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Title: EVALUATION OF EARLY GENERATION TESTING IN A DIALLEL CROSS INVOLVING FOUR WINTER WHEAT CULTIVARS (TRITICUM AESTIVUM VILL., HOST)

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Factors which influence the effectiveness of making early generation selections within bulk populations were investigated. Material utilized included the parents, F_1, and F_2 through F_5 bulk populations resulting from a diallel cross. Information concerning the response of two traits, plant height and grain yield, was obtained for these populations at three diverse experimental sites.

Estimates of gene action were determined by calculating heterosis, inbreeding depression, narrow-sense heritability, and combining ability values. Results obtained suggested that selections for plant height could be effectively made as early as the F_2 generation since this trait was largely controlled by additive gene action. Grain yield was found to be influenced significantly by non-additive gene action; however most populations were stabilized by the F_3 generations where

high yielding populations could be identified and effective selection practiced.

Results from this study suggested that genotype x environment interaction could influence early generation selection by masking the additive genetic effects. Under very favorable growing conditions the non-additive gene action x environment interaction dominated the additive effects for grain yield and to a lesser degree plant height. However, under dry land conditions both non-additive and additive genetic effects were masked by the environment and could not be expressed fully for grain yield. It is evident that for simply inherited traits like plant height, selection in the F_2 generation must be practiced under an environment where there is full expression for that trait, while selection for grain yield must be conducted under the same environments where the potential varieties are to be grown.

The use of Average Combining Ability as an indirect method to evaluate the contribution of parents to performance of the progency was found to be valid by the predicted results obtained for the simply inherited trait plant height. This method could be used with some confidence to estimate contribution of parents for a complex trait like grain yield. Two parents were identified as the best combiners for grain yield. This confirms what was learned about them after fifteen years of actual experience indicating the importance of a technique whereby the breeder can determine in a very short period of time which parents to cross and then concentrate his efforts within the more promising segregating populations.

Evaluation of Early Generation Testing in a Diallel Cross Involving Four Winter Wheat Cultivars (*Triticum aestivum* Vill., Host)

by

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Typed by Susie Kozlik for Abderrazak Daaloul

In dedication to my mother and father

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INTRODUCTION

A major technological breakthrough to increase the world food supply has been made by the development of high yielding semi-dwarf wheat varieties. Several techniques have been used to realize this objective. The most common breeding method employed involved hybridization followed by selection in segregating generations. Two approaches to increase grain yield have been utilized. The first has been to breed for specific traits affecting yield such as disease and lodging resistance; while the second is to breed for grain yield *per se*. The latter approach has not always been successful in wheat and certainly the methods employed have not been very efficient. This is mainly due to the fact that grain yield is a quantitatively inherited trait which is greatly influenced by the environment. Also, a possible plateau for yielding ability may have been attained. In attempting to breed for grain yield a tremendous amount of genetic variability must be utilized so successful combinations can be created. To obtain large amounts of genetic variability the breeder has had to work with a large number of crosses and large population sizes. This is difficult to realize in most breeding programs because of the restrictions imposed on resources such as money, time and space available to the breeder.

It would be more desirable if a plant breeder could create elite genetic variability by being able to identify the most promising parental combinations and then be able to select only the most valuable segregating progeny. If this latter practice is to be successful the breeder must be able to predict the potentialities of how selected progeny in early generations will perform in later generations.

Many investigators have evaluated early generation testing methods and are in agreement that effective early generation selections can be made for qualitatively inherited traits. However, for quantitatively inherited traits, and in particular grain yield where a large environmental influence is present, a controversy has resulted as to which generation can be utilized for the initial selection.

This study was conducted to determine if and when effective early generation selection can be practiced for plant height and grain yield. Those factors investigated included (1) the type of gene action involved in the control of each trait, (2) the genotype and environmental interactions, and (3) the parental contributions to the performance of the resulting progeny.

LITERATURE REVIEW

Early Generation Testing

The concept of early generation testing to predict later generations performances arose when plant breeders realized the necessity of utilizing a large number of crosses and the need to work with large populations. If potential yielding ability, height or other agronomic characteristics could be predicted from data obtained in early generations, many crosses would be discarded early and thus provide more space and time for other more desirable material to be tested (Elliott, 1959). Also by knowing which crosses have the greatest likelihood of producing high yielding segregates, the breeder could make more selections within those promising populations in early generations. Another purpose of early generation testing is the possibility of identifying those varieties or selections which are most likely to be good combining parents in further crosses (Briggs and Knowles, 1967).

Investigators do not agree as to the value of predictions based on early generation performance, particularly for quantitatively inherited traits. Harlan *et al.*, (1940) examined 379 barley crosses involving 28 parent varieties. They observed that yield of F_1 generations was a sound indication of the crosses from which high yielding segregates might be expected. It was their conclusion that low yielding crosses could have been discarded without loss on the basis of their F_1 generation yields. Grafius, Nelson and Dirks (1952) examined the data of Harlan et al. (1940) and suggested that it might be possible to select the high yielding crosses on the basis of the parental yield before any crosses were actually made. However, Briggs and Knowles (1967) reported that evaluations on F_1 generations might not give good results for the following reasons (1) the number of seeds available from crosses is not large enough to permit yield testing (2) these seeds are usually space-planted and (3) the heterosis in F_1 may mislead the breeders. For these reasons they suggest that early generation evaluations for yield should be delayed until later generations.

Harlan, Martini and Stevens (1940) concluded that predictions on basis of F_2 and F_3 were reliable for later generations. Harrington (1940) conducted replicated yield trials with bulk unselected seeds of ten wheat crosses in F_2 and six crosses in F_3. The latter six crosses were evaluated in F_6, F_7 and F_8 generations. Harrington concluded that replicated bulk F_2 tests could be used to indicate the yielding potentialities of wheat crosses and that bulk F_3 tests had supplementary value in this regard. Immer (1941) studied six barley crosses and planted bulk F_2, F_3, and F_4 generations in replicated yield trials. His results showed that the two crosses that produced the highest yields in F_2 and F_3 were among the highest in F_4, while two other crosses were relatively low yielding in all generations tested. He concluded that such yield trials may be used to discard certain crosses since the proportion of high yielding genotypes in the low yielding crosses would be less than in crosses with a higher average yield. Taylor (1951) evaluated bulk F_2 and F_5 populations of twenty barley crosses at four locations. He measured changes in gene frequencies for simply inherited morphological characters. His results indicated that bulk yield trials might have been used for discarding entire crosses without much loss of desirable germ plasm. Raeber and Weber (1953) studied the effectiveness of early generation selections for yield in soybean crosses. An appreciable degree of genic fixation for yield in the F_4 generationwas obtained when they measured the performances of F_5 high and low yielding pedigree lines based on their yield rank in the F_4 generation. Their conclusion was that early generation evaluations are effective in F_3 and F_4 generations.

McKenzie and Lambert (1961) compared yields of families in the F_3 and F_6 generations for two barley crosses. They measured the associations between F_3 and F_6 and found a small association in one cross and a good association in the second cross. They concluded that elimination of some families in the F_3 generation may be useful.

In addition to the replicated bulk yield trials, other methods utilizing some type of diallel analyses have been employed in early generation testing. Leffel and Hanson (1961) used forty-five diallel crosses among ten soybean parents and evaluated the yield in space planted F_1, F_2 and solid seeded F_2 bulk, F_3 bulk and F_3 line generations. Average and specific contributions of parents to progenies and the presence or absence of epistasis, dominance and additive gene action were determined. They found that performances of parents or their crosses in early bulk generations were reliable predictors of the performance of lines obtained from the crosses in the F_3 line generation. Smith and Lambert (1968) worked on bulks in F_2 and F_3 diallel crosses among ten barley parents. They measured Combining Ability and developed predictive values with respect to yield and kernel weight of six of the parents and the early generation bulks of their respective crosses. These predictive values were measured by the performance of F_5 lines derived from the crosses. Their results showed (1) large and significant variances for General Combining Ability for seed yield, kernel weight, maturity and plant height; (2) good and reliable performances of parents and individual crosses in F_2 and F_3 as indication of parental transmissibility and the potential value of the crosses; and (3) the performances of F_1 top crosses was of limited value for either yield or kernel weight in evaluating the parents.

All the investigators mentioned previously were in favor of early generation testing as a good tool for predicting later generation performance; however many others have presented evidence that early generation tests for yield are not reliable criteria for predicting later generation performance.

Kalton (1948) used replicated yield trials to test 25 soybean crosses in the F_2, F_3 and F_4 generations for seed yield, date of maturity, plant height and lodging resistance. He found that seed yield measurements made on spaced F_2 plants were not valuable in predicting yield potential of their F_3 and F_4 progenies. He also observed that F_3 line yield tests are not very closely correlated with those of lines extracted from them in later generations. He found, however, that plant height and maturity measurements made on spaced F_2 plants in each cross were good estimates of average progeny performance for these simply inherited traits in F_3 and F_4 generations.

Fifty segregates from each of ten oat crosses were tested for yield in the F_2 to F_8 generations by Atkins and Murphey (1949). Their results showed that considerable high yielding germplasm may be lost if bulk crosses were discarded on the basis of early generation evaluations.

Early generation tests were conducted by Fowler and Heyne (1955). They used progeny resulting from a diallel cross involving ten hard red winter wheats. Eight selections were made from F_5 generations and were compared to the early generation yield trials in order to determine whether or not the early generation test had been a reliable index in predicting later performances. Parental and early generations performances were not valuable in predicting yields of selections. However, for more simply inherited traits such as plant height, maturity and test weight, predictions were reliable. Fowler and Heyne (1955) explained that the lack of reliability of yield predictions in early generations was due to (1) the year to year variation in relative yield and (2) the inadequate technique for measuring yield.

Results of Fowler and Heyne (1955) are in agreement with those of Weiss _et al._ (1948) who showed that even though yield had attained a high degree of genic fixation in the F_4 generation, correlations between F_2 and F_4 generations for yield were very low. Mahmud and Kramer (1951) showed that this lack of good correlation is primarily due to year to year variation in yield; in effect they grew all generations in replicated trials with the parents and found high estimates of heritabilities from regression of F_4 on F_3 lines. It was consequently concluded, that F_3 lines should provide good estimates of the average yield potential of segregates obtained from these lines.

Most of these studies involving early generation testing were done at one location; thus, genotype-location interactions could not be partitioned out of the analyses.

Gene Action

The nature of the gene action for the character under selection is an important element to consider in early generation testing. Heterotic effects involving mainly non-additive gene action may be detrimental in that they mask the true performance in early generations in conventional breeding programs. These effects are lost by selfing, and this loss may be assessed by inbreeding depression. Additive gene action is fixed throughout the generations and it may be estimated by narrow sense heritability. The following review will cover pertinent literature regarding estimates of gene action as determined by heterosis, inbreeding depression, heritability and Combining Ability.

Heterosis and Inbreeding Depression

Briggs and Knowles (1967) have defined heterosis as a manifestation of heterozygosity expressed as increased vigor, size, fruitfulness and resistance to diseases, insects or adverse conditions. They have also defined inbreeding depression as a manifestation of homozygosity expressed as the converse of heterosis. In the utilization of heterosis in self-pollinating crops only that vigor in excess of the better parent is of significance. The term heterobeltiosis was proposed to describe the improvement of the heterozygote in relation to the better parent (Fonseca and Patterson, 1968). However, the term heterosis under current usage still refers to the increase above the mid-parent or above the higher parent and a distinction between the two is required with each usage of the term heterosis.

Heterosis in wheat was observed for the first time by Freeman (1919) who reported that F_1 plants, on the average, were taller than the tall parent in two crosses of durum x common wheat and common x common wheat. Briggle (1963) has made an extensive review concerning heterosis in wheat and reported several instances of significant heterosis in wheat. In this review increases in grain yield above the mean of the parents were listed as 64 percent by Harrington (1940); 72 percent by Varenica (1946); 88 percent by Cho and Chiang (1957) and 131.40 percent by Sikka _et al_. (1959). Increases in grain yield above the higher parents were mentioned as 32.7 percent by Boyce (1948); 44 percent by Lupton (1961) and 84 percent by Sikka _et al_. (1959).

Many recent studies have been concerned with heterosis in wheat. McNeal, _et al_. (1965) measured heterosis in three related spring wheat crosses. They found that related parents produced a hybrid population with little or no heterosis. They concluded that genetic diversity among parents is a determining factor for heterotic effects. Their results are in agreement with those obtained by Moll, Salhuana and Robinson (1962) who worked on heterosis and genetic diversity in maize. They indicated that greater genetic diversity of the parental varieties is associated with greater heterosis in the hybrids. Those studies suggest the high potential for heterosis from widely divergent parents in both self- and cross-pollinated crops.

Brown, Weibel and Seif (1966) evaluated heterosis in 16 crosses of common winter wheat. They found that five crosses had significant heterobeltiosis and twelve produced more than their mid-parent. The range for grain yield for all the 16 hybrids was 96 to 131 percent of the high parent and 107 to 138 percent of the mid-parent.

Gyawali; Qualset and Yamazaki (1968) estimated heterosis in winter wheat with a seven-parent diallel cross using soft red, soft white and hard red winter varieties. They found that ten of the 21 F_1 hybrids yielded significantly more grain than the better parent in a space-planting experiment. The average yield of all hybrids was 24 percent greater than the better parent. They also showed that soft red x soft red and soft red x hard red hybrids gave similar heterosis values indicating that interclass diversity is not a factor necessary for the expression of heterosis.

Walton (1971) studied the expression of heterosis in spring wheat varieties of Canadian, Mexican and American origin. Two complete diallel crosses with eight and five parents were used. He obtained a range of 10 to 26 percent of heterobeltiosis in the first year but in the second year there was only a range of - 11 to 4 percent of heterobeltiosis. He concluded that the decline of heterobeltiosis from year to year must indicate an F_1 x year interaction. Thus, this suggests that genetic diversity alone will not guarantee the expression of heterosis if the environmental conditions are not suitable.

Evidences of heterosis in wheat have also been reported by Kronstad and Foote (1964), Knott (1965); Johnson et al. (1966); Briggle, Cox and Hayes (1967); Briggle, Peterson and Hayes (1967); Nettevich (1968) and Fonseca and Patterson (1968).

In all the investigations mentioned above, estimates of heterosis were made on either space-planted or hill-planted F_1 plants because of the difficulty of producing large amounts of cross-pollinated wheat seeds. This might have led to an overestimation of the advantages of hybrids compared with parents because of the lack of competition among plants. There is little evidence in the literature of heterosis for yield in wheat from solid seedings.

Peterson (1970) simulated solid seeding by mixing the hybrid seeds with a very short semi-dwarf wheat WA. 4303. He used 20 hybrid seeds per plot. Significant heterosis and heterobeltiosis values were noted for all measured traits.

While several studies have been conducted to estimate heterosis in wheat, very few investigators have subsequently determined the amount of inbreeding depression in wheat or in self-pollinated crops in general.

Immer (1941) working with crosses of barley measured heterosis not only on F_1 hybrids but also on the following segregating generations. He found that as homozygosity increased heterosis decreased markedly. The values of heterosis he obtained were 27.3, 24, 13 and five percent for F_1, F_2 F_3 and F_4 generations, respectively. His results may be open to question since different generations were grown in different years and in such a way that the reduction of heterotic effects was not only due to inbreeding depression but also to generation x year interaction. However, the consistency of the reduction from year to year shows that inbreeding depression was the main contributing factor.

Matzinger, Mann, and Cockerham (1962) estimated heterosis and inbreeding depression for different characteristics in flue-cured tabacco crosses. Heterosis was expressed as the percent increase of the F_1 hybrid above the mid-parent. Inbreeding depression was expressed as the percent of F_2 reduction below the F_1 performance. Their results showed significant average heterosis and inbreeding depression for all characters measured except for leaf axil suckers. Their values for heterosis for plant height averaged 2.17 percent with a maximum of 11.20 percent. For yield the values were 1.16 percent for heterosis with a maximum of 9.50 percent and 3.49 percent for inbreeding depression with a maximum of 8.67 percent.

Miller and Marani (1963) estimated heterosis and inbreeding depression for several characters in cotton. They found significant heterosis values for all the characters measured but found that inbreeding depression was significant only for some characters. Results of this study suggested that inbreeding depression was greatest when heterotic effects were largest such as for lint yield. The F_1 hybrids showed an average increase of 27.5 percent over the mid-parent and the F_2 had an average inbreeding depression of 17.4 percent for all characters considered.

Chiang and Smith (1967) determined heterosis and inbreeding depression of several quantitative characters in grain sorghum. They used the same method of calculation as Matzinger _et al._ (1962). Highly significant inbreeding depression for all the characters measured was found. They also found as did Miller and Marani (1963), that those characters which showed highest heterosis had the greatest inbreeding depression. It was suggested that non-additive gene action might be involved in the inheritance of those characters.

Briggle, Cox and Hayes (1967) observed that in general the yield of F_2 spring wheat population was lower than that of the F_1, and yield of the F_3 was slightly lower than that of the F_2. They suggested that this reduction is somewhat linear to the increase in homozygosity.

Heritability

The observed variability in segregating populations is not all heritable since a portion of it is due to varying environment conditions. Heritability estimates may be used to measure that portion which is under genetic control. Heritability estimates are of two types (Lush, 1945): (1) Broad-sense heritability which measures the total genetic variance including both additive and non-additive gene effects and as such is not an index of transmissibility. (2) Narrow-sense heritability which measures the additive genetic variance and may be considered as an index of transmissibility, especially in self-pollinated crops, where only additive gene action can be fixed in succeeding generations.

There are several techniques to estimate heritability. They include: (1) those based on variance components from analysis of variance (2) those using parent-offspring regression (3) those based on approximations of environmental variance from non segregating populations (Warner, 1952).

Numerous studies have been conducted using these techniques to estimate broad-sense and narrow-sense heritability values. The following review will be restricted to studies where heritability values were obtained for plant height and grain yield in cereal crops with emphasis on wheat.

Fiuzat and Atkins (1953) used the variance component technique to determine heritability estimates for six different traits in two barley crosses. Their estimates ranged from 43.9 to 50.7 percent for grain yield and from 44.4 to 74.7 percent for plant height.

Heritability values for yield and the primary components of yield were determined by McNeal (1960) in a Lemhi X Thatcher wheat cross using regression of F_3 lines on F_2 plants. He found very low values and concluded that selection for yield and yield components in the F_2 generation is of little value.

Narrow-sense heritabilities using parent-F_1 regressions were obtained by Kronstad and Foote (1964) for yield, yield components and plant height in 45 crosses of winter wheat. On the average the values were 25.9 percent for yield and 82.9 percent for plant height.

Anwar and Chowdhry (1969) determined heritability values for plant height, heading date, and yield in four spring wheat crosses. They computed both broad and narrow-sense heritabilities using the variance component technique. Their results were 21 to 40 percent and 50 to 65 percent respectively for narrow-sense and broad-sense heritability estimates of plant height. For grain yield they found 12 to 41 percent and 61 to 70 percent respectively, for narrow-sense and broad-sense heritabilities. They concluded that grain yield is controlled by much less additive gene action than plant height.

Narrow-sense heritability for grain yield has been obtained by Busch et al. (1971) who worked with three crosses of spring wheat. The variance component technique was used among random F_5 lines. Their results ranged from 13.4 to 44.8 percent.

Combining Ability

Combining Ability may be defined as the ability of an inbred line to transmit desirable performance to its hybrid progenies. There are two types of Combining Ability. They are defined by Sprague and Tatum (1942) as: (1) General Combining Ability which refers to the average performance of a particular inbred in a series of hybrid combinations (2) Specific Combining Ability which refers to the ability of inbred lines to combine in specific single, three way, and double crosses.

Those characters that respond primarily to General Combining Ability effects are responding primarily to additive gene action (Frakes, 1963); therefore they are of primary interest to the plant breeder of self-pollinating species such as wheat. Those characters that respond to the effects of Specific Combining Ability may be thought of as responding to a gross gene system that deviates from the additive scheme; that means non-additive gene action (Frakes, 1963).

This concept of Combining Ability has been used widely in both animal and plant breeding. Plant breeders of cross-pollinated species have used this concept for selecting inbred lines to be used in hybrid production (Sprague and Tatum, 1942; Rojas and Sprague (1952); Matziner, Sprague and Cockerham (1959) and others).

For self-pollinated species Combining Ability was used in early generation evaluation of parental material in breeding programs; for instance the work of Leffel and Hanson (1961) on soybeans; of Smith and Lambert (1968) on barley; of Fowler and Heyne (1955); Kronstad and Foote (1963), Brown, Weibel and Seif (1966) on winter wheat.

Most of these studies have used a diallel crossing system. They have estimated General and Specific Combining Ability following Griffing's model of diallel analysis. In this model Griffing (1956) listed four methods of analysis depending on the absence or presence of the parents or the reciprocal F_1's in the array. For each method of analysis there are two models, fixed or random, depending on the assumptions underlying the selection of parents.

The General Combining Ability effects were reported as the main constituent of variation in plant height and yield in wheat by Kronstad and Foote (1964) and by Brown, Weibel and Seif (1966) and by many other investigators. Gyawali, Qualset and Yamazaki (1968) found that both General Combining Ability and Specific Combining Ability effects were significant for grain yield and plant height in wheat.

In a review on testing for Combining Ability, Allard (1966) noted that diallel crosses are important not only because they allow estimates of General Combining Ability and Specific Combining Ability, but also because they give the plant breeder a rapid evaluation of the Average Combining Ability. Jenkins and Branson (1932) as cited by Allard (1966) ranked their inbred lines using both General Combining Ability and Average Combining Ability and found similar results. The correlations between General Combining Ability and Average Combining Ability effects were also computed and ranged from 53 to 90 percent.

The literature review concerning gene action and Combining Ability indicates their importance as to the effectiveness of early generation testing. Two main factors have to be considered as to their influence on the success of early generation selections. They are: (1) the type of gene action controlling the trait under selection and (2) the selection of parents and resulting progenies. The type of gene action determines the degree that non-additive genetic effects control the trait and how much of these effects are lost by selfing. This allows the breeder to be not mislead by masking heterotic effects. The estimation of General Combining Ability effects of the parents would permit selection of the good combiners for further crosses and would point out the good crosses where more selection should be made.

MATERIALS AND METHODS

A diallel cross involving four agronomically diverse winter wheat parents was used in this study. The four parental lines were: Pullman Selection 101; Moro; Brevor and Corvallis Selection 55-1744. These four parents will be referred to as P_1; P_2; P_3 and P_4, respectively. A detailed description and pedigree of each parental line is given in the appendix. Pullman Selection 101 and Corvallis Selection 55-1744 are semi-dwarf and have Norin-10x Brevor as a common parent. Brevor is a standard height variety with the variety Moro being a tall club wheat.

Crosses were first made in 1966 and subsequently the F_1, F_2, F_3, F_4 and F_5 generations were grown as bulk populations from 1967 through 1971. This has resulted in six possible crosses with five generations per cross in 1971.

This study was conducted at three different locations in Oregon. These locations were Malheur, Pendleton and North Willamette Experiment Stations. These locations constitute three vastly different environments.

The Malheur Experiment Station provided a silty clay loam soil type. The experiment was planted October 8th following a previous planting of barley. It was conducted under irrigated conditions to minimize any possibility of water stress. Seventy-two kilograms per hectare of nitrogen (ammonium nitrate) were applied early in the spring.

The Pendleton Experiment Station has a Walla Walla silt loam soil type. Rainfall recorded on the station during the year 1970-1971 was 420 millimeters (Appendix Table 1). The experiment was planted on October 22nd on land which had been previously summer-fallowed. Seventy-two kilograms per hectare of nitrogen (ammonium nitrate) were applied before seeding.

The soil type on the North Willamette Experiment Station is a Willamette soil. The rainfall of the year 1970-71 was 1452 millimeters (Appendix Table 1). The experiment was planted on October 15th following a bean rotation. With the estimation of the nitrogen residue of the beans at 24 kilograms per hectare, 170 kilograms per hectare of additional nitrogen brought the total nitrogen to 194 kilograms per hectare.

In each location the six crosses were planted in a split plot design where the main plots were sets composed of two parents and five generations for each cross. This has resulted in 42 entires per replication which were analyzed as a randomized block with four replications. Individual plots consisted of three rows with a 30 centimeter spacing between rows. Two hundred and eighty six seeds were planted per row. The seeding rate differed from one location to another. At the Pendleton station the rows were 5 meters long which corresponds to a seeding rate of 75 kilograms per hectare. At the Malheur and North Willamette stations the rows were 3.50 meters long which corresponds to a seeding rate of 106 kilograms per hectare.

Because of the difficulty of producing large quantities of F_1 seeds, only 20 F_1 seeds were available for each plot. In order to simulate solid seedings the blend method of seeding was used (Peterson, 1970). The 20 F_1 seeds were mixed with a semi-dwarf, brown-chaffed winter wheat selection 172-RR-69-214. Mixed seeds were grown in the central row of each F_1 plot with two border rows planted with the 172-RR-69-214 selection.

Grain yield and plant height data were collected on these experiments. Grain yield was obtained for the parents and the F_2, F_3, F_4 and F_5 bulk populations by harvesting 2.40 meters from the central row of the plot. The grain yield data for the F_1 generation were handled in a different manner, since there were only 20 seeds per row. All F_1 plants in the row were harvested and the yield for 2.40 meters was calculated on the basis of 286 seeds per row. Grain yields are reported in grams. Plant height measurements were taken from the crown to the tip of the tallest spike in centimeters and represent the average of three observations per plot.

Data from each location were analyzed separately for the character measured (grain yield or plant height). In this analysis of variance each cross was considered as one group; the general error term (Entries x replications) was used to test differences among and within crosses. The mean value of the F_1, F_2, F_3, F_4 and F_5 generations and of the two parents of each cross were compared using the least significant difference at the five percent level ($LSD_{0.05}$).

Heterosis and inbreeding depression values were calculated for evaluation of gene action. According to the formulae of Matzinger et al. (1962) heterosis was expressed as percent increase of the F_1 hybrid means above the average of the two parents (Mid-parent = MP).

$$\text{Heterosis} = \frac{F_1 - MP}{MP} \times 100$$

According to the same investigators inbreeding depression was expressed as percent F_2 reduction below F_1 performance.

$$\text{Inbreeding depression} = \frac{F_1 - F_2}{F_1} \times 100$$

For further segregating generations inbreeding depressions were calculated in the same manner. They were expressed as the percent reduction of one generation below the performance of the previous generation.

$$\text{Inbreeding depression for } F_n = \frac{F_{n-1} - F_n}{F_{n-1}} \times 100$$

Using these formulae a positive heterosis value is an increase in performance while a negative heterosis value is a decrease in performance. This is reversed for inbreeding depression where a positive value is equivalent to a decrease in performance while a negative value is an increase in performance.

Heterobeltiosis values were calculated only for grain yield. They were expressed as the percent increase of the F_1 hybrid means above the higher parent (H. P.) (Fonseca and Patterson, 1968).

$$\text{Heterobeltiosis} = \frac{F_1 - \text{H. P}}{\text{H. P}} \times 100 \ .$$

Narrow-sense heritability estimates were calculated by the regression of the F_2 on the F_1 using mean values of the six crosses for both plant height and grain yield.

Effects of General and Specific Combining Ability were tested by the Griffing's method of analysis of diallel crosses (Griffing; 1956). Only the F_1's were included in the matrix and neither the reciprocals nor the parents were in the array so method four was used. Also, the parents represented a selected population upon which inferences were made, so the fixed model or model I was used. The same technique was used to test General and Specific Combining Ability effects in the F_2, F_3, F_4 and F_5 generations.

The average contribution of each parent was evaluated using Average Combining Ability values. Average Combining Ability was calculated by adding the average performances of the crosses in which the particular parent was involved and dividing the sum by the number of crosses.

EXPERIMENTAL RESULTS

Plant height and grain yield were recorded for the F_1, F_2, F_3, F_4 and F_5 generations of each cross along with the two parents of the cross. The per plot mean values at the three locations (Malheur, Pendleton and North Willamette Experiment Stations) are summarized in Table 11 and Table 12 for plant height and grain yield, respectively. These tables also show the ranking of the mean values within each cross which will be described in the early generation evaluation section of the experimental results.

The mean yields of all entires are 519.7, 398.8 and 466.8 grams at the Malheur, Pendleton and North Willamette locations respectively. The mean heights also differ greatly from one location to another; they are 95.5; 119.8 and 129.8 centimeters for Malheur, Pendleton and North Willamette, respectively.

Analysis of Variance

The results of the analysis of variance for plant height and grain yield data at the three locations are summarized in Table 1 and Table 2, respectively. Coefficients of variation at each location and for each character are also presented in the Tables 1 and 2.

Table 1. Summary of the observed mean squares from analysis of variance for plant height obtained at three locations.

Source of variation	D. F	Observed mean squares		
		Malheur	Pendleton	North Willamette
Replications	3	223.93 **	126.42 *	907.77 **
Entries	41	254.66 **	942.39 **	794.75 **
Among crosses	5	848.12 **	2039.07 **	1706.60 **
Within crosses	36	172.24 **	790.07 **	668.11 **
Within P_1 x P_2	6	134.82 **	642.30 **	664.57 **
Within P_1 x P_3	6	71.98 **	461.98 **	330.82 **
Within P_1 x P_4	6	224.62 **	880.48 **	814.57 **
Within P_2 x P_3	6	38.20	344.33 **	383.03 **
Within P_2 x P_4	6	366.66 **	1531.21 **	1096.37 **
Within P_3 x P_4	6	197.14 **	880.14 **	719.32 **
Replications x Entries	123	19.79	38.63	37.51
Total	167	---	---	---
Coefficient of variation		4.66	5.19	4.72

*Significant at the 5% level

**Significant at the 1% level

Table 2. Summary of the observed mean squares from analysis of variance for grain yield obtained at three locations.

Source of variation	D.F.	Observed mean squares		
		Malheur	Pendleton	North Willamette
Replications	3	1411.25	8142.12	18182.30 **
Entries	41	21086.25 **	13758.21 **	17593.27 **
Among crosses	5	17157.58 **	31098.01 **	36978.90 **
Within crosses	36	21631.89 **	11349.91 **	14900.82 **
Within $P_1 \times P_2$	6	17903.41 **	22044.33 **	27766.42 **
Within $P_1 \times P_3$	6	8923.53	5828.73	4920.56
Within $P_1 \times P_4$	6	16359.15 *	7935.95	13821.33 **
Within $P_2 \times P_3$	6	26806.50 **	6437.39	6710.41 *
Within $P_2 \times P_4$	6	51296.66 **	15510.07 **	16467.70 **
Within $P_3 \times P_4$	6	8502.04	10342.96 *	19709.48 *
Replications x Entries	123	6264.86	4326.43	2889.49
Total	127	---	---	---
Coefficient of variation		15.23	16.49	11.52

*Significant at the 5% level

**Significant at the 1% level

Differences among all 42 entries were highly significant for the two characters and at all three locations. When the 42 entries were considered as six groups (each cross being a group) differences among and within crosses were also significant at the one percent level for all locations except for the Malheur station where differences among crosses for grain yield were significant at the five percent level only.

Differences within crosses (among the F_1, F_2, F_3, F_4 and F_5 generations and the parents of the given cross) were partitioned for each of the six crosses. For plant height highly significant differences were detected within each cross at the three locations, except for the $P_2 \times P_3$ cross at Malheur where no significant differences for this cross were detected. For grain yield, highly significant differences were detected within $P_1 \times P_2$ and $P_2 \times P_4$ at the three locations and within $P_1 \times P_4$ at Malheur and $P_2 \times P_3$ at North Willamette. No significant differences were detected within $P_1 \times P_4$ and $P_2 \times P_3$ at Pendleton, $P_3 \times P_4$ at Malheur and within $P_1 \times P_3$ at the three locations.

Coefficients of variation were rather high for grain yield (Table 2) as compared to those for plant height (Table 1). They are 15.23, 16.49 and 11.52 percent for grain yield at Malheur, Pendleton and North Willamette respectively. However, for plant height the coefficients of variation are 4.66; 5.19 and 4.72 percent at the same respective locations.

Heterosis and Inbreeding Depression

Values for heterosis and inbreeding depression were calculated for plant height and grain yield at the three locations using the formulae developed by Matzinger et al. (1962).

Results for plant height are summarized in Table 3 for heterosis and in Table 4 for inbreeding depression. Most of the F_1's were approximately equal or below the mid-parent for plant height; thus heterosis values for plant height were low and often negative (Table 3).

Table 3. Estimates of heterosis (1) for plant height for six single crosses grown at the three locations.

Crosses	Heterosis		
	Malheur	Pendleton	North Willamette
$P_1 \times P_2$	0.13	-7.89	-1.54
$P_1 \times P_3$	-0.13	-3.29	0.00
$P_1 \times P_4$	0.31	-2.67	0.48
$P_2 \times P_3$	-6.31	-8.45	-8.89
$P_2 \times P_4$	-0.95	-3.40	-0.52
$P_3 \times P_4$	3.37	-2.67	-3.75
Averages	-0.57	-4.72	-2.37

(1) Heterosis $= \frac{F_1 - MP}{MP} \times 100$

They ranged from -6.31 to +3.37 percent at Malheur; from -8.45 to 2.67 percent at Pendleton and from -8.89 to +0.48 percent at North Willamette. The inbreeding depression values from F_1 to F_2 were

Table 4. Inbreeding depression values (1) for plant height in four segregating generations involving six single crosses grown at three locations.

Locations	Crosses	Inbreeding depression values in percent			
		F_2	F_3	F_4	F_5
Malheur	$P_1 \times P_2$	-7.75	2.98	-1.02	-2.03
	$P_1 \times P_3$	-4.57	-0.02	-0.51	1.01
	$P_1 \times P_4$	-12.19	-5.01	0.27	0.50
	$P_2 \times P_3$	-6.53	-0.74	-2.43	1.19
	$P_2 \times P_4$	-19.13	7.57	-6.20	0.93
	$P_3 \times P_4$	-3.37	1.06	-2.42	0.00
	Average	-8.92	0.97	-2.05	0.27
Pendleton	$P_1 \times P_2$	-15.75	-1.78	1.16	-1.37
	$P_1 \times P_3$	-15.05	-1.90	0.41	-2.70
	$P_1 \times P_4$	-34.89	6.52	-6.54	3.68
	$P_2 \times P_3$	-20.39	1.60	-3.26	4.47
	$P_2 \times P_4$	-22.77	-2.29	-8.04	3.98
	$P_3 \times P_4$	-22.20	4.69	-7.99	3.98
	Average	-21.84	1.14	-4.04	2.05
North Willamette	$P_1 \times P_2$	-18.83	5.63	0.56	6.94
	$P_1 \times P_3$	-6.83	-2.20	-1.56	2.12
	$P_1 \times P_4$	-27.03	3.77	-3.52	1.70
	$P_2 \times P_3$	-19.92	2.37	-3.65	1.01
	$P_2 \times P_4$	-24.07	4.01	-5.05	2.49
	$P_3 \times P_4$	-20.13	3.96	-5.07	1.43
	Average	-19.47	2.92	-3.05	0.30
General average		-16.74	1.67	-3.04	0.87

(1) Inbreeding depression $= \dfrac{F_{n-1} - F_n}{F_n} \times 100$

negative (Table 4) showing an increase of plant height in F_2. They were -8.92; -21.84 and -19.47 percent for the Malheur, Pendleton and North Willamette locations, respectively. In the following segregating generations (F_3, F_4 and F_5) the average inbreeding depression values for plant height were positive but small in the F_3, negative in the F_4 and positive in the F_5. These fluctuations were consistent in all three locations.

Heterosis values for grain yield are summarized in Table 5 and inbreeding depression values are presented in Table 6. Heterosis values for grain yield were high ranging from -4.25 to 51.25 percent at Malheur, from 5.36 to 27.56 percent at Pendleton and from 9.14 to 32.62 percent at North Willamette. The average heterosis values were 26.59, 15.11 and 22.50 percent at Malheur, Pendleton and North Willamette respectively. Inbreeding depression values for grain yield were also high and positive in the F_2 generation (Table 6). These values averaged 19.39; 12.28 and 15.17 percent at Malheur, Pendleton and North Willamette, respectively. In the F_3, F_4 and F_5 generations the inbreeding depression values were smaller showing that the decrease in yield is not as great as in the F_2 generation. In the F_3 the inbreeding depression values averaged 1.24, 9.56 and 10.70 percent at Malheur, Pendleton and North Willamette, respectively. In the F_4 and F_5 generations the inbreeding depression values were small and often negative reflecting a stabilization of the yielding ability.

Table 5. Estimates of heterosis (1) for grain yield for six single crosses grown at the three locations.

Crosses	Heterosis		
	Malheur	Pendleton	North Willamette
$P_1 \times P_2$	17.33	27.27	32.62
$P_1 \times P_3$	18.84	10.75	9.14
$P_1 \times P_4$	30.32	14.02	24.92
$P_2 \times P_3$	46.05	27.56	19.90
$P_2 \times P_4$	51.25	5.72	37.86
$P_3 \times P_4$	-4.25	5.36	10.60
Averages	26.59	15.11	22.50

(1) Heterosis $= \frac{F_1 - MP}{MP} \times 100$

Close examination of heterosis values in the F_1 and of inbreeding depression values in the F_2, especially for grain yield (Tables 5 and 6), shows that the crosses which had the highest heterosis value exhibited the highest inbreeding depression value. Crosses with high heterosis and inbreeding depression values involve P_2 such as $P_2 \times P_4$ at Malheur; $P_2 \times P_3$ at Pendleton, $P_2 \times P_4$ at North Willamette and $P_1 \times P_2$ at the three locations. Also the crosses which had the lowest heterosis value exhibited the lowest inbreeding depression value; for example, $P_3 \times P_4$ at Malheur and $P_1 \times P_4$ at North Willamette.

Table 6. Inbreeding depression values (1) for grain yield in four segregating generations of six single crosses grown at three locations.

Locations	Crosses	Inbreeding depression values in percent			
		F_2	F_3	F_4	F_5
Malheur	P_1 x P_2	17.33	7.28	-2.67	10.26
	P_1 x P_3	16.13	1.90	1.32	1.24
	P_1 x P_4	23.01	6.18	-3.45	-10.06
	P_2 x P_3	31.85	-5.42	4.54	-0.94
	P_2 x P_4	32.48	10.56	-7.45	11.27
	P_3 x P_4	-4.44	-13.06	19.44	-4.44
	Average	19.39	1.24	1.95	1.22
Pendleton	P_1 x P_2	25.46	1.29	-8.21	9.27
	P_1 x P_3	10.70	4.28	-0.88	-2.31
	P_1 x P_4	10.68	20.66	-20.04	0.97
	P_2 x P_3	25.53	-9.24	5.38	-2.58
	P_2 x P_4	-1.32	18.97	14.93	-4.12
	P_3 x P_4	2.63	21.40	-0.55	-13.31
	Average	12.28	9.56	-9.37	-2.33
North Willamette	P_1 x P_2	13.36	27.09	-9.73	1.72
	P_1 x P_3	19.04	-10.60	8.67	-6.08
	P_1 x P_4	7.39	20.57	-1.67	-10.37
	P_2 x P_3	18.78	2.75	7.46	11.60
	P_2 x P_4	15.25	11.12	3.43	-10.87
	P_3 x P_4	17.21	13.29	-7.60	-1.95
	Average	15.17	10.70	0.56	-6.52
General average		15.61	7.16	-2.28	-2.54

(1) Inbreeding depression $= \frac{F_{n-1} - F_n}{F_n} \times 100$

Heterobeltiosis values were also calculated for grain yield using the formulae of Fonseca and Patterson (1968). These values are summarized in Table 7. They range from -13.83 to 49.07 percent at Malheur from -7.17 to 19.09 percent at Pendleton and from -3.26 to 28.42 percent at North Willamette. The average heterobeltiosis values were higher at Malheur and North Willamette (20.77 and 15.09 percent respectively) when compared to the value of heterobeltiosis at Pendleton (3.75 percent). Here also, close examination shows that: (1) crosses involving parent P_2 had the highest heterobeltiosis values such as $P_2 \times P_3$ and $P_2 \times P_4$ crosses at Malheur, and (2) crosses involving related parental lines (P_1, P_3 and P_4) exhibited low heterobeltiosis such as $P_3 \times P_4$ cross at Malheur and $P_1 \times P_3$ cross at Pendleton.

Table 7. Estimates of heterobeltiosis (1) for grain yield for six single crosses grown at three locations.

Crosses	Heterobeltiosis		
	Malheur	Pendleton	North Willamette
$P_1 \times P_2$	4.72	3.47	21.72
$P_1 \times P_3$	18.09	-1.80	3.63
$P_1 \times P_4$	22.05	13.92	22.60
$P_2 \times P_3$	44.54	19.09	17.40
$P_2 \times P_4$	49.07	-4.98	28.42
$P_3 \times P_4$	-13.83	-7.17	-3.26
Averages	20.77	3.75	15.09

(1) Heterobeltiosis $= \dfrac{F_1 - H.P}{H.P} \times 100$

Heritability

Narrow-sense heritability estimates were calculated for grain yield and plant height to obtain more information about the type of gene action involved. Heritability estimates were calculated by the regression of F_2 on F_1 using the mean values and are summarized in Table 8. Narrow-sense heritability values were high for plant height. They ranged from 65.0 to 84.8 percent. The narrow-sense heritability values were low for grain yield and ranged from 11.5 to 29.5 percent. The heritability value for grain yield at North Willamette was 114.4 percent which is an unrealistic value and may have resulted from sampling error.

Table 8. Narrow-sense heritability estimates h^2 (1) for grain yield and plant height obtained at three locations.

	Malheur	Pendleton	North Willamette
Grain yield	11.5	29.5	114.4
Plant height	84.8	65.0	80.4

(1) $h^2 = F_2$ on F_1 regression

General and Specific Combining Ability

The analyses of variance for General and Specific Combining Ability were also computed to evaluate the type of gene action involved in these two traits. Analyses of variance for Combining Ability were computed according to Griffing's technique (1956) (method four, model I).

General and Specific Combining Ability mean squares were obtained for both plant height and grain yield in the F_1, F_2, F_3, F_4 and F_5 generations at the three locations. The observed mean squares for General and Specific Combining Ability are summarized in Table 9 for plant height and in Table 10 for grain yield.

Table 9. Observed mean squares from General and Specific Combining Ability analyses for plant height involving six single crosses.

Location	Generations	General Combining Ability	Specific Combining Ability	Error
Malheur	F_1	185.24 **	40.04	26.75
	F_2	222.46 **	117.17 *	24.85
	F_3	65.88 **	40.63 **	0.63
	F_4	132.58 **	75.54 *	17.57
	F_5	133.70 **	38.62	20.67
Pendleton	F_1	456.70 **	24.00	17.69
	F_2	305.25	97.75	137.65
	F_3	505.70 **	6.13	19.34
	F_4	677.33 **	20.13	27.52
	F_5	376.08 **	41.25	36.35
North Willamette	F_1	245.88 **	56.29 *	16.08
	F_2	544.13 **	22.16	38.35
	F_3	336.58 **	12.75	46.71
	F_4	510.08 **	41.62	41.56
	F_5	483.58 **	19.63	44.13

* Significant at the 5% level ** Significant at the 1% level

Table 10. Observed mean squares from General and Specific Combining Ability analyses for grain yield involving six single crosses.

Location	Generations	General Combining Ability	Specific Combining Ability	Error
Malheur	F_1	31044.75	72536.50 *	15737.95
	F_2	641.25	6244.28	2945.06
	F_3	6828.00	5352.50	4436.66
	F_4	913.70	7151.50	4989.20
	F_5	4737.87	7933.75	3048.59
Pendleton	F_1	11850.75 *	1759.00	3179.32
	F_2	13073.46	2640.13	6897.99
	F_3	3878.17	1311.13	2663.42
	F_4	18357.88 *	3531.63	5417.66
	F_5	11151.08	1987.63	4498.43
North Willamette	F_1	21245.00 **	5643.00	2103.00
	F_2	42682.75 **	6039.54	3042.31
	F_3	2575.00	4920.00	3605.00
	F_4	7203.00 **	1615.00	862.80
	F_5	9731.08 *	1103.38	2517.27

* Significant at the 5% level
** Significant at the 1% level

For plant height, General Combining Ability effects were highly significant at all locations and for each generation except the F_2 at Pendleton. Specific Combining Ability effects were significant at the one percent level in the F_3 generation alone at Malheur location. Also significant Specific Combining Ability effects at the five percent level were detected for plant height for the F_2 and the F_4 generations at Malheur location and in the F_1 at North Willamette. However, no significant Specific Combining Ability effects were detected elsewhere.

For grain yield General Combining Ability effects were significant only in the F_1, F_2, F_4 and F_5 generations at North Willamette and in the F_1 and F_4 generation at Pendleton. No significant General Combining Ability effects were detected at the Malheur location. Specific Combining Ability effects for grain yield were not significant except for the F_1 generation at the Malheur location.

Early Generation Evaluation

The evaluation of early generation performances of the bulk populations for plant height and grain yield of the F_1, F_2, F_3, F_4 and F_5 generations and of the parents were compared for the individual crosses at each location using the least significant difference at the five percent level. Results of these comparisons are summarized in Tables 11 and 12 for plant height and grain yield, respectively. Mean values which are ranked under the same alphabetic letter do not differ significantly at the five percent level.

It is clear from Tables 11 and 12 that those crosses which had shown a significance within cross component in the general analyses of variance are those which show significant differences among F_1,

Table 11. Mean values for plant height obtained at three locations.

Crosses at different generations and parents	Malheur (2)		Pendleton (2)		North Willamette (2)	
	means	LSD (1) ranking	means	LSD (1) ranking	means	LSD (1) ranking
P_1	85.25 cms	B	96.75 cms	C	107.00 cms	C
P_2	101.50	A	127.00	A	135.75	A
$P_1 \times P_2$ F_1	93.50	A	109.50	B	119.50	B
$P_1 \times P_2$ F_2	100.75	A	126.75	A	142.00	A
$P_1 \times P_2$ F_3	97.75	A	129.00	A	134.00	A
$P_1 \times P_2$ F_4	98.75	A	127.50	A	133.25	A
$P_1 \times P_2$ F_5	100.75	A	129.25	A	142.50	A
P_1	87.75	B	95.00	B	105.00	B
P_3	98.50	A	118.00	A	129.50	A
$P_1 \times P_3$ F_1	93.00	A	103.00	B	117.25	A
$P_1 \times P_3$ F_2	97.25	A	118.50	A	125.25	A
$P_1 \times P_3$ F_3	98.75	A	120.75	A	128.00	A
$P_1 \times P_3$ F_4	99.25	A	120.25	A	130.00	A
$P_1 \times P_3$ F_5	98.25	A	123.50	A	127.25	A
P_1	83.75	B	98.50	A	103.75	B
P_4	75.75	B	88.50	B	104.25	B
$P_1 \times P_4$ F_1	80.00	B	91.00	A	104.50	B
$P_1 \times P_4$ F_2	89.75	A	122.75	A	132.75	A
$P_1 \times P_4$ F_3	94.25	A	114.75	A	127.75	A
$P_1 \times P_4$ F_4	94.00	A	122.25	A	132.25	A
$P_1 \times P_4$ F_5	93.50	A	117.75	A	130.00	A
P_2	103.25	A	128.75	B	138.00	B
P_3	100.75	A	125.75	B	132.00	B
$P_2 \times P_3$ F_1	95.75	B	116.50	C	123.00	C
$P_2 \times P_3$ F_2	102.00	A	140.25	A	147.50	A
$P_2 \times P_3$ F_3	102.75	A	138.60	A	144.00	A
$P_2 \times P_3$ F_4	105.25	A	142.50	A	149.25	A
$P_2 \times P_3$ F_5	104.00	A	135.75	A	147.75	A

Table 11. Continued.

Crosses at different generations and parents	Malheur (2)		Pendleton (2)		North Willamette (2)	
	means	LSD (1) ranking	means	LSD (1) ranking	means	LSD (1) ranking
P_2	102.25 cms	A	130.75 cms	A	135.00 cms	B
P_4	82.50	C	89.75	C	107.25	D
$P_2 \times P_4$ F_1	91.50	B	106.50	B	120.50	C
$P_2 \times P_4$ F_2	109.00	A	130.75	A	149.50	A
$P_2 \times P_4$ F_3	100.75	A	133.75	A	143.50	A
$P_2 \times P_4$ F_4	107.00	A	144.50	A	150.75	A
$P_2 \times P_4$ F_5	106.00	A	138.75	A	147.00	A
P_3	94.75	A	124.25	A	134.50	A
P_4	76.00	B	91.00	C	105.50	C
$P_3 \times P_4$ F_1	88.25	A	104.75	B	115.50	B
$P_3 \times P_4$ F_2	94.00	A	128.00	A	138.75	A
$P_3 \times P_4$ F_3	93.00	A	122.00	A	133.25	A
$P_3 \times P_4$ F_4	95.25	A	131.75	A	140.00	A
$P_3 \times P_4$ F_5	95.25	A	126.50	A	138.00	A
Grand mean	95.50		119.77		129.81	

(1) Malheur LSD$_{.05}$ = 6.17 cm

Pendleton LSD$_{.05}$ = 8.61 cm

North Willamette LSD$_{.05}$ = 8.49 cm

(2) Means followed by a different upper case letter differ significantly at the five percent level.

Table 12. Mean values for grain yield obtained at three locations.

Crosses at different generations and parents	Malheur (2)		Pendleton (2)		North Willamette (2)	
	means	LSD (1) ranking	means	LSD (1) ranking	means	LSD (1) ranking
P_1	582.75 gms	A	504.00 gms	A	518.00 gms	B
P_2	457.50	B	315.00	B	432.75	C
$P_1 \times P_2$ F_1	610.25	A	521.50	A	630.50	A
$P_1 \times P_2$ F_2	504.50	A	388.75	B	546.25	B
$P_1 \times P_2$ F_3	467.75	A	383.50	B	398.25	C
$P_1 \times P_2$ F_4	480.25	A	415.25	B	437.00	C
$P_1 \times P_2$ F_5	431.00	A	367.75	B	429.50	C
P_1	546.00	A	473.25	A	475.25	A
P_3	500.50	A	366.00	A	427.25	A
$P_1 \times P_3$ F_1	644.75	A	464.75	A	492.50	A
$P_1 \times P_3$ F_2	540.75	A	415.00	A	398.75	A
$P_1 \times P_3$ F_3	530.50	A	397.25	A	441.00	A
$P_1 \times P_3$ F_4	523.50	A	400.75	A	402.75	A
$P_1 \times P_3$ F_5	517.00	A	410.00	A	427.25	A
P_1	534.00	B	454.25	A	478.25	A
P_4	466.25	B	453.50	A	496.75	A
$P_1 \times P_4$ F_1	651.75	A	517.50	A	609.00	A
$P_1 \times P_4$ F_2	501.75	B	462.25	A	564.00	A
$P_1 \times P_4$ F_3	470.75	B	366.75	A	448.00	A
$P_1 \times P_4$ F_4	487.00	B	440.25	A	455.50	A
$P_1 \times P_4$ F_5	536.00	B	436.00	A	502.75	A
P_2	472.75	B	320.25	A	402.00	B
P_3	482.75	B	369.25	A	419.50	B
$P_2 \times P_3$ F_1	497.75	A	439.75	A	492.50	A
$P_2 \times P_3$ F_2	475.50	B	327.50	A	400.00	B
$P_2 \times P_3$ F_3	501.25	B	357.75	A	389.00	B
$P_2 \times P_3$ F_4	478.50	B	338.50	A	360.00	B
$P_2 \times P_3$ F_5	483.00	B	347.25	A	401.75	B

Table 12. Continued.

Crosses at different generations and parents	Malheur (2)		Pendleton (2)		North Willamette (2)	
	means	LSD (1) ranking	means	LSD (1) ranking	means	LSD (1) ranking
P_2	521.00 gms	B	364.75 gms	A	410.25 gms	B
P_4	536.50	B	457.25	A	475.00	B
P_2 x P_4 F_1	799.75	A	434.50	A	610.00	A
P_2 x P_4 F_2	540.00	B	440.25	A	517.00	B
P_2 x P_4 F_3	483.00	B	356.75	A	459.50	B
P_2 x P_4 F_4	519.00	B	303.50	B	443.75	B
P_2 x P_4 F_5	460.50	B	316.00	B	492.00	B
P_3	433.75	B	342.75	A	424.75	B
P_4	542.25	A	449.75	A	582.75	A
P_3 x P_4 F_1	467.25	A	417.50	A	563.50	A
P_3 x P_4 F_2	488.00	A	406.50	A	466.50	B
P_3 x P_4 F_3	551.75	A	319.50	A	404.50	B
P_3 x P_4 F_4	444.50	A	321.25	A	435.25	B
P_3 x P_4 F_5	464.25	A	364.00	A	443.75	B
Grand mean	519.69		398.76		466.77	

(1) Malheur LSD$_{.05}$ = 109.70 gms

Pendleton LSD$_{.05}$ = 91.16 gms

North Willamette LSD$_{.05}$ = 74.49 gms

(2) Means followed by a different upper case letter differ significantly at the five percent level.

F_2, F_3, F_4 and F_5. However in most cases the F_2, F_3, F_4 and F_5 performances were not significantly different.

For grain yield the same result was obtained with no significant differences existing among the F_2, F_3, F_4 and F_5 generations. The only exceptions to this general result are those crosses which showed significant difference among the F_2, F_3, F_4 and F_5 generations such as the case of P_2 x P_4 at Pendleton and P_1 x P_2 at North Willamette.

Parent Evaluations

To evaluate the contribution of each of the parents, Average Combining Ability was calculated for each parent in each generation and at each location. The Average Combining Ability values are summarized in Table 13 for plant height and Table 14 for grain yield. In these tables a parent with high Average Combining Ability will, on the average, produce progeny that have high level of performance, conversely, a parent with low Average Combining Ability will, on the average, produce progeny with a low level of performance.

Results for plant height (Table 13) show that: (1) P_2 consistently had the highest Average Combining Ability in all generations at all locations; (2) P_1 and P_4 had alternatively the lowest Average Combining Ability, while (3) P_3 was always second after P_2.

Results for grain yield (Table 14) were the most consistent at North Willamette where P_4 had the highest Average Combining Ability

Table 13. Average Combining Ability (A. C. A.) for plant height of the parental lines in the F_1, F_2, F_3, F_4 and F_5 generations grown at the three locations.

Generation	Parents	Malheur		Pendleton		North Willamette	
		A.C.A.	Rank	A.C.A.	Rank	A.C.A.	Rank
F_1	P_1	88.83	3	101.17	3	113.75	3
	P_2	93.58	1	110.83	1	121.00	1
	P_3	92.33	2	108.08	2	118.58	2
	P_4	86.58	4	100.75	4	113.13	4
F_2	P_1	95.92	4	122.67	4	133.33	4
	P_2	103.92	1	132.58	1	146.33	1
	P_3	97.75	2	128.92	2	137.17	3
	P_4	97.58	3	127.17	3	140.33	2
F_3	P_1	96.92	4	121.50	4	129.92	4
	P_2	100.42	1	133.58	1	140.50	1
	P_3	98.17	2	126.92	2	135.08	2
	P_4	96.00	3	123.50	3	134.83	3
F_4	P_1	97.33	4	123.33	4	131.83	4
	P_2	103.67	1	138.17	1	144.42	1
	P_3	99.92	2	131.50	2	139.75	3
	P_4	98.75	3	132.83	3	141.00	2
F_5	P_1	97.50	3	123.50	4	133.25	4
	P_2	103.58	1	134.58	1	145.75	1
	P_3	99.17	2	128.58	2	140.67	2
	P_4	98.25	4	127.67	3	138.33	3

Table 14. Average Combining Ability (A.C.A.) for grain yield of the parental lines in the F_1, F_2, F_3, F_4 and F_5 generations grown at the three locations.

Generations	Parents	Malheur		Pendleton		North Willamette	
		A.C.A.	Rank	A.C.A.	Rank	A.C.A.	Rank
F_1	P_1	635.58	3	501.17	1	577.33	3
	P_2	702.58	1	465.25	2	577.66	2
	P_3	603.25	4	440.58	4	516.17	4
	P_4	639.50	2	456.50	3	594.17	1
F_2	P_1	515.66	1	422.00	2	503.00	2
	P_2	506.76	3	385.50	3	487.75	3
	P_3	501.42	4	382.83	4	421.75	4
	P_4	509.92	2	436.16	1	515.83	1
F_3	P_1	489.67	3	382.58	1	429.08	2
	P_2	484.00	4	366.00	2	415.58	3
	P_3	504.91	1	358.16	3	411.50	4
	P_4	501.83	2	347.66	4	437.33	1
F_4	P_1	496.92	1	418.75	1	431.75	2
	P_2	492.58	2	352.41	4	413.58	3
	P_3	482.16	4	353.50	3	399.33	4
	P_4	483.50	3	355.00	2	444.83	1
F_5	P_1	494.66	1	404.58	1	453.16	2
	P_2	458.16	4	343.66	4	441.08	3
	P_3	486.83	3	373.75	2	440.33	4
	P_4	486.92	2	372.00	3	479.50	1

followed successively by P_1, P_2 and P_3. At the other locations, however, the results were not as consistent. In Pendleton, for example, P_1 had the highest Average Combining Ability in the F_1, F_3, F_4 and F_5 generations, but not in the F_2 generation where it was replaced by P_4. The ranking of the other parents was different from one generation to another: P_3 was the lowest in F_1 and F_2 generations; P_4 was the lowest in F_3 and P_2 was the lowest in F_4 and F_5. At Malheur P_1 had the highest Average Combining Ability in F_2, F_4 and F_5 generations; P_4 was always second after P_1 except in F_4 generation. Here it should be noted that P_2 had the highest Average Combining Ability in the F_1 generation while P_3 was the highest in the F_3 generation.

The above results may be summarized in two general statements: (1) for plant height the ranking of the parents as to the value of Average Combining Ability may be as follows: P_2, P_3 and P_1 or P_4. (2) For grain yield the parents can be ranked as follows: P_1 or P_4, P_3 and P_2.

DISCUSSION

The most important method of obtaining new improved varieties of self-pollinated species is through hybridization followed by some type of selection made within segregating populations. To be successful the plant breeder needs genetic variability, therefore he must deal with extensive number of crosses and utilize large population sizes. This is particularly emphasized in breeding for quantitatively inherited traits like grain yield where a possible plateau is being reached in wheat. This feature is particularly disturbing when it is realized that time and space are limiting factors in most breeding programs. An effective early generation method of testing would aid in reducing the number of crosses needed and would allow the plant breeder to concentrate his efforts on larger population sizes from more promising segregating generations.

To be effective early generation testing must provide the plant breeder with a reliable method of identifying superior yielding progeny by at least the F_3 generation. Those factors which will influence the success of such testing are (1) the nature of gene action controlling the expression of a specific trait, (2) environmental interactions with the genetic effects and (3) the contribution of potential parents.

To determine the extent to which these factors influence early generation selections two traits, three environments and four parents were used in this study. The two traits were plant height and grain yield, which have been studied extensively from a breeding and genetic viewpoint. Grain yield has been found to be a complex character which is quantitatively inherited and greatly influenced by the environment. Plant height is less complex in its pattern of inheritance and as a consequence is less influenced by the environment.

Evaluation of the type of gene action involved in the expression of a trait is particularly important in the breeding of self-pollinated species. In a conventional breeding program, the breeder can be mislead during early generations for traits which respond largely to non-additive gene action, since this form of gene action will be reduced by fifty percent each generation of selfing following a cross. This is in contrast with a hybrid program where the F_1 generation is utilized and both non-additive and additive genetic effects are of basic importance.

Heterosis is due primarily to the non-additive form of gene action. In this study heterosis values were high for grain yield and zero or slightly negative for plant height. This confirms other reports that non-additive gene action is more involved in the expression of grain yield than in plant height. Heterosis and heterobeltiosis values for grain yield differed among crosses, with progeny from unrelated parents, such as Pullman Selection 101 x Moro; Moro x Brevor and Moro x Corvallis Selection 55-1744, showing the highest values.

Those from related parents, such as Pullman Selection 101 x Brevor; Pullman Selection 101 x Corvallis Selection 55-1744 and Brevor x Corvallis Selection 55-1744, had lower values. This is in keeping with the generally held concept that the expression of hybrid vigor or heterosis is associated with the diversity of the parents as found by McNeal _et al._ (1965), Moll _et al._ (1969) and Watson (1970). It consequently confirms the importance of non-additive genetic effects in controlling the expression of grain yield and suggests that a problem could be encountered with certain crosses when making early generation selections for yield using conventional methods.

Evaluation of the relative amount of non-additive gene action controlling a specific trait can also be calculated by the resulting inbreeding depression following selfing. This enables the breeder to know how fast the masking heterotic effects are lost and how soon genetic stabilization is realized in the populations. In this investigation crosses with the highest heterosis values for grain yield showed the highest inbreeding depression values from F_1 to F_2 generation. Also, locations with high heterotic effects showed high inbreeding depression values. Inbreeding depressions for grain yield from F_2 to F_3, F_3 to F_4 and F_4 to F_5 decreased bringing about genetic stabilization by the F_3 generation. Inbreeding depression values were calculated for plant height and were negligible from F_1 to F_2. However, from F_2 to F_3 and from F_3 to F_4 the values were negative indicating an increase of plant height from one generation to another in the bulk populations. This increase in plant height took place after genetic stabilization and is therefore mainly controlled by additive gene action. It is due to the apparent natural selective advantage of the tall plants.

Narrow-sense heritability estimates for both traits were in agreement with those obtained by McNeal (1960), Kronstad and Foote (1964) and Anwar and Chowdhry (1969). High narrow-sense heritability values were found for plant height at all locations indicating that additive gene action is predominate in the expression of plant height. Low narrow-sense heritability estimates were found for grain yield again confirming that the additive gene action contribution to the expression of this trait is small as compared to that of plant height.

Earlier reports on General and Specific Combining Ability effects indicated that General Combining Ability effects or additive gene action effects are usually significant for both traits used in this study (Kronstad and Foote, (1964); Brown et al. (1966); and Guyawali et al. (1968). Results of the current study substantiated earlier findings for plant height where General Combining Ability effects were highly significant for almost all generations at the three locations. This indicates again that additive gene action constitutes a major portion of the genetic variation in plant height. However, results of Combining Ability analyses for grain yield were in agreement with earlier findings at only one location (North Willamette). At Malheur and Pendleton no significant General Combining Ability effects were detected even though estimated mean squares indicated that a noticeable portion of the total genetic variation in the populations was due to additive genetic effects.

All estimates obtained concerning the nature of the gene action were greatly influenced by the different environments. Most investigators evaluating early generation testing have conducted their experiments under a single environment and therefore were not able to measure possible genotype x environment interactions. Their varying results have led to much of the controversy concerning the validity of this type of testing. This study differs from the previous investigations in that it was conducted under three different environments. This permitted a better understanding of the genotype x environment interactions to be obtained in order to provide more valid predictions.

The mean yields and heights of all entries substantiated that the three environments did have a marked influence on the expression of both traits. The highest grain yield was obtained at the Malheur site followed by North Willamette and Pendleton, while the greatest expression of plant height was found in North Willamette followed by Pendleton and Malheur. These differences in the expression of grain yield and plant height at the three locations appear to be related to differences in environmental factors such as temperature, moisture and possibly light intensity. The average temperatures from April through August were higher at Malheur, intermediate at Pendleton and lower at North Willamette, (Appendix Table 2). It would appear that lower temperatures at North Willamette location resulted in slower development of the plants resulting in greater vegetative growth and consequently taller plants. By the same token intermediate temperatures at Pendleton resulted in intermediate plant heights compared to North Willamette and Malheur. Differences in moisture stress among the three locations resulted in corresponding differences in grain yield. Optimal moisture conditions at Malheur resulted in the highest yields. A slight moisture stress during early maturity resulted in yield reduction at North Willamette. A more severe moisture stress was realized at Pendleton and consequently an even greater reduction in grain yield was noted. Thus, genotype x environment interactions appear to be important and must be considered if an early generation testing program is to be successful. It is generally thought that the environment has a greater influence on the non-additive genetic effects. Results of this study agreed with such findings. The highest heterosis values for grain yield were found at the Malheur location where optimal conditions for development of the plants were provided. These large values at the Malheur site resulted from a favorable non-additive gene action x environment interaction. However, Peterson (1970) noted that the environment interacts with the additive form of gene action as well. Using General Combining Ability effects, Peterson found that in certain crosses the amount of additive gene action was expressed differently under different environments. The Combining Ability Analysis for grain yield in this study indicated that additive gene action made up a noticeable portion of the genetic variation in the populations at all locations. However, significant additive genetic effects were detected only at North Willamette and not at other locations. Peterson (1970) attributed such differences in the significance of additive genetic effects to the masking of their full expression by certain factors of the environment. It appears in the current study that the masking effects are also associated with the magnitude of the interaction of non-additive gene action with the environment. At the Malheur station, where a favorable non-additive gene action x environment interaction resulted in the highest heterosis expression, no significant additive gene action was detected. The reverse was true at North Willamette site. This reasoning is consistent for the Pendleton station even though heterotic effects were the lowest among the three locations. The water stress to which the populations were exposed in Pendleton did not permit full expression of either type of gene action controlling grain yield. Therefore the interaction of the non-additive gene action with the environment further misleads the breeder by masking the additive genetic effects.

From the previous considerations it appears that selection for grain yield must be practiced under the same environment where the potential varieties will be grown. Nevertheless the most effective site for early generation selections for grain yield is where additive genetic effects could be better expressed as in the North Willamette station. On the other hand sites where non-additive genetic effects have been inflated by their interaction with the environment, as in Malheur, would be good sites for conducting hybrid wheat program.

For plant height, where additive genetic effects are the most important, genotypes and phenotypes are well correlated. Effective early generation selections for this trait can take place at any one of the three environments. However, the largest differences in plant height were expressed at the North Willamette site which would provide the most effective location to select for plant height especially when semi-dwarf parents are involved.

Year to year variations have also contributed to misinterpretation of the value of early generation testing. The varying results from generations grown in different years resulted in the controversy of the earlier workers concerning the earliest generation in which meaningful selections should start. In this study all generations (F_1 through F_5) were grown in the same trial with the potential genotype x year interaction being estimated by going to different locations. This made this method a more valid evaluation of early generation testing. The results of this study agree with the preceding reports by Immer (1941) and Taylor (1951) who suggested that selection should start as early as the F_3 generation. These findings do not agree with the conclusions of Harlan et al. (1941), Harrington (1941) and Raeber and Weber (1953) who suggested to start early selections earlier or later than the F_3 generation. In the current study genetic stabilization for both traits was shown to be established in the F_3 generation. Also comparisons of the mean performances of the F_1 through F_5 generations for each trait showed (1) no significant differences among the F_2, F_3, F_4 and F_5 means for plant height in different crosses and at the three locations. This suggested that selections for plant height may start as early as the F_2 generation without loss of valuable germplasm. (2) For grain yield, even though no significant differences were detected among F_2, F_3, F_4 and F_5 generations in certain crosses at North Willamette, the more general result is that differences among F_3, F_4 and F_5 generations were not detected for most of the crosses at the three locations. Thus, it appears that selection for grain yield can be started as early as the F_3 generation.

The success of early generation selection also depends on the knowledge of the contribution of each parent to the resulting progeny. This information would indicate which crosses will produce the highest percentage of high yielding segregates, thereby allowing the breeder to make more selections in these superior populations. The specific contribution of each parent to their respective crosses was estimated using Average Combining Ability as an indirect measurement of the General Combining Ability effects. The validity of this technique in determining the contributions of each parent was supported by the results obtained for plant height. As expected, Moro, the tallest parent, was found to be the best combiner for increased plant height, while the semi-dwarf selections, Pullman Selection 101 and Corvallis Selection 55-1744, were shown to be good combiners for shortness. Therefore this method may be used with a degree of confidence to evaluate parent contributions for a more complex trait such as grain yield. For this trait Pullman Selection 101 and Corvallis Selection 55-1744 were the best combiners for yield in this study since they made the highest contribution to progeny performance in most of the crosses at all locations. At Pendleton and Malheur, Pullman Selection 101 was classified first while Corvallis Selection 55-1744 ranked first at North Willamette. This difference may be related to the fact that Corvallis Selection 55-1744 flowers earlier than Pullman Selection 101 which could be an advantage at North Willamette where a moisture stress did occur during maturity. However, at Pendleton and Malheur Corvallis Selection 55-1744 was susceptible to shattering which resulted in reducing yield. At North Willamette temperatures were not as high and less shattering occurred. Pullman Selection 101 performed well under the three environments and may be considered a widely adapted parent. This is supported by the fact that Pullman Selection 101 has been extensively used by many conventional breeding programs throughout the world and is known through experience to be a good combining parent. Corvallis Selection 55-1744 is also a good combining parent for grain yield as noted from the results of Kronstad (1963), but it is not as widely adapted as Pullman Selection 101. The good combining ability of these two selections is widely recognized, but it took many years before breeders capitalized on this fact. If studies such as this investigation had been conducted earlier, breeders could have made more extensive use of these parents in their crosses and more efficient and rapid progress could have been made for grain yield.

These two parents, Pullman Selection 101 and Corvallis Selection 55-1744 would also be valuable to include in a hybrid program; however best results are obtained when they are crossed with an unrelated parent such as Moro.

In conclusion, the following recommendations can be made for the success of early generation selections: (1) Selections for plant height or other traits involving mainly additive gene action may be started as early as the F_2 generation, particularly under optimum environment; (2) Effectiveness of early generation selection for a more complex trait such as grain yield is made difficult by the non-additive genetic effects, particularly in certain crosses, and their interaction with the environment. Therefore genetic stabilization must be obtained before effective selection can be practiced. The results of this study suggest that selection for grain yield could have been practiced as early as the F_3 generation. (3) The contributions of the parents is a primary factor influencing the effectiveness of early generation selection in any trait. This study substantiated that Pullman Selection 101 and Corvallis Selection 55-1744 are good combiners for high yielding ability and that Pullman Selection 101 is more widely adapted than Corvallis Selection 55-1744. This last factor is important to the breeder not only because it permits identification of parents for crossing but also because it allows the breeder to concentrate his efforts within the best segregating progenies in early generations.

SUMMARY AND CONCLUSIONS

The objectives of this study were (1) to gain information about those factors which might influence the effectiveness of early generation testing within bulk populations (2) to determine the specific contributions of each parent within the crosses and consequently identify those parents which are most likely to be good combiners for further crosses, and (3) to identify which crosses will give the highest yielding segregates in order to make more selections in those populations.

Data were obtained from the parents, the F_1 generation, and from F_2 through F_5 bulk populations resulting from a four-parent diallel cross. These experimental populations were grown in 1970 at the Malheur Experiment Station, Pendleton Experiment Station and North Willamette Experiment Station in Oregon.

Grain yield and plant height were measured with differences among and within crosses being determined by analysis of variance. In determining the effectiveness of early generation testing the predominate type of gene action controlling the expression of the two traits was evaluated using (1) heterosis and inbreeding depression calculations as formulated by Matzinger _et_ _al_. (1962) (2) narrow-sense heritability estimates using regression of the F_2 on the F_1 and (3) Combining Ability analysis as outlined by Griffing (1956). Comparisons of the grain yield and plant height means of different generations using the least significant difference (LSD) at the five percent level served to detect the establishment of genetic stabilization in the populations. Average Combining Ability estimates were used as an indirect method for estimating the contributions of each parent in the performance of the crosses where they were involved.

From the results of this study the following conclusions can be stated:

(1) The expression of plant height is predominately controlled by additive gene action making early generation selection for this trait effective at the three locations.

(2) Selection for plant height may start as early as the F_2 generation at all locations. However, in a program involving semi-dwarf lines, environments where a full expression of plant height is obtained would be most effective for selection.

(3) The expression of grain yield is predominately controlled by non-additive gene action which can mislead the breeder by masking the additive genetic effects.

(4) These masking effects may be enlarged by the non-additive gene action x environment interaction under favorable environmental conditions.

(5) Environments where the non-additive gene action x environment interactions are minimum and favor the expression of the

additive portion of gene action are good sites for effective early generation selection. The opposite is true for good sites for a hybrid wheat program.

(6) Due to genotype x environment interactions, selection for grain yield should be practiced under the same environment where the potential varieties are to be grown.

(7) Effectiveness of early generation selection for grain yield depends upon the establishment of the genetic stabilization. In this study, genetic stabilization was achieved in the F_3 generation for grain yield.

(8) Average Combining Ability method for estimating the contribution of parents in the performances of the crosses where they were involved is a valid technique since it substantiated expected results for plant height. Therefore it may be used with some degree of confidence for more complex traits such as grain yield.

(9) For grain yield Pullman Selection 101 and Corvallis Selection 55-1744 were confirmed to be very good combiners for crosses in a conventional breeding program. They may also be used in crosses with Moro for a hybrid wheat program.

(10) Pullman Selection 101 is more widely adapted than Corvallis Selection 55-1744 since it has performed well under the three different environments of this study.

(11) Crosses involving Pullman Selection 101 or Corvallis

Selection 55-1744, such as Pullman Selection 101 x Brevor; Pullman Selection 101 x Corvallis Selection 55-1744 and Brevor x Corvallis Selection 55-1744, were identified as the best crosses for high yielding segregates and early selections should be concentrated in these crosses.

(12) This method has, then, provided a fast technique to evaluate parental contributions and may help in identifying the good combiners soon enough to realize better progress in breeding for grain yield.

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APPENDIX

APPENDIX I

Pedigrees and Description of the Four Parental Lines

1. Pullman Selection 101 (C. I. 13438) is a selection from the cross of C. I. 12697 with Norin 10 x Brevor. Developed at Washington State University, it is a high yielding semi-dwarf awned winter wheat.

2. Moro is a variety developed at the Pendleton Experiment Station in Oregon from the cross P. I. 178383 x Omar^2. It has brown chaff and is a white club winter wheat recommended for the 250-400 millimeter rainfall areas where shallow soils are a problem. The variety is tall with weak straw and tends to lodge in high rainfall areas particularly under heavy nitrogen fertilization.

3. Brevor was a selection made at Washington State University from the cross between (Turkey x Florence) and (Fortyfold-Federation). It is a white chaffed, soft white winter wheat. The variety is of standard height, stiff and highly resistant to lodging straw.

4. Corvallis Selection 55-1744 was selected from a cross between Norin 10 and Staring. It is a high yielding semi-dwarf soft red winter wheat developed at Oregon State University. It is susceptible to shattering under high temperatures coupled with moisture stresses.

Appendix Table 1. Precipitation data from Pendleton and North Willamette Experiment Station. *

Months		Pendleton	North Willamette
September	1970	25.9 mms	34.0 mms
October	"	35.6	88.6
November	"	56.4	200.9
December	"	25.9	205.7
January	1971	36.6	422.7
February	"	19.6	97.5
March	"	32.5	143.3
April	"	41.9	94.2
May	"	42.2	52.6
June	"	79.8	66.5
July	"	16.0	2.0
August	"	8.4	44.2
Total		420.8	1452.2

* From climatological records at each location

Appendix Table 2. Average temperature from the three locations during the growing season.*

Months		North Willamette	Pendleton	Malheur
October	1970	15.7° C	8.6° C	8.6° C
November	"	12.5	5.0	4.9
December	"	4.6	2.0	-1.2
January	1971	3.9	3.3	0.0
February	"	5.0	4.2	2.9
March	"	5.7	4.4	4.5
April	"	8.6	8.2	10.6
May	"	12.5	13.5	16.4
June	"	13.9	14.6	18.5
July	"	19.1	21.0	24.6
August	"	20.2	23.1	25.5

* From climatological records of the weather service at O.S.U.