares for general and specific combining ability estimates for (6 x 2) crosses

m.s.		Expectation of m.s.
General combining ability(6)	A	$\sigma^2_e + r\sigma^2_{SCA} + rn_1\sigma^2_{GCA(6)}$
General combining ability(2)	B	$\sigma^2_e + r\sigma^2_{SCA} + rn_2\sigma^2_{GCA(2)}$
Specific combining ability	C	$\sigma^2_e + r\sigma^2_{SCA}$
Error	D	σ^2_e
$r = \# \text{ reps}$		$n_1 = \# \text{ two-rowed parents}$ $n_2 = \# \text{ six-rowed parents}$

$$\sigma^2_{GCA} = \frac{A - B^*}{r(P - 2)} = \frac{1}{2} \text{ additive variance}$$

$$\sigma^2_{SCA} = \frac{B - C}{r} = \text{Non-additive variance}$$

$$h^2_{ns} = \frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_e}$$

*When the error variance was larger than SCA, C was used instead of B.

The components of general and specific combining ability and narrow-sense heritability estimates for the (6 x 2) crosses were obtained from Table 2 in the following manner:

$$\sigma^2_{(GCA)(6)} = \frac{A - C^a}{rn_1} = \frac{1}{2} \text{ additive variance (six-rowed)}$$

$$\sigma^2_{(GCA)(2)} = \frac{B - C^a}{rn_2} = \frac{1}{2} \text{ additive variance (two-rowed)}$$

$$\sigma^2_{(GCA)^b} = \frac{n_1 + n_2 - 2}{r(2n_1n_2 - n_1 - n_2)} \frac{(n_1 - 1)SS(GCA)(2) + (n_2 - 1)SS(GCA)(6)}{n_1 + n_2 - 2} - SS(SCA)$$

$$\sigma^2_{(SCA)} = \frac{C - D}{r} = \text{Non-additive variance}$$

$$h^2_{ns} = \frac{2\sigma^2_{(GCA)}}{2\sigma^2_{(GCA)} + \sigma^2_{(SCA)} + \sigma^2_e}$$

Where:

a = When the error variance was larger than SCA, D was used instead of C

b = Weighted average of general combining ability

Numerical examples of the computation of estimates of general and specific combining ability; of components of general and specific combining ability; and of narrow-sense heritability for the (2 x 2) crosses and the (6 x 2) crosses are given in Appendix Tables 3 and 4.

RESULTS

Yield and Components of Yield

A summary of average yield per plant, tiller per plant, kernels per head, and weight per kernel for the 21 F_1 crosses and the seven parents is given in Table 3. This table includes the averages for the crosses when grouped according to the row number of their respective parents. The four groups consisted of (6 x 6), (2 x 2), (6 x 2) crosses and the parents.

Functional analyses of variance were computed for each trait where the three types of crosses (6 x 6), (2 x 2), and (6 x 2) and parents were considered as different groups. A summary of the mean squares from these analyses is given in Table 4. The appropriate individual error mean squares were used to determine significances of the various sources of variation.

The among group mean square for grain yield was not significant; however, significant differences were found among groups for the three components. This result is possible, providing there is a compensating effect between the components that comprise the complex trait. The term compensation is used to describe the situation where the marked effect of a low value for one component is offset by a corresponding high value for a second component.

An illustration of compensation for grain yield is given in Table 5, where the group averages for grain yield, tillers per plant, kernels per head, and weight per kernel for the (6 x 6),

Table 3

A summary of the means for grain yield, tillers per plant, kernels per head and weight per kernel for the (6x6), (2x2), (6x2) crosses and seven parental varieties

Group	Entry	Yield	Tillers/plant	Kernels/head	Weight/kernel
6x6	T ₁ XA	63.7	29.6	60.3	0.052
	T ₁ XT ₂	57.3	24.0	53.1	0.051
	T ₂ XA	<u>63.9</u>	<u>31.3</u>	<u>57.2</u>	<u>0.048</u>
	Ave.	61.6	28.3	56.9	0.050
2x2	HXD	61.2	54.3	25.7	0.052
	HXP	62.1	53.0	25.4	0.053
	HXAD	53.6	43.7	26.3	0.051
	DXP	59.5	48.0	25.8	0.061
	DXAD	55.5	46.4	26.8	0.055
	PXAD	<u>53.0</u>	<u>45.0</u>	<u>26.4</u>	<u>0.051</u>
	Ave.	57.5	48.4	26.1	0.054
6x2	AXD	44.2	31.9	22.2	0.070
	AXAD	54.5	41.9	24.6	0.064
	AXP	50.2	46.6	23.8	0.062
	AXH	55.0	40.7	22.8	0.065
	T ₁ XD	59.1	39.4	29.4	0.064
	T ₁ XAD	65.1	43.0	30.5	0.063
	T ₁ XP	61.0	34.2	43.7	0.049
	T ₁ XH	68.0	48.4	32.3	0.056
	T ₂ XD	61.5	41.4	24.1	0.078
	T ₂ XAD	53.1	36.7	25.5	0.073
	T ₂ XP	52.5	39.0	24.7	0.071
	T ₂ XH	<u>44.9</u>	<u>32.0</u>	<u>24.9</u>	<u>0.070</u>
	Ave.	55.8	39.6	27.4	0.065
Parents					
Traill	= T ₁	60.2	27.5	62.1	0.045
Atlas 46	= A	54.7	28.7	42.0	0.047
Trebi	= T ₂	64.8	28.6	54.6	0.051
Domen	= D	46.9	42.5	24.0	0.059
Pirolina	= P	51.6	49.3	25.6	0.051
Hannchen	= H	55.3	49.3	26.2	0.058
Abed Denso	= AD	<u>50.0</u>	<u>45.2</u>	<u>26.1</u>	<u>0.046</u>
	Ave.	54.8	38.7	37.2	0.051

Table 4
A summary of the mean squares from the functional analyses of variance
for grain yield and components of yield

Source of variation	df	Yield ms	Tillers/plant ms	Kernels/head ms	Weight/kernel ms
Replications	3	26.380 N.S.	29.370 N.S.	11.277 N.S.	0.000071667*
Entries	27	156.965**	278.541**	656.978**	0.000335148**
Among groups	3	148.010 N.S.	1,129.540**	3,339.700**	0.001738333**
¹ Within groups	24	158.085**	172.166**	321.263**	0.000159750*
w/in (6x6) crosses	2	56.225 N.S.	59.400*	52.175 N.S.	0.000019500 N.S.
w/in (6x2) crosses	11	223.277**	110.261**	145.527**	0.000249000**
w/in (2x2) crosses	5	62.388 N.S.	74.386 N.S.	1.136 N.S.	0.000059800*
w/in parents	6	150.600 N.S.	404.732**	1,001.588**	0.000126167**
² Reps x entries	81	51.167	25.563	11.140	0.000018802
³ R x w/in groups	9	25.931	26.907	12.327	.000038111
⁴ R x w/in (6x6) crosses	6	118.878	10.892	27.282	.000038333
⁵ R x w/in (6x2)	33	43.886	20.788	10.692	.000078788
⁶ R x w/in (2x2)	15	42.945	52.462	2.669	.000020533
⁷ R x w/in parents	18	61.413	16.117	13.046	.000021222
Total	111				

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 for within groups

⁴ = Error term for within (6x6) crosses

⁵ = Error term for within (6x2) crosses

⁶ = Error term for within (2x2) crosses

⁷ = Error term for within parents

Table 5

A comparison of the average yield, tillers per plant, kernels per head and weight per kernel for the (6 x 6), (2 x 2), and (6 x 2) crosses

Crosses	Yield	Tillers/plant	Kernels/head	wt/kernel
6 x 6	61.6	28.3	56.9	0.050
2 x 2	57.5	48.4	26.1	0.054
6 x 2	55.8	39.6	27.1	0.065

(2 x 2), and (6 x 2) crosses are compared. Tillers per plant and kernels per head were the compensating factors which enabled the average yield of the (6 x 6) and (2 x 2) crosses to be approximately equal. The average yield of the (6 x 2) crosses was not different from the average yield of the (6 x 6) and (2 x 2) crosses. Tillers per plant and weight per kernel compensated for the low value for kernels per head in the (6 x 2) crosses.

The within parent mean squares for grain yield were not significant; however, significant differences within the parents were found for the three components of yield (Table 4). The crosses within the (6 x 6) group and within the (2 x 2) group were similar in their grain yield and components of grain yield. The (6 x 6) crosses differed significantly only for tillers per plant and the (2 x 2) crosses differed significantly only for weight per seed. The F_1 's produced by crossing six-rowed x two-rowed parents were variable but with significant differences occurring for yield and for all of the yield components.

A method of studying the contributions of the components of yield in relation to each other as they influence yield is through a procedure commonly referred to as pathway coefficient analysis. The direct and indirect effects of the components on grain yield for the six-rowed and two-rowed barleys are given in Table 6. Tiller number per plant had the largest direct effect on yield for both the two-rowed and six-rowed barleys. The direct effect of tillers per plant in the two-rowed barleys was much larger than the direct effect of kernel number per head or kernel weight. Kernel number had a direct effect almost as large as tiller number per plant in the six-rowed barleys.

The examination of the pathway coefficients for the (6 x 2) crosses showed that the contributions of the various components to yield was not the same as those for either the six-rowed barleys or the two-rowed barleys (Table 6). Instead of tillers per plant having the largest direct effect on yield in the (6 x 2) group, kernels per head exerted the largest direct effect. Tillers per plant had a slightly larger direct effect on yield than weight per kernel, but weight per kernel was more important in the (6 x 2) crosses than in the six-rowed or two-rowed barleys.

The interrelationships between the components as indicated by the indirect effects in Table 6, were different for the six-rowed, two-rowed, and six-rowed x two-rowed groups. The most striking differences were found for the indirect effect of kernel number via the other components on yield. An extremely large negative, indirect effect was present in the (6 x 2) crosses for weight per

Table 6

The direct and indirect effects of the components of yield for three types of barleys

Components	Six-rowed	Groups	
		Two-rowed	(6x2) crosses
Tillers/plant			
Direct effect on yield	0.72768	0.80466	0.78547
Indirect effect via			
kernels/head on yield	-0.13268	0.01523	-0.03621
Indirect effect via			
weight/kernel on yield	-0.05012	-0.00381	-0.14613
Simple r	0.54488	0.81608	0.60313
Kernels/head			
Direct effect on yield	0.60374	0.32905	1.12270
Indirect effect via			
tillers/plant on yield	-0.15991	0.03725	-0.02534
Indirect effect via			
weight/kernels on yield	0.06944	-0.09945	-0.51051
Simple r	0.51327	0.26685	0.58685
Weight/kernel			
Direct effect on yield	0.36048	0.28896	0.64095
Indirect effect via			
tillers/plant on yield	-0.10118	-0.01061	-0.17908
Indirect effect via			
kernels/head on yield	0.11630	-0.11325	-0.89422
Simple r	0.03756	0.16510	-0.43235
$R^2 =$	0.84178	0.79219	0.85549

kernel via kernels per head. The simple correlation coefficient for these two traits in the (6 x 2) crosses was $r = -0.796$.

Estimates of the amounts of heterosis for yield and the components of yield measured by the amount that the F_1 exceeded the parental average and by the amount that the F_1 exceeded the better parent are given in Tables 7, 8, 9, and 10, respectively. There was a general lack of heterosis for grain yield. Only two hybrids in the (2 x 2) group had grain yields which were 20 percent larger than the midparental mean. None of the crosses in the (6 x 6) and the (6 x 2) groups produced more than 20 percent in excess of their parental midpoint. The average increase in yield over the midparent for the (6 x 6), (2 x 2), and (6 x 2) crosses was 2.9, 12.8, and 0.1 percent, respectively. One cross in the (6 x 6) group, five crosses in the (2 x 2) group, and three crosses in the (6 x 2) group produced more grain than the better parent, but none of these differences were significant. The range in heterosis for yield based on the parental averages was 20.7 to -26.3 percent.

The average percent increase over the parental average for tillers per plant for the (6 x 6), (2 x 2), and (6 x 2) crosses was -0.1, 3.9, and 8.3 percent, respectively (Table 8). None of the crosses in the (6 x 6) and (2 x 2) groups had 20 percent more tillers than the parental average, while two crosses in the (6 x 2) group had 20 percent more tillers per plant than the parental average. Only one cross in the (6 x 2) group had more tillers than the high parent and this difference was not significant. None of the (6 x 6) crosses had more tillers per plant than the high

Table 7

The amounts of heterosis for grain yield of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	63.7	60.2	54.7	57.5	6.2	3.5	10.1
	AXT ₂	63.9	64.8	54.7	59.8	4.1	- 0.9	6.9
	T ₂ XT ₁	57.3	64.8	60.2	62.5	- 5.2	- 7.5	- 8.4
							Ave.	2.9
2x2	ADXD	55.5	50.0	46.9	48.5	7.0	5.5	14.4
	ADXP	53.0	51.6	50.0	50.8	2.2	1.4	4.3
	ADXH	53.6	55.3	50.0	52.7	0.9	- 1.7	1.7
	PXH	62.1	55.3	51.6	53.5	8.6	6.8	16.0
	PXD	59.5	51.6	46.9	49.3	10.2a	7.9	20.7
	HXD	61.2	55.3	46.9	51.1	10.1a	5.9	19.8
							Ave.	12.8
6x2	AXD	44.2	54.7	46.9	50.8	- 6.6	-10.5	-13.0
	AXP	50.2	54.7	51.9	53.2	- 3.0	- 4.5	- 5.3
	AXH	55.0	55.3	54.7	55.0	0.0	- 0.3	0.0
	AXAD	54.5	54.7	50.0	52.4	2.1	- 0.2	4.0
	T ₁ XD	59.1	60.2	46.9	53.6	5.5	- 1.1	10.3
	T ₁ XP	61.0	60.2	51.6	55.9	5.1	0.8	10.9
	T ₁ XH	68.0	60.2	55.3	57.8	10.2	7.8	17.6
	T ₁ XAD	65.1	60.2	50.0	55.1	10.0	4.9	18.1
	T ₂ XD	61.5	64.8	46.9	55.9	5.6	- 3.3	10.0
	T ₂ XP	52.5	64.8	51.6	58.2	- 5.7	-12.3*	- 9.8
	T ₂ XH	44.9	64.8	55.3	60.1	-15.2	-19.9*	-26.3
	T ₂ XAD	53.1	64.8	50.0	57.4	- 4.3	-11.7	7.5
							Ave.	0.1

Parents		\bar{X}
Traill	=T ₁	60.2
Atlas 46	=A	54.7
Trebi	=T ₂	64.8
Domen	=D	46.9
Pirolina	=P	51.6
Hannchen	=H	55.3
Abed Denso	=AD	50.0

a = $F_1 > 20$ percent of parental average

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 10.0

P = 28 SSR = 12.8

Table 8

The amounts of heterosis for tillers per plant of
(6x6), (2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	$\bar{M}\bar{P}$	$>\bar{M}\bar{P}$	$F_1 >$ High \bar{P}	% $>\bar{M}\bar{P}$
6x6	T ₁ XA	29.6	28.7	27.5	28.1	1.5	- 0.6	5.3
	AXT ₂	31.3	28.7	28.6	28.7	2.6	0.0	9.1
	T ₂ XT ₁	24.0	28.6	27.5	28.1	- 4.1	- 4.6	-14.6
							Ave.	- 0.1
2x2	ADXD	46.4	45.2	42.5	43.9	2.5	1.2	5.7
	ADXP	45.0	49.3	45.2	47.3	- 2.3	- 4.3	- 4.9
	ADXH	43.7	49.3	45.2	47.3	- 3.6	- 5.6	- 7.6
	PXH	53.0	49.3	49.3	49.3	3.7	3.7	7.5
	PXD	48.0	49.3	42.5	45.9	2.1	- 1.3	4.6
	HXD	54.3	49.3	42.5	45.9	8.4	5.0	18.3
							Ave.	3.9
6x2	AXD	31.9	42.5	28.7	35.6	- 3.7	-10.6*	-10.4
	AXP	46.6	42.5	28.7	35.6	11.0a	4.1	30.9
	AXH	40.7	49.3	28.7	39.0	1.7	- 8.6*	4.4
	AXAD	41.9	45.2	28.7	37.0	4.9	- 3.3	13.2
	T ₁ XD	39.4	42.5	27.5	35.0	4.4	- 3.1	12.6
	T ₁ XP	34.2	42.5	27.5	35.0	- 0.8	- 8.3*	- 2.3
	T ₁ XH	48.4	49.3	27.5	38.4	10.0a	- 0.9	26.0
	T ₁ XAD	43.0	45.2	27.5	36.4	6.6	- 2.2	18.1
	T ₂ XD	41.4	42.5	28.6	35.6	5.8	- 1.1	16.3
	T ₂ XP	36.7	45.2	28.6	36.9	- 0.2	- 8.5*	- 0.6
	T ₂ XH	32.0	49.3	28.6	39.0	- 7.0	-17.3*	-17.9
	T ₂ XAD	39.0	42.5	28.6	35.6	3.4	- 3.5	9.6
							Ave.	8.3

Parents		\bar{X}
Traill	=T ₁	27.5
Atlas 46	=A	28.7
Trebi	=T ₂	28.6
Domen	=D	42.5
Pirolina	=P	45.2
Hannchen	=H	49.3
Abed Denso	=AD	42.5

a = $F_1 > 20$ percent of parental average

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 7.1

P = 28 SSR = 9.1

Table 9

The amounts of heterosis for kernels/head of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	$\%>\bar{MP}$
6x6	T ₁ XA	60.3	62.1	42.0	52.1	8.2	- 1.8	15.7
	AXT ₂	53.1	54.6	42.0	48.3	4.8	- 1.5	9.9
	T ₂ XT ₁	57.2	62.1	54.6	58.4	- 1.2	- 4.9	- 2.1
	Ave.							7.8
2x2	ADXD	26.8	26.1	24.0	25.1	1.7	0.7	6.8
	ADXP	26.4	26.1	25.6	25.9	0.5	0.3	1.9
	ADXH	26.3	26.2	26.1	26.2	0.1	0.1	0.4
	PXH	25.4	26.2	25.6	25.9	- 0.5	- 0.8	- 1.9
	PXD	25.8	25.6	24.0	24.8	1.0	0.2	4.0
	HXD	25.7	26.2	24.0	25.1	0.6	- 0.5	2.4
	Ave.							2.3
6x2	AXD	22.2	42.0	24.0	33.0	-10.8	-19.8*	-33.4
	AXP	23.8	42.0	25.6	33.8	-10.0	-19.8*	-29.6
	AXH	22.8	42.0	26.2	34.1	-11.3	-19.2*	-33.1
	AXAD	24.6	42.0	26.1	34.1	- 9.5	-17.4*	-27.9
	T ₁ XD	29.4	62.1	24.0	43.1	-13.7	-32.4*	-31.8
	T ₁ XP	43.7	62.1	25.6	43.9	- 0.2	-18.4*	- 0.5
	T ₁ XH	32.3	62.1	26.2	44.2	-11.9	-29.8*	-26.9
	T ₁ XAD	30.5	62.1	26.1	44.1	-13.6	-31.6*	-30.8
	T ₂ XD	24.1	54.6	24.0	39.3	-15.2	-30.5*	-38.7
	T ₂ XP	24.7	54.6	25.6	40.1	-15.4	-29.7*	-38.4
	T ₂ XH	24.9	54.6	26.2	40.4	-15.5	-29.7*	-38.4
	T ₂ XAD	25.5	54.6	26.1	40.4	-14.9	-29.1*	-36.9
	Ave.							-30.5

Parents	\bar{X}
Traill =T ₁	62.1
Atlas 46 =A	42.0
Trebi =T ₂	54.6
Domen =D	24.0
Piroline =P	25.6
Hannchen =H	26.2
Abed Denso=AD	26.1

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 4.7
P = 28 SSR = 6.0

Table 10

The amounts of heterosis for weight/kernel of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$> \bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	0.052	0.047	0.045	0.046	0.006	0.005	13.0
	AXT ₂	0.048	0.051	0.047	0.049	-0.001	-0.003	- 2.0
	T ₂ XT ₁	0.051	0.051	0.045	0.048	0.003	0.000	6.3
							Ave.	5.8
2x2	ADXD	0.055	0.059	0.046	0.053	0.002	-0.004	3.8
	ADXP	0.051	0.051	0.046	0.049	0.002	0.000	4.1
	ADXH	0.051	0.058	0.046	0.052	-0.001	-0.007	- 1.9
	PXH	0.053	0.058	0.051	0.055	-0.002	-0.005	- 3.6
	PXD	0.061	0.059	0.051	0.055	0.005	0.003	10.9
	HXD	0.052	0.059	0.058	0.059	-0.006	-0.006	-11.9
							Ave.	0.2
6x2	AXD	0.070	0.059	0.047	0.053	0.017a	0.011*	32.1
	AXP	0.062	0.051	0.047	0.049	0.013a	0.011*	26.5
	AXH	0.065	0.058	0.047	0.053	0.012a	0.007*	22.6
	AXAD	0.064	0.047	0.046	0.047	0.017a	0.017*	36.2
	T ₁ XD	0.064	0.059	0.045	0.052	0.012a	0.005	23.1
	T ₁ XP	0.049	0.051	0.045	0.048	0.001	-0.002	2.1
	T ₁ XH	0.056	0.058	0.045	0.055	0.001	-0.002	1.8
	T ₁ XAD	0.063	0.046	0.045	0.046	0.017a	0.017*	37.0
	T ₂ XD	0.078	0.059	0.051	0.055	0.023a	0.019*	41.8
	T ₂ XP	0.071	0.051	0.051	0.051	0.020a	0.020*	39.2
	T ₂ XH	0.070	0.058	0.051	0.055	0.015a	0.012*	27.3
	T ₂ XAD	0.073	0.051	0.046	0.046	0.024a	0.022*	49.0
							Ave.	28.1

Parents		\bar{X}
Traill	=T ₁	0.045
Atlas 46	=A	0.047
Trebi	=T ₂	0.051
Domen	=D	0.059
Pirolina	=P	0.051
Hannchen	=H	0.058
Abed Denso	=AD	0.046

a = $F_1\bar{X} > 20$ percent of parental average

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 0.006

P = 28 SSR = 0.008

parent, while three crosses in the (2 x 2) group had more tillers but these increases were not significant. The range of heterosis based on the midparent estimates among all crosses for tillers per plant was 30.9 to -17.9 percent.

A slight amount of heterosis for kernel number per head was found for the (6 x 6) crosses and the (2 x 2) crosses but no heterosis was found for any of the (6 x 2) crosses (Table 9). The average percent increase of the F_1 over the parental average for kernels per head for the (6 x 6), (2 x 2) and (6 x 2) crosses was 7.8, 2.3, and -30.5 percent, respectively. None of the (6 x 6) crosses had more kernels per head than the high parent, while four of the six (2 x 2) crosses had more kernels than the high parent. None of the (6 x 2) crosses had more kernels per head than the parental average. The range in heterosis for kernel number among all crosses based on the midparent estimates was 15.7 to -38.7 percent.

The (6 x 2) crosses exhibited more heterosis for kernel weight than the (6 x 6) or (2 x 2) crosses (Table 10). The average percentage increase of the F_1 's over the parental averages for kernel weight for the (6 x 6), (2 x 2), and (6 x 2) crosses was 5.8, 0.2, and 28.1, respectively. None of the (6 x 6) or (2 x 2) crosses possessed kernels that were significantly larger than the largest parent. Nine of the twelve (6 x 2) crosses had kernels which were significantly larger than the largest parent. The range in heterosis for kernels per head among all crosses was 49.0 to -11.9 percent.

The components of general and specific combining ability estimates and the narrow-sense heritability estimates for yield and

the components of yield for the (2 x 2) and (6 x 2) crosses are presented in Table 11.

A small amount of additive gene action, as indicated by the estimate for general combining ability (GCA), was present for grain yield, number of heads per plant and weight per kernel in the (2 x 2) crosses (Table 11). Non-additive gene action was indicated by the estimate of specific combining ability (SCA) only for weight per kernel in the (2 x 2) crosses. The non-additive component of genetic variance was larger than the additive component for weight per kernel. No genetic variance was found for kernels per head. The environmental component for all traits was much larger than either of the genetic components or both of the genetic components combined. Relatively low narrow-sense heritability estimates were found for grain yield, tiller number per plant and weight per kernel in the (2 x 2) crosses. In general, the genetic portion of the variation among the (2 x 2) crosses was quite small.

The types of gene action estimates for yield and the components of yield for the (6 x 2) crosses are also shown in Table 11. It is possible to determine the additive gene action contributed by the six-rowed parents and by the two-rowed parents to the genetic variances of traits within the (6 x 2) crosses. In all but one case, the additive genetic components (GCA) for the six-rowed parents were much larger than the (GCA) of the two-rowed parents. A weighted average general combining ability estimate ($\overline{\text{GCA}}$) was computed to determine the average additive gene action among the crosses. Additive gene action ($\overline{\text{GCA}}$) was noted for yield, kernel

Table 11

Components of general and specific combining ability
and narrow-sense heritability estimates for yield
and components of yield for (2x2) and (6x2) crosses

Crosses	Component	Grain yield	Kernels/ head	Heads/ plant	Weight/ kernel
2x2	GCA	8.0493	0.0000	5.7307	0.000,003,917
	SCA	0.0000	0.0000	0.0000	0.000,005,117
	E	32.2090	2.6669	52.4620	0.000,020,533
	h^2_{ns}	0.333	0.000	0.179	0.234
6x2	GCA(6)	44.7510	39.6189	0.0000	0.000,069,726
	GCA(2)	0.0000	0.6875	0.0000	0.000,009,367
	\overline{GCA}	12.5200	18.5830	0.0000	0.000,031,221
	SCA	30.1055	11.3178	36.6258	0.000,000,000
	E	43.8860	10.6920	20.7885	0.000,078,788
	h^2_{ns}	0.252	0.628	0.000	0.442

GCA = general combining ability

SCA = specific combining ability

E = environmental

GCA(6) = general combining ability for six-rowed parents

GCA(2) = general combining ability for two-rowed parents

\overline{GCA} = weighted average general combining ability

h^2_{ns} = heritability in narrow-sense

number per head and weight per kernel in the (6 x 2) group. No additive gene action was detected for heads per plant in the (6 x 2) crosses. Some non-additive gene action (SGA) was found for all the traits except weight per kernel. Weight per kernel appeared to be controlled only by additive genes and most of these were contributed by six-rowed parents.

The narrow-sense heritability estimates for the (6 x 2) crosses are given in Table 11 for yield and the components of yield. A high narrow-sense heritability estimate was found for kernels per head, while an intermediate estimate was found for weight per kernel. Grain yield had a relatively low estimate.

Total Leaf Area and Components of Total Leaf Area

Functional analyses of variance were computed for each leaf area trait at both times of measurement. Summaries of the mean squares from these analyses are given in Tables 12 and 13. Appropriate error mean squares were used to determine significance of the various sources of variation.

The 21 crosses and the seven parental varieties differed significantly at the .01 level for total leaf area and all of the components of TLA at both times of measurement. When the crosses were separated according to the row number of their respective parents, only leaf width was found to be significantly different for these groups.

Although the among group sources of variation were not significant for most of the leaf area traits, there appeared to be small

Table 12

A summary of the mean squares from the functional analysis of variance
for total leaf area and components of total leaf area prior to heading

Source of variation	df	TLA ms	Leaf width ms	Leaf length ms	Tillers/plant ms
Replications	3	25,603.967 N.S.	0.04447**	10.167**	2.080 N.S.
Entries	27	965,764.925**	0.14105**	12.748**	17.210**
Among groups	3	34,310.700 N.S.	0.40087*	13.333 N.S.	16.740 N.S.
¹ Within groups	24	104,359.717*	0.10858**	12.675**	17.269**
w/in (6x6) crosses	2	249,993.610**	0.29360**	8.980 N.S.	68.085**
w/in (6x2) crosses	11	122,815.373**	0.06805**	21.663**	9.084**
w/in (2x2) crosses	5	42,410.836 N.S.	0.01840 N.S.	4.032 N.S.	14.300**
w/in parents	6	73,603.767*	0.19637**	4.622**	17.810**
² Reps x entries	81	32,543.519	0.00981	1.863	2.648
³ R x w/in groups	9	21,132.538	0.00730	3.283	2.473
⁴ R x w/in (6x6) crosses	6	11,703.810	0.01063	1.805	1.638
⁵ R x w/in (6x2) crosses	33	30,037.458	0.00845	1.932	2.340
⁶ R x w/in (2x2) crosses	15	59,838.946	0.00709	1.723	3.011
⁷ R x w/in parents	18	27,043.837	0.01555	1.136	3.333
Total	111				

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 for within groups

⁴ = Error term for within (6x6) crosses

⁵ = Error term for within (6x2) crosses

⁶ = Error term for within (2x2) crosses

⁷ = Error term for within parents

Table 13

A summary of the mean squares from the functional analyses of variance for total leaf area and components of total leaf area at heading time

Source of variation	df	TLA ms	Leaf width ms	Leaf length ms	Tillers/plant ms
Replications	3	514,013.333 N.S.	0.02193 N.S.	7.943**	10.580 N.S.
Entries	27	1,471,159.778**	0.15366**	14.822**	39.562**
Among groups	3	801,072.667 N.S.	0.59993**	12.380 N.S.	63.940 N.S.
¹ Within groups	24	1,554,920.667**	0.09787**	15.128**	36.515 N.S.
w/in (6x6) crosses	2	6,065,092.556**	0.07300**	12.720**	64.335**
w/in (6x2) crosses	11	1,413,073.636**	0.06694**	18.925**	28.795 N.S.
w/in (2x2) crosses	5	534,687.660 N.S.	0.00344 N.S.	5.892**	16.500 N.S.
w/in parents	6	904,770.167*	0.24158**	16.667**	58.072*
² Reps x entries	81	328,413.222	0.05428	0.980	18.031
² R x w/in groups	9	300,384.967	0.00594	1.586	16.840
⁴ R x w/in (6x6) crosses	6	434,898.000	0.00625	0.852	4.000
⁵ R x w/in (6x2) crosses	33	247,457.030	0.00479	1.000	25.336
⁶ R x w/in (2x2) crosses	15	491,375.693	0.00661	0.689	12.478
⁷ R x w/in parents	18	322,854.150	0.00509	0.924	14.539
Total	111				

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 replication and entries

³ = Error term for within groups

⁴ = Error term for within (6x6) crosses

⁵ = Error term for within (6x2) crosses

⁶ = Error term for within (2x2) crosses

⁷ = Error term for within parents

but consistent differences between the averages for the (6 x 6), (2 x 2), and (6 x 2) crosses. These same differences were generally found when the parental varieties were compared according to row number. In general, the six-rowed parents had larger TLA, wider leaves, shorter leaves, and fewer tillers than the two-rowed parents. These same trends were also present when the (6 x 6) and the (2 x 2) crosses were compared. The (6 x 2) crosses were intermediate between the six-rowed and two-rowed barleys in their leaf area characters. The only major exception to the intermediate behavior of the (6 x 2) crosses occurred for TLA at heading time when the average of the (6 x 2) crosses was lower than either parental group.

The crosses between the six-rowed parents (6 x 6) differed significantly for all leaf traits at both stages of growth except for leaf length prior to heading (Table 12 and 13). The crosses between the two-rowed parents (2 x 2) differed significantly only for tillers per plant prior to heading and leaf length at heading.

Pathway coefficient analyses were computed to determine the associations between the components of leaf area and TLA of six-rowed barleys and two-rowed barleys at the two stages of growth. The direct and indirect effects of the components of TLA for the six-rowed barleys and the two-rowed barleys prior to heading and at heading are given in Tables 14 and 15 respectively.

The comparison of the pathway coefficient analyses for TLA for the six-rowed and two-rowed barleys indicated that these two groups were different (Tables 14 and 15). Tiller number which represents leaf number per plant had the largest direct effect in both groups

Table 14

The direct and indirect effects of the components of total leaf area for three types of barleys prior to heading

Components	<u>Groups</u>		
	Six-rowed	Two-rowed	(6x2) crosses
Tillers/plant			
Direct effect on TLA	1.65893	1.50665	0.69715
Indirect effect via leaf length on TLA	-0.10395	-0.52108	-0.13218
Indirect effect via leaf width on TLA	-0.79916	-0.24068	-0.11877
Simple r	0.75582	0.74489	0.44620
Leaf length			
Direct effect on TLA	0.36918	0.66353	0.37605
Indirect effect via tiller on TLA	-0.46709	-1.18320	-0.24504
Indirect effect via leaf width on TLA	0.00599	0.20455	0.42335
Simple r	-0.09192	-0.31512	0.55436
Leaf width			
Direct effect on TLA	1.01476	0.29537	0.60682
Indirect effect via tiller on TLA	-1.30646	-1.22767	-0.13645
Indirect effect via leaf length on TLA	0.00218	0.45950	0.26235
Simple r	-0.28952	-0.47280	0.73272
$R^2 =$	0.92614	0.77354	0.96418

Table 15

The direct and indirect effects of the components of total leaf area for three types of barleys at heading time

Components	Six-rowed	<u>Groups</u>	
		Two-rowed	(6x2) crosses
Tillers/plant			
Direct effect on TLA	0.90291	0.84992	0.76937
Indirect effect via leaf length on TLA	-0.40488	-0.10459	-0.16733
Indirect effect via leaf width on TLA	0.23584	-0.36893	0.00654
Simple r	0.73387	0.37640	0.60858
Leaf length			
Direct effect on TLA	0.72193	0.27330	0.54716
Indirect effect via tiller on TLA	-0.50638	-0.32525	-0.23529
Indirect effect via leaf width on TLA	-0.12275	0.42412	0.18677
Simple r	0.09280	0.37217	0.49864
Leaf width			
Direct effect on TLA	-0.29012	0.76844	0.27496
Indirect effect via tiller on TLA	-0.73390	-0.40804	0.01862
Indirect effect via leaf length on TLA	0.30546	0.15084	0.37166
Simple r	-0.71865	0.51124	0.6524
$R^2 =$	0.93812	0.81450	0.92409

at both times of measurement. The direct effects of leaf length and leaf width were not the same in both groups. Tiller number also had a larger direct effect than leaf length and leaf width in the (6 x 2) crosses. The direct effects of leaf length and leaf width in the (6 x 2) group were similar to the direct effects of these components in the six-rowed barleys. The main differences between groups were found in the direct effects of leaf length and leaf width.

The magnitude of direct effects of leaf length and leaf width reversed in the two-rowed and six-rowed barleys as the plant matured. At the measurement prior to heading, leaf width had a larger direct effect than leaf length in the six-rowed group, while at heading time leaf length had the larger direct effect. The two-rowed group also showed a reversal but in the opposite direction. Leaf length had a larger direct effect prior to heading than leaf width, while leaf width had the larger direct effect at heading time. The pathway coefficients indicated that six-rowed and two-rowed barleys, besides differing in the direct effects of the components, also differed in the importance of a component at different stages of maturity. When the direct effects of leaf length and leaf width of the two stages of maturity were compared in the (6 x 2) crosses, a reversal in importance similar to the one for the six-rowed barleys was found.

Estimates of heterosis for TLA and the components of TLA at two stages of growth are given in Tables 16, 17, 18, 19, 20, 21, 22, and 23. The crosses were separated into three groups according to the row number of their respective parents.

Table 16

The amounts of heterosis for total leaf area of (6x6),
(2x2) and (6x2) crosses prior to heading

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	$\% > \bar{MP}$
6x6	T ₁ XA	1346.0	1355.5	1303.1	1329.3	16.7	9.5	1.3
	AXT ₂	1425.0	1303.1	1285.6	1294.4	130.6	121.9	10.1
	T ₂ XT ₁	957.9	1355.5	1285.6	1320.6	-362.7	-397.6	-27.5
							Ave.	- 5.4
2x2	ADXD	1180.8	1175.4	973.7	1074.6	106.2	5.4	9.9
	ADXP	1215.6	1175.4	1099.8	1137.6	78.0	40.2	6.9
	ADXH	1166.9	1175.4	1112.3	1143.9	23.0	- 8.5	2.0
	PXH	992.0	1112.3	1099.8	1106.5	-114.5	-120.3	-10.3
	PXD	1256.7	1099.8	973.7	1036.8	219.9a	156.9	21.2
	HXD	1042.9	1112.3	973.7	1043.0	- 0.1	- 69.4	0.0
							Ave.	5.0
6x2	AXD	788.6	1303.1	973.7	1138.4	-349.8	-514.5	-30.7
	AXP	1012.5	1303.1	1099.8	1201.5	-189.0	-290.6	-15.7
	AXH	1141.7	1303.1	1112.3	1207.7	- 66.0	-161.4	- 5.5
	AXAD	1213.8	1303.1	1175.4	1239.3	- 25.5	- 89.3	- 2.1
	T ₁ XD	1183.1	1355.5	973.7	1164.6	18.5	-107.1	1.6
	T ₁ XP	1348.4	1355.5	1099.8	1227.7	120.7	- 7.1	9.8
	T ₁ XH	1353.6	1355.5	1112.3	1233.9	119.7	- 1.9	9.7
	T ₁ XAD	1353.0	1355.5	1175.4	1265.5	87.5	- 2.5	6.9
	T ₂ XD	1308.4	1285.6	973.7	1129.7	178.7	22.8	15.8
	T ₂ XP	1031.2	1285.6	1099.8	1192.7	-161.5	-254.4	-13.5
	T ₂ XH	1091.5	1285.6	1112.3	1199.0	-107.5	-194.1	- 9.0
	T ₂ XAD	1014.0	1285.6	1175.4	1230.5	-216.5	-271.6	-17.6
							Ave.	4.2
Parents		\bar{X}						
Traill	=T ₁	1355.5						
Atlas 46	=A	1303.1						
Trebi	=T ₂	1285.6						
Domen	=D	973.7						
Pirolina	=P	1099.8						
Hannchen	=H	1112.3						
Abed Denso	=AD	1175.4						

a = $F_1 >$ 20 percent of parental average

Table 17

The amounts of heterosis for leaf length of (6x6),
(2x2) and (6x2) crosses prior to heading

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	32.6	37.4	34.8	36.1	-3.5	-4.8*	-9.7
	AXT ₂	34.9	35.9	34.8	35.4	-0.5	-1.0	-1.4
	T ₂ XT ₁	35.4	37.4	35.9	36.7	-1.3	-2.0	-3.5
							Ave.	-4.9
2x2	ADX _D	37.3	36.5	34.6	35.6	1.7	0.8	4.8
	ADXP	35.4	35.5	34.6	35.1	0.3	-0.1	0.9
	ADXH	36.0	34.6	34.5	34.6	1.4	1.4	4.1
	PXH	36.0	35.5	34.5	35.0	1.0	0.5	2.9
	PXD	36.3	36.5	35.5	36.0	0.3	-0.2	0.8
	HXD	38.1	36.5	34.5	35.5	2.6	1.6	7.3
							Ave.	3.5
6x2	AXD	33.5	36.5	34.8	35.7	-2.2	-3.0*	-6.2
	AXP	32.2	35.5	34.8	35.2	-3.0	-3.3*	-8.5
	AXH	33.3	34.8	34.5	34.7	-1.4	-1.5	-4.0
	AXAD	32.8	34.8	34.6	34.7	-1.9	-2.0	-5.5
	T ₁ XD	39.3	37.4	36.5	37.0	2.3	1.9	6.2
	T ₁ XP	35.3	37.4	35.5	36.5	-1.2	-2.1	-3.3
	T ₁ XH	38.0	37.4	34.5	36.0	2.0	0.6	5.6
	T ₁ XAD	37.6	37.4	34.6	36.0	1.6	0.2	4.4
	T ₂ XD	38.2	36.5	35.9	36.2	2.0	1.7	5.5
	T ₂ XP	35.5	35.9	35.5	35.7	-0.2	-0.4	-0.6
	T ₂ XH	35.2	35.9	34.5	35.2	0.0	-0.7	0.0
	T ₂ XAD	35.4	35.9	34.6	35.3	0.1	-0.5	0.3
							Ave.	-0.5
Parents			\bar{X}					
Traill	=T ₁		37.4					
Atlas 46	=A		34.8					
Trebi	=T ₂		35.9					
Domen	=D		36.5					
Pirolina	=P		35.5					
Hannchen	=H		34.5					
Abed Denso	=AD		34.6					

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 1.92
P = 28 SSR = 2.35

Table 18

The amounts of heterosis for leaf width of (6x6), (2x2) and (6x2) crosses prior to heading

Group	Entry	$F_1\bar{X}$	High \bar{F}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	1.83	1.81	1.34	1.58	0.25	0.02	15.8
	AXT ₂	1.32	1.51	1.34	1.43	-0.11	-0.19	- 7.7
	T ₂ XT ₁	1.72	1.81	1.51	1.66	0.06	-0.09	3.6
							Ave.	3.9
2x2	ADXD	1.35	1.40	1.25	1.32	0.03	-0.05	2.3
	ADXP	1.25	1.25	1.22	1.24	0.01	0.00	0.8
	ADXH	1.26	1.25	1.16	1.20	0.06	0.01	5.0
	PXH	1.24	1.22	1.16	1.19	0.05	0.02	4.2
	PXD	1.16	1.40	1.22	1.31	-0.15	-0.24*	-11.5
	HXD	1.33	1.40	1.16	1.28	0.05	-0.07	3.9
							Ave.	0.8
6x2	AXD	1.21	1.34	1.22	1.28	-0.07	-0.13	- 5.5
	AXP	1.34	1.40	1.34	1.37	-0.03	-0.06	- 2.2
	AXH	1.38	1.34	1.16	1.25	0.13	0.04	10.4
	AXAD	1.49	1.34	1.25	1.30	0.19	0.15	14.6
	T ₁ XD	1.61	1.81	1.40	1.60	0.01	-0.20*	0.6
	T ₁ XP	1.63	1.81	1.22	1.52	0.11	-0.18*	7.2
	T ₁ XH	1.48	1.81	1.16	1.48	0.00	-0.33*	0.0
	T ₁ XAD	1.67	1.81	1.25	1.53	0.14	-0.14	9.2
	T ₂ XD	1.52	1.51	1.40	1.46	0.06	0.01	4.1
	T ₂ XP	1.44	1.51	1.22	1.36	0.08	-0.07	5.9
	T ₂ XH	1.38	1.51	1.16	1.34	0.04	-0.13	3.0
	T ₂ XAD	1.43	1.51	1.25	1.38	0.05	-0.08	3.6
							Ave.	4.2

Parents	\bar{X}
Traill =T ₁	1.81
Atlas 46 =A	1.34
Trebi =T ₂	1.51
Domen =D	1.40
Pirolina =P	1.22
Hannchen =H	1.16
Abed Denso=AD	1.25

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 0.14
P = 28 SSR = 0.17

Table 19

The amounts of heterosis for tillers per plant of (6x6), (2x2) and (6x2) crosses prior to heading

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	$\% >\bar{MP}$
6x6	T_1XA	13.0	16.0	11.5	13.9	-0.9	-3.3*	- 6.5
	AXT_2	17.0	16.3	12.8	14.6	2.4	0.7	16.4
	T_2XT_1	8.8	12.8	11.5	12.2	-3.4	-4.0*	-27.9
	Ave.							6.0
2x2	$ADX D$	13.5	15.8	11.5	13.7	-0.2	-2.3	- 1.5
	$ADXP$	14.5	15.8	14.8	15.3	-0.8	-1.2	- 5.2
	$ADXH$	14.8	16.0	15.8	15.9	-1.1	-1.2	- 6.9
	PXH	12.8	16.0	14.8	15.4	-2.6	-3.2*	-16.9
	PXD	16.3	14.8	11.5	13.2	3.1a	1.5	23.5
	HXD	10.8	16.0	11.5	13.8	-3.0	-5.2*	-21.7
	Ave.							- 4.8
6x2	AXD	10.0	16.3	11.5	13.9	-3.9	-6.3*	-28.1
	AXP	14.8	16.3	14.8	15.6	-0.8	-1.5	- 5.3
	AXH	14.2	16.3	16.0	16.2	-2.0	-2.1	-12.3
	$AXAD$	14.2	16.3	15.8	16.1	-1.9	-2.1	-11.8
	T_1XD	10.8	11.5	11.5	11.5	-0.7	-0.7	- 6.1
	T_1XP	13.0	14.8	11.5	13.2	-0.2	-1.8	- 1.5
	T_1XH	13.8	16.0	11.5	13.8	0.0	-2.2	0.0
	T_1XAD	12.3	15.8	11.5	13.7	-1.4	-3.5*	-10.2
	T_2XD	12.8	12.8	11.5	12.2	0.6	0.0	4.9
	T_2XP	11.5	14.8	12.8	13.8	-2.3	-3.3*	-16.7
	T_2XH	11.8	16.0	12.8	14.4	-2.6	-4.2*	-18.1
	T_2XAD	11.5	15.8	12.8	14.3	-2.8	-4.3*	-19.6
	Ave.							-10.4

Parents		\bar{X}
Traill	$=T_1$	11.5
Atlas 46	$=A$	16.3
Trebi	$=T_2$	12.8
Domen	$=D$	11.5
Pirolina	$=P$	14.8
Hannchen	$=H$	16.0
Abed Denso	$=AD$	15.8

a = F_1 20 percent of parental average

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 1.92
P = 28 SSR = 2.35

Table 20

The amounts of heterosis for total leaf area of (6x6),
(2x2) and (6x2) crosses at heading time

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	MP	$>\bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	3415.6	4313.2	3780.8	4047.0	- 631.4	- 897.6	-15.6
	AXT ₂	5481.2	4313.2	4070.4	4191.8	1288.4a	1168.0*	30.8
	T ₂ XT ₁	3287.0	4070.4	3780.8	3925.6	- 638.6	- 783.4	-16.3
							Ave.	- 0.4
2x2	ADXD	3859.9	3742.8	3096.7	3419.8	440.1	117.1	12.9
	ADXP	3010.3	3742.8	3275.5	3509.2	- 498.9	- 732.5	-14.2
	ADXH	3717.9	3742.8	3129.1	3436.0	281.9	- 24.9	8.2
	PXH	3204.4	3275.5	3129.1	3202.3	2.1	- 71.1	0.1
	PXD	3914.5	3275.5	3096.7	3124.1	790.4a	639.0	25.3
	HXD	3506.9	3129.1	3096.7	3112.9	394.0	377.8	12.7
							Ave.	7.5
6x2	AXD	2662.7	4313.2	3096.7	3705.0	-1042.3	-1650.5*	-28.1
	AXP	3290.2	4313.2	3275.5	3794.4	- 504.2	-1023.0*	-13.3
	AXH	3078.1	4313.2	3129.1	3721.2	- 643.1	-1235.1*	-17.3
	AXAD	3229.1	4313.2	3742.8	4028.0	- 798.9	-1084.1*	-19.8
	T ₁ XD	3662.9	3780.8	3096.7	3438.8	224.1	- 117.9	6.5
	T ₁ XP	3930.5	3780.8	3275.5	3528.2	402.3	149.7	11.4
	T ₁ XH	4661.2	3780.8	3129.1	3455.0	1206.2a	880.4	34.9
	T ₁ XAD	4134.1	3780.8	3742.8	3761.4	372.7	353.3	9.9
	T ₂ XD	3509.4	4070.4	3096.7	3583.6	- 74.2	- 561.0	- 2.1
	T ₂ XP	2925.9	4070.4	3275.5	3673.0	- 747.1	-1144.5*	-20.3
	T ₂ XH	2698.2	4070.4	3129.1	3599.8	- 901.6	-1372.2*	-25.0
	T ₂ XAD	3395.7	4070.4	3742.8	3906.6	- 510.9	- 674.7	-13.1
							Ave.	- 6.4

Parents		\bar{X}
Traill	=T ₁	3,780.8
Atlas 46	=A	4313.2
Trebi	=T ₂	4070.4
Domen	=D	3096.7
Pirolina	=P	3275.5
Hannchen	=H	3129.1
Abed Denso	=AD	3742.8

a = $F_1 >$ 20 percent of parental average

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 806.6
P = 28 SSR = 988.5

Table 21

The amounts of heterosis for leaf length of (6x6),
(2x2) and (6x2) crosses at heading time

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	33.3	36.5	31.8	34.2	- 0.9	- 3.2*	- 2.7
	AXT ₂	36.4	37.1	31.8	34.5	1.9	- 0.7	5.5
	T ₂ XT ₁	36.4	37.1	36.5	36.8	- 0.4	- 0.7	- 1.1
	Ave.							0.6
2x2	ADXD	37.8	38.3	35.5	36.9	0.9	- 0.5	2.4
	ADXP	35.0	35.5	34.9	35.2	- 0.2	- 0.5	- 0.6
	ADXH	38.0	35.5	35.1	35.3	2.7	2.5*	7.6
	PXH	36.8	35.1	34.9	35.0	1.8	1.7*	5.1
	PXD	37.0	38.3	34.9	36.6	0.4	1.3	1.1
	HXD	38.6	38.3	35.1	36.7	1.9	0.3	5.2
	Ave.							3.5
6x2	AXD	34.9	38.3	31.8	35.1	- 0.2	- 3.4*	- 0.6
	AXP	32.5	34.9	31.8	33.4	- 0.9	- 2.4*	- 2.7
	AXH	34.0	35.1	31.8	33.5	0.5	- 1.1	1.5
	AXAD	33.6	35.5	31.8	33.7	- 0.1	- 1.9*	- 0.3
	T ₁ XD	39.5	38.3	36.5	37.4	2.1	1.2	5.6
	T ₁ XP	36.2	36.5	34.9	35.7	0.5	0.3	1.4
	T ₁ XH	38.3	36.5	35.1	35.8	2.5	1.8*	7.0
	T ₁ XAD	38.1	36.5	35.5	36.0	2.1	1.6*	5.8
	T ₂ XD	38.4	38.3	37.1	37.7	0.7	0.1	1.9
	T ₂ XP	36.3	37.1	34.9	36.0	0.3	- 0.8	0.8
	T ₂ XH	37.0	37.1	35.1	36.1	0.9	- 0.1	2.5
	T ₂ XAD	35.9	37.1	35.5	36.3	- 0.4	- 1.2	- 1.1
	Ave.							1.9

Parents		\bar{X}
Traill	=T ₁	36.5
Atlas 46	=A	31.8
Trebi	=T ₂	37.1
Domen	=D	38.3
Pirolina	=P	34.9
Hannchen	=H	35.1
Abed Denso	=AD	35.5

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 1.39
P = 28 SSR = 1.71

Table 22

The amount of heterosis for leaf width of (6x6),
(2x2) and (6x2) crosses at heading time

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	$\%>\bar{MP}$
6x6	T ₁ XA	2.04	1.98	1.67	1.83	0.21	0.06	11.5
	AXT ₂	1.79	1.92	1.67	1.80	-0.01	-0.13	- 0.6
	T ₂ XT ₁	2.01	1.98	1.92	1.95	0.06	-0.03	- 3.1
							Ave.	4.7
2x2	ADXD	1.55	1.54	1.51	1.53	0.03	0.01	1.3
	ADXP	1.46	1.54	1.39	1.47	-0.01	-0.08	- 0.7
	ADXH	1.48	1.54	1.36	1.45	0.03	-0.06	2.1
	PXH	1.46	1.39	1.36	1.38	0.08	0.05	5.8
	PXD	1.46	1.51	1.39	1.45	0.01	-0.05	0.7
	HXD	1.48	1.51	1.36	1.44	0.04	-0.03	2.8
							Ave.	2.0
6x2	AXD	1.57	1.67	1.51	1.59	-0.02	-0.10	- 1.3
	AXP	1.49	1.67	1.39	1.53	-0.04	-0.18	- 2.6
	AXH	1.61	1.67	1.36	1.52	0.09	-0.06	5.9
	AXAD	1.67	1.67	1.54	1.61	0.06	0.00	3.7
	T ₁ XD	1.81	1.98	1.51	1.75	0.06	-0.17	3.4
	T ₁ XP	1.90	1.98	1.39	1.69	0.21	0.08	12.4
	T ₁ XH	1.76	1.98	1.36	1.67	0.09	-0.31	5.4
	T ₁ XAD	1.93	1.98	1.54	1.76	0.17	-0.05	9.7
	T ₂ XD	1.69	1.92	1.51	1.72	0.03	-0.40*	- 1.7
	T ₂ XP	1.72	1.92	1.39	1.66	0.06	-0.20	3.6
	T ₂ XH	1.64	1.92	1.36	1.64	0.00	-0.28	0.0
	T ₂ XAD	1.66	1.92	1.54	1.73	-0.07	-0.33	- 4.0
							Ave.	2.9

Parents		\bar{X}
Traill	=T ₁	1.98
Atlas 46	=A	1.67
Trebi	=T ₂	1.92
Domen	=D	1.51
Pirolina	=P	1.39
Hannchen	=H	1.36
Abed Denso	=AD	1.54

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR - 0.33
P = 28 SSR - 0.40

Table 23

The amounts of heterosis for tillers per plant of
(6x6), (2x2) and (6x2) crosses at heading time

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	$\bar{M}\bar{P}$	$>\bar{M}\bar{P}$	$F_1 >$ High \bar{P}	$\% >\bar{M}\bar{P}$
6x6	T ₁ XA	20.3	24.5	19.8	22.2	- 1.9	- 4.2	- 8.6
	AXT ₂	23.8	24.5	18.3	21.4	2.4	- 0.7	11.2
	T ₂ XT ₁	15.8	19.8	18.3	19.1	- 3.3	- 4.0	-17.3
							Ave.	- 4.9
2x2	ADXD	24.0	25.3	19.8	22.6	1.4	- 1.3	6.2
	ADXP	22.3	27.5	25.3	26.4	- 4.1	- 5.2	-15.5
	ADXH	27.8	27.0	25.3	26.2	1.6	0.8	6.1
	PXH	24.0	27.5	27.0	27.3	- 3.3	- 3.5	-12.1
	PXD	26.0	27.5	19.8	23.7	2.3	- 1.5	9.7
	HXD	23.0	27.0	19.8	23.4	- 0.4	- 4.0	- 1.7
							Ave.	- 1.2
6x2	AXD	19.5	24.5	19.8	22.2	- 2.7	- 5.0	-12.2
	AXP	26.5	27.5	24.5	26.0	0.5	- 1.0	1.9
	AXH	24.3	27.0	24.5	25.8	- 1.5	- 2.7	- 5.8
	AXAD	22.3	25.3	24.5	24.9	- 2.6	- 3.0	-10.4
	T ₁ XD	20.3	19.8	19.8	19.8	0.5	0.5	2.5
	T ₁ XP	23.5	27.5	19.8	23.7	- 0.2	- 4.0	- 0.8
	T ₁ XH	25.8	27.0	19.8	23.4	2.4	- 1.2	10.3
	T ₁ XAD	24.0	25.3	19.8	22.6	1.4	- 1.3	6.2
	T ₂ XD	20.3	19.8	18.3	19.1	1.2	0.5	6.3
	T ₂ XP	18.5	27.5	18.3	22.9	- 4.4	- 9.0*	-19.3
	T ₂ XH	19.0	27.0	18.3	22.7	- 3.7	- 8.0*	-16.3
	T ₂ XAD	21.8	25.3	18.3	21.8	- 0.0	- 3.5	0.0
							Ave.	- 3.1

Parents		\bar{X}
Traill	=T ₁	19.8
Atlas 46	=A	24.5
Trebi	=T ₂	18.3
Domen	=D	19.8
Pirolina	=P	27.5
Hannchen	=H	27.0
Abed Denso	=AD	25.3

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 5.97
P = 28 SSR = 7.31

The amount of heterosis measured as the amount that the F_1 exceeded the parental average for TLA at both stages of growth was quite small for all crosses. Average amounts of heterosis for TLA prior to heading for the (6 x 6), (2 x 2), and (6 x 2) crosses were -5.4, 5.0, and 4.2 percent, respectively. The average amount of heterosis for TLA at heading time for the (6 x 6), (2 x 2), and the (6 x 2) crosses was -0.4, 7.5, and -6.4 percent, respectively. The range in heterosis for TLA in all crosses at heading was from -28.1 to 34.9 percent. The Atlas 46 x Trebi hybrid at heading time was the only cross that had a significantly larger TLA than the better parent, although the Traill x Hannchen cross approached significance.

There were three crosses which exhibited a large amount of heterosis for TLA at heading time. These were as follows: Atlas 46 x Trebi (6 x 6), Pirolina x Domen (2 x 2), and Traill x Hannchen (6 x 2), which exceeded the parental averages by 30.8, 25.3, and 34.9 percent, respectively. A comparison of the TLA and the components of TLA of these three F_1 's and their respective parents is given in Table 24.

The parental varieties in Table 24 exhibited reciprocal differences for the components of TLA. One parent had a low mean value for one component and the other parent had a high mean value for this component. There was almost perfect complementation between the parents of these three crosses. All of the (6 x 2) crosses had parents which complemented each other but not all of the crosses exhibited heterosis.

Table 24

A comparison of the total leaf area and the components of TLA of three F_1 's and their respective parents that exhibited heterosis.

Cross	6 x 6			2 x 2			6 x 2		
	Parent	F_1	Parent	Parent	F_1	Parent	Parent	F_1	Parent
Traits	Atlas 46	AXT ₂	Trebi	Pirolina	DXP	Domen	Traill	T ₁ XH	Hannchen
Leaf length	31.8	36.4	37.1	34.9	37.0	38.3	36.5	38.3	35.1
Leaf width	1.67	1.79	1.92	1.39	1.46	1.51	1.98	1.76	1.36
Tiller number	24.5	23.8	18.3	27.5	26.0	19.8	19.8	25.8	27.0
TLA	4313.2	5481.2	4070.4	3275.5	3914.5	3096.7	3780.8	4661.2	3129.1
	Percent heterosis - 30.8			Percent heterosis - 25.3			Percent heterosis - 34.9		

Estimates of general and specific combining ability effects associated with the leaf area traits were made in order to obtain an indication of the types of gene action controlling the various traits. The variance components of general combining ability (additive gene action), specific combining ability (non-additive gene action), and environment for TLA and its components with the narrow-sense heritability estimate at two stages of growth are given in Tables 25 and 26, respectively.

No genetic variation was found for TLA for the (2 x 2) crosses prior to heading (Table 25). At heading time, a slight amount of non-additive gene action was found for TLA in this group (Table 26). The predominant factor which contributed to differences in TLA in this group was the environment. The narrow-sense heritability estimates for TLA were zero at both stages of growth for the (2 x 2) crosses. The additive genetic component was the only genetic factor found at both stages which influenced leaf length. The narrow-sense heritability estimates for leaf length were 0.396 and 0.760 for the two stages of growth. The differences in these estimates were due to an increase in the additive component at heading time associated with a smaller environmental component. A small amount of additive gene action at heading time was found for leaf width, while non-additive gene action was found to comprise a larger amount of the genetic variation at this time. The narrow-sense heritability estimate for leaf width was small. No genetic variance was found for leaf width at heading time in the (2 x 2) crosses. Only non-additive genetic factors were found for tiller

Table 25

Components of general and specific combining ability and narrow-sense heritability estimates for total leaf area and components of total leaf area for (2x2) and (6x2) crosses prior to heading

Crosses	Components	TLA	Leaf length	Leaf width	Tiller/plant
2x2	GCA	0.000	0.5641	0.000163	0.0000
	SCA	0.000	0.0000	0.002625	3.9659
	E	59,838.946	1.7233	0.00710	3.0113
	h^2_{ns}	0.000	0.396	0.032	0.0000
6x2	GCA(6)	1,105.130	7.0928	0.0128	0.00000
	GCA(2)	0.000	0.7313	0.0000	0.14716
	\overline{GCA}	0.000	3.0195	0.0064	0.10226
	SCA	0.000	0.2661	0.0000	1.52759
	E	300,374.580	1.932	0.0845	2.34091
	h^2_{ns}	0.000	0.733	0.132	0.050

GCA = general combining ability
 SCA = specific combining ability
 E = environmental
 GCA(6) = general combining ability for six-rowed parents
 GCA(2) = general combining ability for two-rowed parents
 \overline{GCA} = weighted average general combining ability
 h^2_{ns} = heritability in narrow-sense

Table 26

Components of general and specific combining ability and narrow-sense heritability estimates for total leaf area and components of total leaf area for (2x2) and (6x2) crosses at heading time

Crosses	Components	TLA	Leaf length	Leaf width	Tiller/ plant
2x2	GCA	0.000	1.09164	0.0000	0.0000
	SCA	32,640.170	0.00000	0.0000	6.2868
	E	491,375.693	0.68933	0.0661	12.4780
	h^2_{ns}	0.000	0.760	0.000	0.000
6x2	GCA(6)	385,652.482	6.5563	0.02236	1.2776
	GCA(2)	0.000	0.8389	0.00000	0.0000
	\overline{GCA}	114,083.130	2.9060	0.00766	0.4056
	SCA	115,093.848	0.0000	0.00357	0.0000
	E	247,457.030	1.0003	0.00479	25.3357
	h^2_{ns}	0.386	0.853	0.647	0.003

GCA = general combining ability
 SCA = specific combining ability
 E = environmental
 GCA(6) = general combining ability for six-rowed parents
 GCA(2) = general combining ability for two-rowed parents
 \overline{GCA} = weighted average general combining ability
 h^2_{ns} = heritability in narrow-sense

number per plant at both stages of growth.

The (GCA) components associated with the two-rowed parents in the (6 x 2) crosses were in good agreement with the (GCA) components for the (2 x 2) crosses. Prior to heading and at heading time, the only sizeable (GCA) component for the two-rowed parents in the (6 x 2) group was for leaf length.

Additive gene action for the six-rowed parents was found for all traits at both stages of growth with the exception of tiller number per plant prior to heading (Tables 25 and 26). In every case, except for tiller number per plant prior to heading, the (GCA)(6) components were much larger than the (GCA)(2) components.

Additive gene action (\overline{GCA}) was not found for TLA prior to heading but was present for TLA at heading time. The additive genetic difference present in the (6 x 2) crosses was mostly contributed by the six-rowed parents. Some non-additive gene action (SCA) was found at heading time for TLA but none was found prior to heading. The narrow-sense heritability estimate for TLA was zero prior to heading and 0.386 at heading. Large amounts of additive gene action (\overline{GCA}) were found for leaf length and leaf width at both stages of growth in the (6 x 2) group. Narrow-sense heritability estimates of 0.733 and 0.853 for leaf length and 0.132 and 0.647 for leaf width at the two stages of growth respectively were found.

The associations of leaf area measurements with yield and its components were determined in order to obtain information on the importance of these relationships. Simple correlation coefficients

between the leaf area characteristics at two stages of development with grain yield are presented for six-rowed, two-rowed, and six-rowed x two-rowed crosses in Tables 27, 28, and 29, respectively.

It would appear that leaf length and leaf width are negatively associated with the components of yield in the six-rowed barleys (Table 27); however, none of these associations between the leaf size characters and the components of yield were significant. Because of the size of the population of six-rowed barleys, an "r" value of 0.811 is required to be significantly different from zero at the .05 level. Tiller number at both times of measurement was positively associated with all of the components of yield, with three of these relations being significant.

The relationships between the leaf measurements and grain yield were generally small and not significantly different from zero in the two-rowed barleys (Table 28). Several significant associations were found between the leaf measurements and the components of yield. There were no clear relationships between leaf size and leaf number with yield or the components of yield in the two-rowed barleys.

Several significant positive associations were found for the leaf measurements and grain yield in the (6 x 2) crosses (Table 29.) Larger leaves and greater TLA were positively associated with grain yield. The relationships between the yield components and the leaf area measurements varied from component to component.

Table 27

The relationships between leaf area measurements and grain yield and components of grain yield for six-rowed barley

Trait	Grain yield	Heads/ plant	Kernels/ head	Weight/ kernel
TLA ¹	0.488	0.920**	0.556	0.302
Leaf length ¹	0.114	-0.355	-0.642	-0.319
Leaf width ¹	0.476	-0.481	-0.682	-0.409
Tillers/plant ¹	0.101	0.870*	0.840*	0.224
TLA ²	0.143	0.724	0.806	0.464
Leaf length ²	-0.992**	-0.221	-0.626	-0.504
Leaf width ²	0.239	-0.437	-0.459	-0.389
Tillers/plant ²	0.379	0.775	0.922**	0.469

1 = Measurements prior to heading

2 = Measurements at heading

* = r is significant at five percent level if greater than 0.811 n = 6

** = r is significant at one percent level if greater than 0.917 n = 6

Table 28

The relationships between leaf area measurements and grain yield and components of grain yield for two-rowed barley

Trait	Grain yield	Heads/ plant	Kernels/ head	Weight kernel
TLA ¹	-0.515	-0.330	0.734*	-0.680*
Leaf length ¹	0.324	0.229	0.509	0.278
Leaf width ¹	-0.309	-0.253	-0.376	-0.607
Tillers/plant ¹	-0.133	-0.268	-0.376	-0.227
TLA ²	0.217	-0.747*	0.424	-0.408
Leaf length ²	0.226	0.704*	-0.298	0.285
Leaf width ²	-0.168	-0.386	0.802*	-0.231
Tillers/plant ²	0.162	0.141	0.524	-0.174

1 = Measurements prior to heading

2 = Measurements at heading

* = r is significant at five percent level if greater than 0.6325 n = 10

** = r is significant at one percent level if greater than 0.7650 n = 10

Table 29

The relationship between leaf area measurements and grain yield and components of grain yield for (6x2) crosses

Trait	Grain yield	Heads/ plant	Kernels/ head	Weight/ kernel
TLA ¹	0.884**	0.450	0.633*	-0.463
Leaf length ¹	0.668*	0.162	0.351	0.371
Leaf width ¹	0.718**	-0.116	0.656*	-0.297
Tillers/plant ¹	0.317	0.681*	0.805**	-0.410
TLA ²	0.931**	0.603	0.672*	-0.586*
Leaf length ²	0.561	-0.106	0.357	0.640*
Leaf width ²	0.727**	0.151	0.772**	-0.446
Tillers/plant ²	0.472	0.702**	0.304	-0.639*

1 = Measurements prior to heading

2 = Measurements at heading

* = r is significant at five percent level if greater than 0.576 n = 12

** = r is significant at one percent level if greater than 0.684 n = 12

Malting Quality

Values of the 21 F_1 's and seven parental varieties for barley nitrogen, diastatic power, and extract are given in Table 30. This table includes the averages for the crosses when they are grouped according to the row number of their respective parents. The four groups consisted of the (6 x 6), (2 x 2), and (6 x 2) crosses and the parents. The means for the 21 crosses and seven parents for the malting quality characters, nitrogen, diastatic power, and extract, are given in Appendix Table 5.

Functional analyses of variance were computed for the barley quality traits and the mean squares from the analyses are given in Table 31. Significant differences were determined by the use of the appropriate error mean squares. The 21 crosses and seven parents differed significantly at the .01 level for barley nitrogen, diastatic power, and extract. The separation of the crosses into groups according to row number produced significant differences at the .01 level for barley nitrogen and barley extract. The differences between groups of crosses and parents for barley diastatic power approached the "F" value at the .05 level. The (2 x 2) crosses and the (6 x 6) crosses had lower amounts of barley nitrogen than the (6 x 2) crosses. The average diastatic power for the (6 x 6) crosses was lower than the average for the (2 x 2) crosses, and the (6 x 2) group of crosses had the highest average diastatic power. The average barley extract for the (6 x 2) crosses was intermediate in barley extract between these two groups of crosses.

Table 30

A summary of the means of the 21 crosses and seven parents for barley nitrogen, barley diastatic power and barley extract and the group averages for (6x6), (2x2), (6x2) crosses and parents

Group	Entry	Barley nitrogen	Barley D.P.	Barley ext.
6x6	T ₁ XA	2.15	179.0	76.3
	T ₁ XT ₂	2.18	225.8	77.2
	T ₂ XA	<u>2.26</u>	<u>185.2</u>	<u>76.1</u>
	Ave.	2.20	196.7	76.5
2x2	HXD	2.28	235.2	80.3
	HXP	2.30	231.2	79.6
	HXAD	2.32	201.8	79.9
	DXP	2.26	238.2	79.9
	DXAD	2.21	213.5	80.2
	PXAD	<u>2.21</u>	<u>220.2</u>	<u>79.1</u>
	Ave.	2.26	223.4	79.8
6x2	AXD	2.36	238.2	77.4
	AXAD	2.26	183.5	78.4
	AXP	2.33	196.2	76.7
	AXH	2.37	185.5	78.7
	T ₁ XD	2.43	268.5	78.2
	T ₁ XAD	2.48	265.0	78.6
	T ₁ XP	2.31	243.2	78.2
	T ₁ XH	2.53	283.2	77.7
	T ₂ XD	2.44	287.2	78.2
	T ₂ XAD	2.44	246.0	78.5
	T ₂ XP	2.47	267.5	78.8
	T ₂ XH	<u>2.55</u>	<u>278.0</u>	<u>77.7</u>
	Ave.	2.41	245.1	78.1
Parents				
Traill	= T ₁	2.14	210.5	77.0
Atlas 46	= A	2.09	136.0	75.4
Trebi	= T ₂	2.22	257.2	76.0
Domen	= D	2.39	236.2	79.0
Pirolina	= P	2.29	218.5	79.6
Hannchen	= H	2.38	217.2	79.9
Abed Denso	= AD	<u>2.33</u>	<u>227.5</u>	<u>78.2</u>
	Ave.	2.26	214.8	77.9

Table 31

A summary of the mean squares from the functional analyses of variance for barley nitrogen, barley diastatic power and barley extract

Source of variation	df	Barley N. ms	Barley D.P. ms	Barley extract ms
Replications	3	0.01130 N.S.	482.223 N.S.	1.803**
Entries	27	0.56804**	5,088.520**	7.397**
Among groups	3	0.25773**	10,460.140 N.S.	33.603**
¹ Within groups	24	0.03169**	4,417.067**	4.122**
w/in (6x6) crosses	2	0.01280 N.S.	2,576.585*	1.440**
w/in (6x2) crosses	11	0.03176**	5,652.325**	1.469**
w/in (2x2) crosses	5	0.00808 N.S.	799.374 N.S.	0.774 N.S.
w/in parents	6	0.05750**	5,780.667**	12.670**
² Reps x entries	81	0.004219	358.596	0.336
³ R x w/in groups	9	0.00410	376.957	0.431
⁴ R x w/in (6x6) crosses	6	0.00593	306.917	0.042
⁵ R x w/in (6x2) crosses	33	0.00251	321.930	0.196
⁶ R x w/in (2x2) crosses	15	0.07653	279.042	0.473
⁷ R x w/in parents	18	0.00397	500.159	0.527
Total	111			

N.S. = Non-significant at five percent level

* = Significant at five percent level

** = Significant at 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 (6x6) crosses

⁵ = Error term for within (6x2) crosses

⁶ = Error term for within (2x2) crosses

⁷ = Error term for within parents

Significant "F" values were found for the within parent source of variation for the three quality traits. The six-rowed parents had lower nitrogen and extracts than the two-rowed parents. The two-rowed parents were uniform for diastatic power for the most part, but the six-rowed parents were quite different, with Trebi having the highest diastatic power and Atlas 46 the lowest of all parents.

Significant differences were found within the (6 x 6) crosses for diastatic power and barley extract (Table 31). The crosses between the two-rowed parents (2 x 2) did not differ significantly for any of the quality traits. Differences for all three quality traits were found to be significant in the (6 x 2) crosses. The (6 x 2) crosses can be placed into three groups according to the common six-rowed parent for barley nitrogen and diastatic power (Table 30). This cannot be done for barley extract where large amounts of variation occurred between the (6 x 2) crosses within the same six-rowed parents.

In order to obtain one value which might provide a single numerical rating for malting quality, an index was constructed using barley nitrogen, barley diastatic power, and barley extract where the correlation between barley and malt values were taken into account. Barley nitrogen, diastatic power, and extract values obtained from Hannchen were used as a standard. The quality indexes for the 21 crosses and seven parents are provided in Table 32.

The individual quality indexes associated with each variety within a group were quite uniform. Crosses within the (6 x 6) group

Table 32

The malting quality index for 21 crosses and seven parents and the averages for these crosses when grouped according to the row number characteristic

Group	Cross	Quality index	Parent	Quality index
(6x6) crosses and six-rowed parents	T ₁ XA	- 9.91	T ₁ =Traill	- 7.93
	T ₁ XT ₂	- 7.12	A ₁ =Atlas 46	- 13.86
	T ₂ XA	- 8.44	T ₂ =Trebi	- 9.47
	Ave.	- 8.49	Ave.	- 10.42
(2x2) crosses and two-rowed parents	HXD	- 1.60	D=Domen	- 2.16
	HXP	- 2.15	P=Piroline	- 1.16
	HXAD	- 1.48	H=Hannchen	0.00
	DXP	- 2.59	AD=Abed Denso	- 3.55
	DXAD	- 2.22		
	PXAD	- 3.76	Ave.	- 2.55
	Ave.	- 2.30		
(6x2) crosses	AXP	- 6.13		
	AXD	- 4.69		
	AXH	- 3.08		
	AXAD	- 5.22		
	T ₁ XP	- 4.47		
	T ₁ XD	- 5.17		
	T ₁ XH	- 7.93		
	T ₁ XAD	- 5.18		
	T ₂ XP	- 4.87		
	T ₂ XD	- 6.04		
	T ₂ XH	- 8.01		
	T ₂ XAD	- 4.00		
	Ave.	- 5.40		

had the poorest index values among the parents. The (2 x 2) crosses had the best index values among the crosses, and the two-rowed parents were almost exactly intermediate in their index values between the two parental groups.

The amounts of heterosis for the quality index, barley nitrogen, diastatic power, and extract are given in Tables 33, 34, 35, and 36, respectively. The crosses were grouped according to the row number of their respective parents and the average amounts of heterosis for the quality traits for each group are included in these tables.

The F_1 exceeded the parental average by 20 percent in one cross in each of the (6 x 6) and (2 x 2) groups, and four crosses in the (6 x 2) group (Table 33). Only the Atlas 46 x Trebi and the Atlas 46 x Abed Denso crosses had index values which were better than the best parent. The average amounts of heterosis for the quality index for the (6 x 6), (2 x 2), and the (6 x 2) groups were 17.0, -61.2, and 8.0 percent, respectively. The crosses between the six-rowed parents (6 x 6) were all better than their respective parental averages. The crosses between the two-rowed parents (2 x 2) were evenly divided with one-half being better and one-half being poorer than their respective parental averages. Five of the crosses between the six-rowed and the two-rowed parents (6 x 2) were better than their respective parental averages.

None of the 21 crosses in this study exhibited heterosis for barley nitrogen that was in excess of 20 percent of the parental average (Table 34). Five crosses in the (6 x 2) group possessed

Table 33

The amounts of heterosis for the quality index of
(6x6), (2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	Best \bar{P}^*	Poor \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ Best \bar{P}	% $>\bar{MP}$
6x6	T ₁ XA	-9.91	-7.93	-13.86	-10.90	0.99	-1.98	9.1
	AXT ₂	-7.12	-9.43	-13.86	-11.67	4.55a	2.35	39.0
	T ₂ XT ₁	-8.44	-7.93	-9.47	-8.70	1.03	-0.51	3.0
							Ave.	17.0
2x2	ADXD	-1.60	-2.16	-3.55	-2.86	1.26a	0.56	44.1
	ADXP	-2.15	-1.80	-3.55	-2.68	0.53	-0.35	19.8
	ADXH	-1.48	0.00	-3.55	-1.78	0.30	-1.48	16.9
	PXH	-2.59	0.00	-1.80	-0.90	-1.69	-2.59	-187.8
	PXD	-2.22	-1.80	-2.16	-1.98	-0.24	-0.42	-12.1
	HXD	-3.76	0.00	-2.16	-1.08	-2.68	-3.76	-248.1
							Ave.	-61.2
6x2	AXD	-4.69	-1.80	-13.86	-7.83	3.14a	-2.89	41.1
	AXP	-5.22	-2.61	-13.86	-8.01	2.79a	-3.06	35.8
	AXH	-6.13	0.00	-13.86	-6.93	0.80	-6.13	11.6
	AXAD	-3.08	-3.55	-13.86	-8.71	5.63a	0.47	64.6
	T ₁ XD	-5.17	-2.16	-7.93	-5.04	-0.13	-3.01	-2.6
	T ₁ XP	-5.18	-1.80	-7.93	-4.86	-0.32	-3.38	-6.6
	T ₁ XH	-4.47	0.00	-7.93	-3.96	-0.51	-4.47	-12.9
	T ₁ XAD	-7.93	-3.55	-7.93	-5.74	-2.19	-4.38	-38.2
	T ₂ XD	-6.04	-2.16	-9.47	-5.82	-0.22	-3.88	-3.8
	T ₂ XP	-4.00	-1.80	-9.47	-5.64	1.64a	-2.20	-29.1
	T ₂ XH	-4.87	0.00	-9.47	-4.74	-0.13	-4.87	-2.7
	T ₂ AD	-8.01	-3.55	-9.47	-6.51	-1.46	-4.46	-23.0
							Ave.	8.0

Parents	\bar{X}
Traill T ₁	-7.93
Atlas 46 =A	-13.86
Trebi =T ₂	-9.47
Dómen =D	-2.16
Pirolina =P	-1.80
Hannchen =H	0.00
Abed Denso=AD	-3.55

* = Parent with largest quality index is considered best parent
a = $F_1 > 20$ percent of parental average

Table 34

The amounts of heterosis for barley nitrogen of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	$M\bar{P}$	$>M\bar{P}$	$F_1 >$ High \bar{P}	% $>M\bar{P}$
6x6	T ₁ XA	2.15	2.14	2.09	2.12	0.03	0.01	1.4
	AXT ₂	2.26	2.22	2.09	2.16	0.10	0.04	4.6
	T ₂ XT ₁	2.18	2.22	2.14	2.18	0.00	-0.04	0.0
							Ave.	2.0
2x2	ADXD	2.21	2.39	2.33	2.36	-0.15	-0.18*	-6.4
	ADXP	2.21	2.33	2.29	2.31	-0.10	-0.12*	-4.3
	ADXH	2.32	2.38	2.33	2.36	-0.04	-0.06	-1.7
	PXH	2.30	2.38	2.29	2.34	-0.04	-0.08	-1.7
	PXD	2.26	2.39	2.29	2.34	-0.08	-0.13*	-3.4
	HXD	2.28	2.39	2.38	2.38	-0.10	-0.11*	-4.2
							Ave.	-3.6
6x2	AXD	2.33	2.29	2.09	2.19	0.14	0.04	6.4
	AXP	2.36	2.39	2.09	2.24	0.12	-0.03	5.4
	AXH	2.37	2.38	2.09	2.24	0.13	-0.01	5.8
	AXAD	2.26	2.33	2.09	2.21	0.05	-0.07	2.3
	T ₁ XD	2.43	2.39	2.14	2.26	0.17	0.04	7.5
	T ₁ XP	2.31	2.29	2.14	2.22	0.09	0.02	4.1
	T ₁ XH	2.53	2.38	2.14	2.26	0.27	0.15*	11.9
	T ₁ AD	2.48	2.33	2.14	2.24	0.24	0.15*	10.7
	T ₂ XD	2.44	2.39	2.22	2.30	0.14	0.05	6.1
	T ₂ XP	2.47	2.29	2.22	2.26	0.21	0.18*	9.3
	T ₂ XH	2.55	2.38	2.22	2.30	0.25	0.17*	10.9
	T ₂ XAD	2.44	2.33	2.22	2.28	0.16	0.11*	7.0
							Ave.	7.3

Parents		\bar{X}
Traill	= T ₁	2.14
Atlas 46	= A	2.09
Trebi	= T ₂	2.22
Domen	= D	2.39
Pirolina	= P	2.29
Hannchen	= H	2.38
Abed Denso	= AD	2.33

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 0.09
P = 28 SSR = 0.11

Table 35

The amounts of heterosis for diastatic power of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	\bar{MP}	$>\bar{MP}$	$F_1 >$ High \bar{P}	$\%>\bar{MP}$
6x6	T ₁ XA	179.0	210.5	136.0	173.2	5.8	-31.5*	3.3
	AXT ₂	185.2	257.2	136.0	196.6	-11.4	-72.0*	- 5.8
	T ₂ XT ₁	225.8	257.2	210.5	233.8	- 8.0	-31.4*	- 3.4
							Ave.	- 2.0
2x2	ADXD	213.5	236.0	227.5	231.8	-18.3	-22.5	- 7.9
	ADXP	220.2	227.5	218.5	223.0	- 2.8	- 7.3	- 1.3
	ADXH	201.8	227.5	217.2	222.4	-20.6	-25.7	- 9.3
	PXH	231.2	218.5	217.2	217.8	13.4	12.7	6.2
	PXD	238.2	236.0	218.5	227.2	11.0	2.2	4.8
	HXD	235.2	236.0	217.2	226.6	8.6	- 0.8	3.8
							Ave.	- 0.6
6x2	AXD	196.2	218.5	136.0	177.2	19.0	-22.3	10.7
	AXP	238.2	236.0	136.0	186.0	52.2a	2.2	28.1
	AXH	185.5	217.5	136.0	176.6	8.9	-31.7*	5.0
	AXAD	183.5	227.5	136.0	181.8	1.7	-44.0*	0.9
	T ₁ XD	268.5	236.0	210.5	223.2	45.3a	32.5*	20.3
	T ₁ XP	243.2	218.5	210.5	214.5	28.7	24.7	13.4
	T ₁ XH	283.2	217.2	210.5	213.8	69.4a	66.0*	32.5
	T ₁ XAD	265.0	227.5	210.5	219.0	46.0a	37.5*	21.0
	T ₂ XD	287.2	257.2	236.2	246.6	40.6	30.0*	16.5
	T ₂ XP	267.5	257.2	218.5	237.8	29.7	10.3	12.5
	T ₂ XH	278.0	257.2	217.5	237.2	40.8	20.8	17.2
	T ₂ XAD	246.0	257.2	227.5	242.4	3.6	-11.2	1.5
							Ave.	15.0

Parents	\bar{X}
Traill. =T ₁	210.5
Atlas 46 =A	136.0
Trebi =T ₂	257.2
Domen =D	236.0
Piroline =P	218.5
Hannchen =H	217.2
Abed Dendo=AD	227.5

a = $F_1 > 20$ percent of parental average

* = Significant at five percent level (Duncan's new multiple range test)

P = 2 SSR = 26.6

P = 29 SSR = 34.2

Table 36

The amounts of heterosis for barley extract of (6x6),
(2x2) and (6x2) crosses

Group	Entry	$F_1\bar{X}$	High \bar{P}	Low \bar{P}	$\bar{M}\bar{P}$	$>\bar{M}\bar{P}$	$F_1 >$ High \bar{P}	$\%>\bar{M}\bar{P}$
6x6	T ₁ XA	76.3	77.0	75.4	76.2	0.1	-0.7	0.1
	AXT ₂	76.1	76.0	75.4	75.7	0.4	0.1	0.5
	T ₂ XT ₁	77.2	77.0	76.0	76.5	0.7	0.2	0.9
							Ave.	0.5
2x2	ADXD	80.2	79.0	78.2	78.6	1.6	1.2*	2.0
	ADXP	79.1	79.6	78.2	78.9	0.2	-0.5	0.3
	ADXH	79.9	79.9	78.2	79.0	0.9	0.0	1.1
	PXH	79.6	79.9	79.6	79.8	-0.2	-0.3	-0.3
	PXD	79.9	79.6	79.0	79.3	0.6	0.3	0.8
	HXD	80.3	79.9	79.0	79.4	0.9	0.4	1.1
							Ave.	0.8
6x2	AXD	76.7	79.6	75.4	77.5	-1.2	-2.9*	1.0
	AXP	77.4	79.0	75.4	77.2	0.2	-1.6*	0.3
	AXH	78.7	79.9	75.4	77.6	1.1	-1.1*	1.4
	AXAD	78.4	78.2	75.4	76.8	1.6	0.2	2.1
	T ₁ XD	78.2	79.0	77.0	78.0	0.2	-0.8	0.3
	T ₁ XP	78.2	79.6	77.0	78.3	-0.1	-1.4*	0.0
	T ₁ XH	77.7	79.9	77.0	78.4	-0.7	-2.2*	0.9
	T ₁ XAD	78.6	78.2	77.0	77.6	1.0	0.4	1.3
	T ₂ XD	78.2	79.0	76.0	77.5	0.7	-0.8	0.9
	T ₂ XP	78.8	79.6	76.0	77.8	1.0	-0.8	1.3
	T ₂ XH	77.7	79.9	76.0	78.0	0.3	-2.2*	0.4
	T ₂ XAD	78.5	78.2	76.0	77.1	1.4	0.3	1.8
							Ave.	0.8

Parents		\bar{X}
Traill	=T ₁	77.0
Atlas 46	=A	75.4
Trebi	=T ₂	76.0
Domen	=D	79.0
Piroline	=P	79.6
Hannchen	=H	79.9
Abed Denso	=AD	78.2

* = Significant at the five percent level (Duncan's new multiple range test)

P = 2 SSR = 0.85
P = 28 SSR = 1.06

significantly higher nitrogen values than the high parent when significance was determined by Duncan's new multiple range test. The average percent of heterosis for barley nitrogen found for the (6 x 6), (2 x 2), and the (6 x 2) groups were 2.0, -3.6, and 7.3 percent, respectively. The (2 x 2) crosses consistently had less barley nitrogen than the parental average, while the (6 x 6) and (6 x 2) crosses consistently had more barley nitrogen than the parental average.

Four of the (6 x 2) crosses exhibited heterosis in excess of 20 percent of the parental average for diastatic power (Table 35). None of the (6 x 6) or the (2 x 2) crosses exceeded the parental averages by 20 percent for diastatic power. Three of the four (6 x 2) crosses that exceeded parental averages by 20 percent had higher diastatic power than the high parent. One additional (6 x 2) cross was also significantly higher than the high parent in diastatic power. The average amount of heterosis for the three groups of crosses was -2.0, -0.6, and 15.0 percent, respectively. The crosses between six-rowed and two-rowed parents (6 x 2), in general exhibited a considerable amount of heterosis for diastatic power. The (6 x 2) crosses with Traill as a common six-rowed parent, exhibited the most heterosis when it was measured by both methods, and Traill was next to the lowest in diastatic power of the parental varieties.

In general, no heterosis was observed for barley extract (Table 36). The Abed Denso x Domen cross had an extract value which was significantly higher than the high parent, Abed Denso. The average amounts of heterosis found for barley nitrogen in the

(6 x 6), (2 x 2), and (6 x 2) crosses were 0.5, 0.8, and 0.8 per cent, respectively.

Estimates of gene action for barley nitrogen, diastatic power and extract were obtained from the combining ability analyses. The components of general and specific combining ability for the (2 x 2) group for the three quality traits are presented in Table 37. Some additive gene action (GCA) was found in the (2 x 2) crosses for diastatic power and extract. No genetic variances were indicated to be present for barley nitrogen in the (2 x 2) group. The best estimates for non-additive gene action (SCA) in the (2 x 2) group for all three traits were zero. A considerable amount of environmental variation was found for all three traits. The narrow-sense heritability estimates for diastatic power and barley extract for the (2 x 2) group were 0.465 and 0.278, respectively.

Additive gene action (\overline{GCA}) was found to be present for barley diastatic power and barley nitrogen in the (6 x 2) group. The six-rowed parents contributed considerably more to this additive gene action component than the two-rowed parents. Non-additive gene action (SCA) was found to be present in the (6 x 2) groups for all three factors. The only type of gene action present for barley extract in the (6 x 2) group was non-additive (SCA). The environmental component was large for barley diastatic power and relatively small for nitrogen and extract. The narrow-sense heritability estimates for barley nitrogen and diastatic power were 0.254 and 0.728, respectively.

The simple correlation coefficients between the three quality

Table 37

Components of general and specific combining ability and narrow-sense heritability estimates for barley diastatic power, barley nitrogen and barley extract for (2x2) and (6x2) crosses

Crosses	Components	Barley DP	Barley N	Barley Ext.
2x2	GCA	121.146	0.0000	0.09115
	SCA	0.000	0.0000	0.00000
	E	279.042	0.7653	0.47330
	h^2_{ns}	0.465	0.000	0.278
6x2	GCA(6)	1,876.236	0.006231	0.0000
	GCA(2)	97.820	0.000914	0.0000
	\overline{GCA}	730.545	0.002844	0.0000
	SCA	203.525	0.002918	0.4307
	E	321.930	0.002510	0.1960
	h^2_{ns}	0.728	0.254	0.000

GCA = general combining ability

SCA = specific combining ability

E = environmental

GCA(6) = general combining ability for six-rowed parents

GCA(2) = general combining ability for two-rowed parents

\overline{GCA} = weighted average general combining ability

h^2_{ns} = heritability in narrow-sense

traits and yield and its components and TLA and its components are given in Table 38. The entries were separated according to row number. The three groups consisted of six-rowed, two-rowed barleys and six-rowed x two-rowed crosses.

Among the simple correlations between the three quality traits and yield and components of yield, only four were found to be significant. A significant positive association between diastatic power and kernels per head was found for the six-rowed barleys. A significant negative association between those two traits was found for the (6 x 2) crosses. A significant negative association between tillers per plant and barley nitrogen was found for the two-rowed barleys. Barley extract was positively correlated with grain yield in the two-rowed barleys. No single large association between yield or components of yield and the quality traits existed in all groups of barley in this study.

Examination of the correlation coefficients found for barley quality traits and leaf area measurements revealed only three associations which were significant. Leaf length was significantly and negatively associated with diastatic power in both the two-rowed barleys and the (6 x 2) crosses. A large positive but non-significant correlation coefficient was found for leaf length and diastatic power in the six-rowed barleys. Total leaf area at heading time was significantly correlated with barley extract in the (6 x 2) crosses. In general, no single leaf area trait was found to be associated with the three quality traits in the three groups.

Table 38

A summary of the simple correlation coefficients for diastatic power, barley nitrogen, and barley extract with yield, components of yield, total leaf area, and components of total leaf area at heading time

Group	Traits	Diastatic power	Barley nitrogen	Barley ext.
1	Yield	0.274	0.748	0.143
2		-0.244	-0.333	0.653*
3		-0.442	-0.169	0.343
1	Tillers/	-0.456	0.290	-0.665
2	plant	-0.224	-0.947**	0.500
3		-0.238	-0.122	-0.106
1	Kernels/	0.865*	0.273	0.806
2	Head	0.521	-0.531	0.265
3		-0.974**	-0.204	0.110
1	Weight/	0.260	0.327	0.464
2	kernel	-0.271	0.137	0.429
3		-0.256	0.152	0.152
1	TLA	0.313	0.488	-0.527
2		-0.301	-0.290	0.219
3		-0.321	-0.260	0.820**
1	Tillers/	-0.688	-0.160	-0.755
2	plant	0.305	0.111	0.251
3		0.263	0.408	-0.208
1	Leaf length	0.770	0.729	0.588
2		-0.733*	-0.238	0.423
3		-0.772**	-0.309	0.292
1	Leaf width	0.765	0.146	0.789
2		-0.404	-0.288	-0.277
3		-0.326	-0.266	0.532
1	Diastatic	--	--	--
2	power	--	--	--
3		--	--	--
1	Barley	0.388	--	--
2	nitrogen	-0.152	--	--
3		0.575*	--	--

Table 38, continued

Group	Traits	Diastatic power	Barley nitrogen	Barley ext.
1	Barley	0.950**	0.136	--
2	extract	-0.449	-0.269	--
3		-0.120	0.229	--

1 = six-rowed barleys

2 = two-rowed barleys

3 = (6 x 2) crosses

n = 6

n = 10

n = 12

* Significant at five percent level

**Significant at one percent level

The associations between the three quality traits found on Table 38 were inconsistent for the three different groups in this study. Barley nitrogen was not associated with barley extract in the three groups. A positive association between barley nitrogen and diastatic power was found for the (6 x 2) crosses, while these two traits were not associated in the six-rowed and two-rowed barleys. Diastatic power was positively associated with extract in the six-rowed barleys.

DISCUSSION

The success of hybrid barleys in commercial production will partly be dependent upon the extent of hybrid vigor present. Heterosis for grain yield will certainly be one of the major objectives in hybrid barley programs. Whether heterotic responses will be sought for leaf area traits and malting quality has not yet been determined. However, total leaf area and its components offer an excellent opportunity to study the expression of heterosis for a complex trait in relationship to the behavior of its components. The economic importances of malting quality traits justifies the investigation of heterosis for malting quality.

It has been suggested by Williams (1959) and Adams and Duarte (1961, 1963) that the interaction between components of a complex trait can produce a large amount of heterosis in the complex trait. Likelihood of this type of component interaction to produce heterosis is obtained when large differences in the components exist between the parental varieties. The existence of two morphologically different species of cultivated barleys enables the barley breeder to obtain parental varieties with large differences in the components.

The parental varieties in this study possessed large differences in their components of grain yield. These differences could be associated with the row number characteristic in the parental varieties. These findings would suggest that the hybrids between six-rowed and two-rowed parents should exhibit more heterosis than

hybrids within six-rowed parents or two-rowed parents.

The pathway coefficient analyses indicated that the direct and indirect effects of the components of grain yield were not the same for six-rowed and two-rowed barleys and six-rowed x two-rowed crosses. As expected, tiller number had the largest direct effect in the two-rowed barleys, while kernel number and tiller number were about equal in their direct effects in the six-rowed barleys. The extremely large direct effect of kernel number in the (6 x 2) crosses were unexpected. The row number character in barley is the primary determining factor of kernel number per head. The two-rowed condition is dominant to the six-rowed condition but there are apparently several modifiers which alter the expected results of some six-rowed x two-rowed crosses. In fact, some (6 x 2) crosses in this study approached the parental mean for kernel number per head, while other (6 x 2) crosses were similar to the two-rowed parent. Those crosses with more kernels per head than expected were also higher yielding crosses; thus, the large direct effect of kernel number was obtained in the (6 x 2) crosses. However, grain yield was not increased as much as expected by increasing kernel number per head because there was a large negative association between kernel number and kernel weight. The extra kernels formed on the (6 x 2) hybrids were in the lateral florets and were quite small in comparison to the kernels of the central florets.

Since large reciprocal differences existed in the components of yield of H. vulgare and H. distichum, larger amounts of heterosis would be anticipated in the (6 x 2) crosses than in the (6 x 6) or

(2 x 2) crosses. If there is perfect additivity (no heterosis) for all the components, there can still be a large amount of heterosis in the complex trait (Williams, 1959). That is to say, if the parents complement one another in their components and the hybrid is exactly intermediate for the components, the hybrid may still express a large amount of heterosis for the complex trait.

The general lack of heterosis in the (6 x 6) and (2 x 2) crosses for grain yield and the components of grain yield may be attributed to the lack of genetic diversity among the parents. The lack of heterosis in the ((6 x 2) crosses cannot be attributed to this cause, since supposedly large genetic and morphological differences existed between H. vulgare and H. distichum parents. Heterosis for grain yield was not found in the (6 x 2) crosses because tiller number and kernel number per head did not behave in an additive manner. The failure of the additive expression for kernel number was expected since the two-rowed character is considered to be dominant over the six-rowed character. There was a large amount of heterosis for kernel weight in these crosses (6 x 2) but this component appears to be of lesser importance than tiller number and kernel number in influencing grain yield; therefore, the occurrence of this heterosis did not offset the lower values obtained for tiller number and number of kernels per head.

There is another possible explanation for the general lack of heterosis for yield, as well as for all the traits in this study. The F₁ plants and parents were grown under very favorable growing conditions. The plants were space planted and the length of the

growing season was prolonged in the protection of the greenhouse. It has been suggested by Suneson (1962) that these conditions tend to minimize the differences between hybrids and their parents. This has been supported by Aastveit (1964), who found that the environmental-genotype interactions were a significant component of heterosis. Therefore, it might be anticipated that under less favorable growing conditions, as in the field, a greater response due to heterosis would be found.

The combining ability estimates for yield and the components of yield for the (2 x 2) and (6 x 6) crosses were in agreement with the results of the expression of heterosis except for weight per kernel. A large component for specific combining ability which indicates non-additive gene action or heterosis, was anticipated for kernel weight in the (6 x 2) crosses. However, all of the genetic variance for kernel weight in this group was found to be additive (\overline{GCA}) in nature. This points out that heterosis can occur when non-additive gene action is not detected by combining ability analysis. This may possibly be due to some additive x additive interaction scheme.

The heritability estimates obtained by manipulation of the components of combining ability estimates reflected the general lack of genetic variance in the (2 x 2) crosses and the higher amount of additive gene action than non-additive in the (6 x 2) crosses. The high narrow-sense heritability estimate for kernel number per head in the (6 x 2) crosses indicated that the modifying genes of the row number character were possibly additive in nature.

It could be concluded from the results of this study that little

will be gained in heterosis for grain yield by crossing H. vulgare with H. distichum in the production of hybrids. This was true, even though these two species would appear to complement each other in the components of grain yield. The interaction of components to produce heterosis apparently did not occur as anticipated. Barley breeders will probably be more successful in producing high yielding hybrids by crossing parents within the same species which possess large reciprocal differences in the components of grain yield.

The two species, H. vulgare and H. distichum, were found to differ reciprocally for the components of total leaf area (leaf length, leaf width, and tiller number). The differences in leaf measurement traits were consistent for the two stages of growth. The lack of significant differences for the leaf area traits for the (2 x 2) crosses indicated that the two-rowed parents were not only phenotypically similar but also genetically similar. This was not the case for the (6 x 6) crosses where large differences in almost all of the components were found. This would suggest that the six-rowed parents were genetically different.

The pathway coefficient analysis indicated that the contributions of the different components for the three groups of barley at two stages of growth were not the same. The fact that leaf length and leaf width behaved differently in the (6 x 6) and (2 x 2) crosses further indicates that inherent differences exist between six-rowed parents and two-rowed parents.

Since larger differences exist in the components of TLA between six-rowed and two-rowed barleys, more heterosis for TLA would

be anticipated in the (6 x 2) crosses than in the (6 x 6) or (2 x 2) crosses. This expectation is based on the concept that additivity in the hybrid for components of complementing parents will produce heterosis in the complex trait. It should be pointed out that although the (6 x 2) crosses met the requirement of complementation between parents as a group, they did not exhibit the expected amounts of heterosis. In fact, only one cross exhibited heterosis in the amounts anticipated in this group of crosses. The principle reason for the failure in the expression of heterosis in crosses of this type was due to the inconsistent additive behavior in the components. When all three components behaved in an additive manner, as was the case for three crosses in this study, the hybrids had TLA's which significantly exceeded the better parent.

Although the selection of parental varieties for the production of hybrids with large complementing differences in their components would enhance the possibility of heterosis in the complex trait, it does not insure its occurrence. If the components are not able to respond in an additive manner due to genetic reasons, such as dominance of the low value, heterosis may not occur in the complex trait. It should also be pointed out that not all components contribute equally to the complex trait. Therefore, failure of additivity in a component with a larger contribution results in more loss than can be offset by a large amount of heterosis for a lesser component. Tiller number as a component of TLA is a good example of this situation. Another factor in the expression of heterosis through the combination of complementing components in a hybrid is

biological limitation. It may not be biologically possible to have high values for all components in one plant. An example of this might be drawn from the response observed in the (6 x 2) crosses for kernel number and kernel weight. Those crosses which had large numbers of kernels per head also had smaller kernels. This could be due to the fact that the plant is able to produce only so much substrate and this can be used either as kernel number per head or kernel weight. If kernel number is increased, weight per kernel will correspondingly decrease when there is a large negative association between these two factors.

The estimates of the components of general and specific combining ability were in good agreement with the expressions of heterosis. More heterosis for TLA was found at heading time than prior to heading and correspondingly the amount of non-additive gene action as indicated by (SCA) component increased. In general, only a small amount of non-additive gene action was found for leaf length and leaf width at both stages of growth and for both groups of crosses. This corresponds to the general lack of heterosis for leaf length and leaf width. More heterosis and correspondingly more non-additive gene action was found for tiller number per plant.

The heritability estimates indicated that leaf dimension characters were controlled primarily by additive genes while tiller number was controlled by non-additive and environmental components.

The changes in the magnitude of the different estimates of gene action for leaf area characteristics at different stages of growth are in agreement with findings of Kheiralla and

Whittington (1962) in tomatoes. These results support the view that extreme caution is necessary in generalizing from a genetic analysis made at only one stage of growth.

The relationships between the leaf area measurements and yield and components of yield were rather inconsistent in this study. The different dimensions of the leaf and leaf number appeared to have different associations with grain yield and components of grain yield for six-rowed, two-rowed, and six-rowed x two-rowed crosses. Large total leaf areas did not appear to be highly associated with grain yield in all barleys. This was in agreement with the findings of Watson and co-workers (1958).

Malting quality can be considered to be a complex trait. It is composed of many physical and chemical components. In this study, malting quality was assumed to be composed of three quality traits. In order to obtain one value for the complex trait, an index value was computed for all the entries in this study. For simplicity and continuity, this index was assumed to be a measure of the complex trait, malting quality, although it is admittedly an artificial value and has no real existence such as grain yield or total leaf area.

The two species, H. vulgare and H. distichum, in general, did not have the same malting quality values. The parental varieties within a particular species were quite uniform for barley nitrogen and barley extract. The construction of the index which was composed of barley nitrogen, diastatic power, and extract measurements also demonstrated the general trend of crosses and parents within a

species to be similar. It was apparent that when the two-rowed parent (Hannchen) was selected as a standard for malting quality, that differences associated with the row number character occurred. This indicates that crossing within H. distichum will produce hybrids with malting quality more similar to Hannchen than crossing within H. vulgare. However, the existence of large differences between H. vulgare and H. distichum in malting quality offers the opportunity to increase or decrease these values through hybridization. If higher diastatic power or lower nitrogen content became desirable quality factors for two-rowed barleys of Oregon, then the H. vulgare sources of variation in these components could be of direct interest. The reverse would be true in areas where six-rowed barleys are the predominant malting barleys.

If hybrid barleys are grown for malting, the existence of heterosis for malting quality may or may not be desirable. It is certain that large heterotic responses for such components of malting quality as nitrogen content and enzymatic activities could greatly modify the quality of the hybrid barley. Heterotic responses for such things as kernel plumpness and malt extract would be very desirable.

Estimates of heterosis for malting quality in this study indicated that very little heterotic response occurred for the three components of malting quality or for the combination of these components in the quality index values. The intermediate behavior of the crosses between H. vulgare and H. distichum would indicate a pre-dominance of additive gene action for the quality traits. If this

is the general trend of results obtained when these two species are crossed, it could be concluded that hybrids with acceptable malting quality can be obtained. Parental varieties which were widely different in their malting quality could be used in the production of hybrid barleys for malting provided the differences in the components of malting quality complemented one another.

The combining ability estimates for diastatic power and extract in the (2 x 2) crosses suggested that only additive differences were present. Barley nitrogen appeared to be influenced only by environmental factors. The slight differences in malting quality in the (2 x 2) crosses was due predominantly to environmental factors for all crosses. Larger genetic variances were found in the (6 x 2) crosses which indicates that the six-rowed and two-rowed parental varieties were genetically dissimilar. Diastatic power appeared to be controlled primarily by additive gene action; thus, a high narrow-sense heritability estimate was found. These results are in agreement with the findings of Rasmusson and Glass (1965).

Since there were only a few significant associations found between the three malting quality traits, yield and its components and total leaf area and its components, it was not possible to determine the plant types which would have high or low malting quality. These few significant correlations suggested that the relationships between these traits were not always the same in six-rowed barleys, two-rowed barleys and six-rowed x two-rowed crosses. The interrelationships between the three malting quality factors indicated that six-rowed barleys, two-rowed barleys and six-rowed x two-rowed crosses did not

behave the same in this study.

SUMMARY AND CONCLUSIONS

The major objective of this study was to measure the amounts of heterosis for three complex traits and their components. A further objective was to investigate the concept of component interactions as a means of producing heterosis in complex traits.

To accomplish these objectives, grain yield, total leaf area, and malting quality were each subdivided into their components and measurements of heterosis were made on 21 F_1 's. In addition, pathway coefficient analyses were computed for grain yield and total leaf area to determine the relative importances of the various components of these complex traits. Estimates of gene action for all traits were obtained by combining ability and heritability estimates and these estimates were related to the occurrence of heterosis. Since two distinct species of barley were included in this study, the parents and crosses were studied separately and differences between and within species were determined.

From the results of this study, the following conclusions can be made:

1. Large differences in the components of grain yield and total leaf area existed between the crosses and parents of H. vulgare and the crosses and parents of H. distichum.
2. There was a general lack of heterosis for grain yield in all crosses. This was true for the (6 x 2) crosses, even though large differences in tillers per plant, kernels per head, and weight per kernel were present in the six-rowed

and two-rowed species. Component interactions to produce heterosis for grain yield apparently did not occur. The principle reason for this was the failure to obtain additivity for kernel number per head and tiller number per plant and these two components are the most important components in determining grain yield in both parental species.

3. A limited amount of heterosis was found for total leaf area in all crosses. There was one cross in each of the (6 x 6), (2 x 2), and (6 x 2) crosses which exhibited a large amount of heterosis. Upon examination of these crosses, it was found that when the parents possessed large differences in the components and these differences complemented each other in the hybrids, heterosis was exhibited. There was no heterosis for the components in the three crosses but a large amount in the complex trait, total leaf area.
4. Estimates of gene action were, in general, in agreement with the observation on heterosis, the major exception being for weight per kernel in the (6 x 2) crosses.
5. There were no clear associations between the leaf area measurements and grain yield and its components in this study.
6. The three malting quality traits were found to be closely associated with the row number characteristic. The construction of a quality index composed of all three traits

also demonstrated this association.

7. There was only a slight amount of heterosis found for barley nitrogen, diastatic power, extract, and the composite of these three (quality index). It was suggested that additive gene action was the predominant type of gene action controlling the quality traits and because of this, hybrids with good malting quality could be obtained.
8. Malting quality was not associated with grain yield and its components and total leaf area and its components in this study.

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APPENDIX

Appendix Table 1
A description of the seven parental spring barley varieties

Parent	C.E. No.	Cross symbol	Pedigree	Row No.	Straw	Heading time	Use	Origin
Traill	9538	T ₁	A selection from Titan x Kindred	Six	Midtall	Midseason	Malting	North Dakota
Atlas 46	7323	A	A bulk from Hanna x Atlas ⁷ and Turk x Atlas ⁸	Six	Midtall	Early to midseason	Malting	California
Trebi	936	T ₂	Unknown	Six	Midtall	Midseason	Feed	Asiatic Turkey
Domen	9562	D	A selection from Opal B x Maskin	Two	Midtall	Late season	Malting	Norway
Hannchen	531	H	A pure line selection from Hanna	Two	Midtall	Midseason to late	Malting	Sweden
Piroline	9558	P	A selection from Weiheimstephaner MPJ x Margensot	Two	Midtall	Midseason	Malting	Holland
Abed Denso	--	AD	A field mutant from Abed Plant Breeding Station	Two	Short	Midseason to late	Not released	Denmark

Appendix Table 2

A numerical example of the computation of the quality index for the variety Trebi

$$\text{Quality Index} = - \left| r_{11}u_1 \right| - \left| r_{22}u_2 \right| + r_{33}u_3$$

	<u>Trebi</u>	<u>Hannchen (standard)</u>
Barley nitrogen	2.22	2.38
Diastatic power	257.2	217.2
Extract	76.0	79.9

Barley nitrogen and malt nitrogen $r_{11} = .955$

Barley diastatic power and malt diastatic power $r_{22} = .739$

Barley extract and malt extract $r_{33} = .828$

$$u_1 = \frac{\text{Trebi } \bar{x} \text{ nitrogen} - \text{Hannchen } \bar{x} \text{ nitrogen}}{\text{Standard deviation for nitrogen}} = \frac{2.22-2.38}{.06495} = -2.46$$

$$u_2 = \frac{\text{Trebi } \bar{x} \text{ D.P.} - \text{Hannchen } \bar{x} \text{ D.P.}}{\text{Standard deviation for D.P.}} = \frac{257.2-217.2}{18.935} = 2.11$$

$$u_3 = \frac{\text{Trebi } \bar{x} \text{ extract} - \text{Hannchen } \bar{x} \text{ extract}}{\text{Standard deviation for extract}} = \frac{76.0-79.9}{.580} = -6.72$$

$$QI = - \left| .955 \times -2.46 \right| - \left| .739 \times 2.11 \right| + .828 \times -6.72$$

$$= -2.35 \quad -1.36 \quad -5.66$$

$$= -9.47$$

Appendix Table 3

Estimates of general and specific combining ability, components of general and specific combining ability and narrow-sense heritability estimates for leaf length in the (2 x 2) crosses

Leaf length

	D	P	H	AD	X _{i.}	
D	-	145.3	152.3	149.3	446.9	$\sum (X_{i.})^2 = 767,876.10$
P	145.3	-	143.9	141.4	430.6	$(X_{..})^2 = 767,726.44$
H	152.3	143.9	-	144.0	440.2	$\sum (X_{ij})^2 = 128,035.04$
A	149.3	141.4	144.0	-	434.7	X _{..}
X _{.j}	446.9	430.6	440.2	434.7	17524	$\div 2 = 287.2$
$4[SS(GCA)] = \frac{1}{P-2} \sum (X_{i.})^2 - \frac{4}{P(P-2)} X_{..}^2 = \frac{1}{2}(767,876.10) - \frac{1}{2}(767,726.44)$						
$= 74.83$						

$$SS(GCA) = \frac{74.83}{4} = 18.7075$$

$$4[SS(SCA)] = \sum (X_{ij})^2 - \frac{1}{P-2} \sum (X_{i.})^2 + \frac{2}{(P-1)(P-2)} X_{..} = 128,035.04 - 383,038.05 + 255,908.81 = 5.80$$

$$SS(SCA) = \frac{5.80}{4} = 1.4500$$

Analysis of Variance Table

Source	df	SS	ms	Expected m.s.
Entries	5	20.16	4.0320	
GCA	3	18.71	6.2367	$\sigma^2_e + 4\sigma^2_{SCA} + 8\sigma^2_{GCA}$
SCA	2	1.45	.7250	$\sigma^2_e + 4\sigma^2_{SCA}$
Error	15	25.85	1.7233	σ^2_e

Components

$$GCA = \frac{6.2367 - 1.7233}{8} = .5641 = \frac{1}{2} \text{ additive variance}$$

$$SCA = 0.0000 \text{ (best estimate)}$$

$$= 1.7233$$

$$h^2_{ns} = \frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_e}$$

$$= \frac{1.1282}{2.8515} = .3956$$

Appendix Table 4

Estimates of general and specific combining ability, components of general and specific combining ability and narrow-sense heritability estimates for leaf length in the (6 x 2) crosses

Leaf length

	T ₁	A	T ₂	X _{..j}	
D	157.3	134.0	152.6	443.9	$\sum (X_{i.})^2 = 972,055.10$
P	141.0	128.9	141.9	411.8	$\sum (X_{.j})^2 = 727,455.78$
H	152.3	133.1	140.8	426.2	$\sum (X_{ij})^2 = 243,262.08$
AD	<u>150.3</u>	<u>131.3</u>	<u>141.7</u>	<u>423.3</u>	$X_{..}^2 = 2,907,707.04$
X _{i.}	600.0	527.3	577.0	1705.2	X _{..}

$$(4) \text{ SSGCA}(6) = \frac{\sum X_{i.}}{4} - \frac{X_{..}^2}{12} = 243,013.78 - 242,308.92 = 704.86$$

$$\text{SSGCA}(6) = \frac{704.86}{4} = 176.22$$

$$(4) \text{ SSGCA}(2) = \frac{\sum X_{.j}}{3} - \frac{X_{..}^2}{12} = 242,485.26 - 242,308.92 = 176.34$$

$$\text{SSGCA}(2) = \frac{176.34}{4} + 44.09$$

$$(4) \text{ SS(SCA)} = \sum X_{ij} - \frac{X_{..}^2}{12} - \text{SSGCA}(6) - \text{SSGCA}(2) - 243,262.08$$

$$- 242,308.92 = 953.16$$

$$\text{SS(SCA)} = \frac{953.16}{4} - 176.22 - 44.09 = 17.98$$

Appendix Table 4, continued

Analysis of Variance Table

Source	df	SS	ms	Expected m.s.
Entries	11	238.29	21.6627	
GCA(6)	2	176.22	88.1100	$\sigma^2_e + 4 \sigma^2_{SCA} + 12 \sigma^2_{GCA(6)}$
GCA(2)	3	44.09	14.6967	$\sigma^2_e + 4 \sigma^2_{SCA} + 16 \sigma^2_{GCA(2)}$
SCA	6	17.98	2.9967	$\sigma^2_e + 4 \sigma^2_{SCA}$
Error	33	63.77	1.932	σ^2_e

Components

$$\sigma^2_{GCA(6)} = \frac{88.1100 - 2.9967}{12} = 7.0928 = \frac{1}{2} \text{ additive (6)}$$

$$\sigma^2_{GCA(2)} = \frac{14.6967 - 2.9967}{16} = .7313 = \frac{1}{2} \text{ additive (2)}$$

$$\sigma^2_{\overline{GCA}} = \frac{5}{68} \left[\frac{2(88.1100) + 3(14.6967)}{5} - 2.9967 \right] = 3.0195 = \frac{1}{2} \text{ additive variance}$$

$$h^2_{ms} = \frac{2\sigma^2_{\overline{GCA}}}{2\sigma^2_{\overline{GCA}} + \sigma^2_{SCA} + \sigma^2_e} = \frac{6.0390}{8.2371} = .7331$$

Appendix Table 5

A summary of the values of the 21 crosses and seven parents for malting nitrogen, diastatic power, and barley extract, and the group averages for the 6 x 6, 2 x 2, and 6 x 2 and parents

Group	Cross	Barley N	Barley DP	Barley ext.
6 x 6	T ₁ XA	2.18	144	73.7
	T ₁ XT ₂	2.18	205	75.0
	T ₂ XA	2.34	124	73.0
	Ave.	2.23	157.7	73.9
2 x 2	HXD	2.21	207	79.3
	HXP	2.36	214	76.7
	HXAD	2.31	177	76.2
	DXP	2.29	237	78.0
	DXAD	2.17	201	79.0
	PXAD	2.23	207	76.8
	Ave.	2.26	207.1	77.7
6 x 2	AXD	2.36	121	72.9
	AXAD	2.30	116	74.8
	AXP	2.35	135	73.8
	AXH	2.44	118	74.5
	T ₁ XD	2.38	231	76.8
	T ₁ XAD	2.56	236	75.6
	T ₁ XP	2.31	221	76.0
	T ₁ XH	2.52	251	75.9
	T ₂ XD	2.45	192	76.4
	T ₂ XAD	2.43	187	75.4
	T ₂ XP	2.46	218	75.3
	T ₂ XH	2.53	217	75.6
	Ave.	2.42	186.9	75.3
Parents	T ₁	2.10	223	75.9
	A	2.09	75	72.7
	T ₂	2.21	148	73.2
	D	2.47	197	76.9
	P	2.34	189	75.9
	H	2.45	175	76.2
	AD	2.38	172	75.7
	Ave.	2.29	168.4	75.2

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	D	2.47	197	76.9
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