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THE EFFECT	IVENESS OF EAP	RLY GENERATION SELECTION
IN A DIALLE	L CROSS INVOLV	ING FOUR WINTER WHEAT
CULTIVARS	TRITICUM AEST	IVUM, VILL., HOST)
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Factors which influence the effectiveness of early generation selection were investigated in a diallel cross involving four agronomically and genetically diverse winter wheat cultivars. Experimental material consisted of (1) parental lines, F_1 and F_2 through F_6 bulk populations grown under solid-seeded conditions and (2) randomly selected F_3 and F_6 populations grown along with parents and F_1 's under space-planted conditions. Information concerning plant height, grain yield, tiller number, 1000 kernel weight, spikelet and kernels number per spike was obtained from solid-seeded experiments. Similar information for the same traits except for spikelet number were also measured under space-planted conditions. These experiments were conducted at three diverse environmental sites.

Estimates of gene action were determined by calculating heterosis, heterobeltiosis, inbreeding depression and narrow-sense heritability and by analyzing for combining ability. The relative contribution of each parent with regard to general combining ability effects was also determined. Under solid-seeded and space-planted conditions, both additive and non-additive genetic effects were involved in the expression of all the traits. Their relative magnitude was different depending on the trait. Plant height, kernel weight, spikelet number and kernel number per spike were largely influenced by additive gene action. Selection for those traits could be made effectively as early as the F₂ generation. In contrast, grain yield and tiller number were significantly influenced by non-additive gene action in the F_1 and F_2 generation; however in the F₃ generation, additive genetic effects prevailed. Identification of high yielding segregates and effective selection for these traits could be practiced in the F₃ generation.

The environment influenced both additive and non-additive genetic effects at the three sites under solid and space-planted conditions. Favorable growing conditions enhanced the expression of non-additive gene action for grain yield and tiller number. However, under dryland conditions, non-additive genetic effects were not fully expressed for grain yield, whereas additive gene action was not as susceptible to moisture stresses. For plant height, kernel weight, spikelet number and kernel number per spike, selection in the F_2 generation must be practiced under an environment where there is full expression of the trait. Selection for grain yield and tillering capacity must, however, be conducted under the same environments where the potential varieties will be grown. When genotype x environmental interactions were tested involving two years data from solid-seeded experiments, spikelet number commonly referred to as head size, was the least sensitive to location and year to year variations. In addition, head size was mainly controlled by additive genetic effects; therefore, selection for yield through this component may start in the F_2 generation.

Parental contribution to the performance of the resulting progeny in terms of general combining ability was considered for grain yield and for the compnents of yield. Because of its good tillering capacity Sel 101 contributed the largest to grain yield under solid-seeded conditions, whereas Moro, a club wheat with high kernel number per head, contributed the greatest under space-planted conditions. Lesscompetitive conditions enhanced tillering capacity for all parental lines and the later developing components of yield became more influential in terms of grain yield. Space-planting of F_2 populations under adequate soil moisture and fertility would permit to raise the genetic potential of yield components related to head size and fertility

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in a general effort to increase yielding ability. However, selection practiced under space-planted conditions may result in the loss of the most competitive genotypes and the discarding of segregating lines which may become superior in commercial production.

To make the most efficient progress in breeding for grain yield, the following procedure would appear the most productive. Selection based primarily on head size and fertility may start in the F_2 generation under space-planted conditions with adequate soil moisture and fertility. The selected space-planted F_2 material should be solidseeded in the F_3 generation with selection for tillering capacity and grain yield <u>per se</u> initiated. Genetic and Environmental Factors Influencing the Effectiveness of Early Generation Selection in a Diallel Cross Involving Four Winter Wheat Cultivars (Triticum aestivum Vill., Host) by

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GENETIC AND ENVIRONMENTAL FACTORS INFLUENCING THE EFFECTIVENESS OF EARLY GENERATION SELECTION IN A DIALLEL CROSS INVOLVING FOUR WINTER WHEAT CULTIVARS (TRITICUM AESTIVUM VILL., HOST)

INTRODUCTION

The main objective of most plant breeding programs is to increase the yielding capacity of a given crop. Two approaches have been utilized to realize that goal in wheat improvement: (1) breeding for specific traits affecting grain yield such as disease or lodging resistance and (2) breeding for grain yield <u>per se</u>. The latter approach has not always been successful for a number of reasons. First, grain yield is a complex quantitatively inherited trait and is greatly influenced by the environment. Secondly, it has been suggested that yield plateaus are now being realized and further increases in yield will be difficult to obtain. Finally, the current methods employed to breed for grain yield <u>per se</u> have not been entirely efficient, and where they have been successful, they have required very large programs.

A wide range of genetic variability must be utilized if successful combinations are to be created to raise the yielding capacity in wheat. To obtain the necessary genetic variability, the breeder must work with a large number of crosses and large population sizes. This is frequently difficult to realize because of the restrictions imposed on resources, i. e., money, time and space available to the breeder. It would be very desirable if a plant breeder could identify the most promising parental combinations and in early generations select only the most valuable segregating progeny. If this latter alternative 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.

The effectiveness of early generation selection has been evaluated by many investigators. The type of gene action involved in the expression of a given trait has been considered as the main factor affecting the effectiveness of early generation selection. Agreement has been reached that effective early generation selection can be made for qualitatively inherited traits; however, for quantitatively inherited traits, particularly grain yield, a controversy has resulted as to if and when selection should be practiced. The controversy has resulted primarily from lack of consideration of environmental influence and the year to year variations. The majority of studies which have refuted the effectiveness of early generation selection for grain yield have been conducted under a single environment.

Recent studies have considered the strategy of early generation selection for grain yield in terms of yield components as a new approach for improving effectiveness of early generation selection. Such a strategy of selection is based on a knowledge of parental

contribution to the performance of the resulting progeny in terms of total grain yield and the different yield components. Because yield components are developed in a sequential pattern which is highly influenced by environmental resources, the management of early generation material becomes an important factor in the success of early generation selection. This study was conducted to determine if and when early generation selection can be practiced for plant height, grain yield and the grain yield components, i.e., tiller number, number of kernels per spike and kernel weight. Those factors investigated included: (1) the type of gene action involved in the control of each trait; (2) the genotype x environmental interactions; and (3) the parental contribution to performance of the resulting progeny. In considering the importance of management of early generation material in the effectiveness of selection, both solid-seeded and spaceplanted experiments were conducted at three locations representing three diverse environmental conditions.

II. LITERATURE REVIEW

Effectiveness of Early Generation Selection

In attempting to breed for high yielding cultivars, plant breeders face the necessity of handling a tremendous amount of genetic variability and an extensive base of germ plasm. They realize this by increasing the number of crosses among a wide range of potential parents and by enlarging the sizes of the segregating populations. These expansions usually exceed the capacity of most breeding programs and some other alternatives should be considered. The creation of elite genetic variability through effective early generation selection is certainly a valuable alternative. If effective selections could be practiced in early generations for grain yield, plant height, maturity and other agronomic traits, a great deal of time and effort could be directed toward testing only the most desirable genetic material. Also, when progeny performances are effectively evaluated in early generations, the plant breeder can readily identify those varieties or selections which are most likely to be good combiners in future crosses.

The effectiveness of early generation selection has been studied for many field crops, especially soybeans and cereal crops (Briggs and Knowles, 1967). In general, the main factor influencing the validity of early generation selection is the genetic nature of a trait

and its sensitivity to the surrounding environment (Elliot, 1959; Briggs and Knowles, 1967). Results on the effectiveness of early generation selection in breeding cereal crops differed when simply inherited traits were compared to complex traits, particularly grain yield (Immer, 1941, Taylor, 1951; Fowler and Heyne, 1955).

Investigations on the effectiveness of early generation selection for simply inherited traits in cereal crops have shown that selection can be practiced as early as the F_2 or F_3 generation after hybridization (Taylor, 1951; Frey, 1954; Fowler and Heyne, 1955; Escuro, Sentz and Myers, 1963; Allard and Harding, 1963; Rasmusson and Glass, 1965, 1967; Briggle, Yamazaki and Hanson, 1968; Daaloul, 1972; Solen, 1973; Alcala, 1973).

Taylor (1951) suggested that effective early generation selection could be practiced after measuring changes in gene frequencies for a series of simply inherited morphological traits. He used F_2 and F_5 populations from 20 barley crosses grown at four locations. Similar conclusions were reported when two barley crosses were utilized to test the validity of predictions for plant height and heading date based on F_2 -derived line performances (Frey, 1954). Using a 10-parent diallel cross in hard red winter wheat, a comparison between selections from the F_2 and F_3 generations and the F_5 generation with respect to plant height, maturity and test weight was studied (Fowler and Heyne, 1955). For those traits under study early generation selection was reliable.

Escuro, Sentz and Myers (1963), in a four-parent diallel cross in oats, compared the relative effectiveness of selection in the F_2 generation for heading date, plant height and kernel weight. By evaluating the relative amounts of additive gene action involved in each of the traits, selection in the F_2 generation was more effective for kernel weight than for plant height and heading date.

The existence of minor modifying genes in the genetic background of a simply inherited trait reducted the effectiveness of selection made in the F_2 generation (Allard and Harding, 1963). By working on the effectiveness of predicting the heading date from F_2 and F_3 generations in one cross of winter wheat, Allard and Harding discovered the existence of minor genes along with a major single gene. Minor genes, which are masked in early generations, may show up in later generations reducing the validity of predictions made in the F_2 and F_3 generations.

Selection for certain quality characteristics in the F_3 generation was shown to be very effective in barley (Rasmusson and Glass, 1965). The quality traits studied were the diastatic power, the plumpness of kernels, the amount of extract and the content of protein. Narrow-sense heritability estimates based on regression of F_4 on F_3 generations means were used to compare the relative effectiveness of F_3 selection for those traits. Similarly, regressions of F_4 , F_5 , F_6 , and F_7 on F_3 generations means in another study of barley indicated that F_3 selections were effective for kernel weight, heading date and plant height (Rasmusson and Glass, 1967). Studies were also made on the effectiveness of F_2 selection for quality characteristics in wheat (Briggle, Yamazaki, and Hanson, 1968). F_2 selection was shown to be highly successful for pearling index and flour yield.

Recent positive evidences for effectiveness of F_2 selection for qualitatively inherited traits in winter wheat have been reported (Daaloul, 1972; Alcala, 1973; Solen, 1973). By estimating the amount of gene action involved in the expression of plant height in crosses involving winter wheat cultivars, estimates of additive gene action were observed to be high and predominant and hence, F_2 selection for this trait could be very effective (Daaloul, 1972; Alcala, 1973). Similar results were obtained for plant height by studying heritability estimates and associations as a measure of additive genetic effects in four winter wheat crosses (Solen, 1973).

In contrast to the general agreement on the effectiveness of F_2 and F_3 selections for simply inherited traits, controversy exists on the value of early generation selection for complex traits, particularly grain yield. Atkins and Murphey (1949) worked with 10 crosses of oat and tested the F_2 through F_8 generations as bulk populations in yield trials. Because there were no significant associations between early

generation performances and their corresponding later generations, high yielding germ plasm may be lost if early generation selections were practiced. Comparisons between selections made in the F_5 generation and early yield trials in a diallel cross involving 10 hard red winter wheats, indicated lack of reliability in early generation performance for grain yield (Fowler and Heyne, 1955). The masking heterotic effects from F_1 through F_4 generations were considered the main reason for the lack of reliability of F_2 , F_3 , or F_4 generations resulting from several intercrosses among potential wheat parents and grown as bulk populations. Similar conclusions were drawn by Escuro, Sentz, and Myers (1963) when studying a fourparent diallel cross of oats and using the F_1 and F_2 generation grain yield performances. To test the effectiveness of early generation selection for grain yield, three hard red spring wheat crosses were used (Busch, Lucken, and Frohberg, 1971). The parents, F_1 through F_4 generations and back crosses were studied. Additive gene action, dominance and epistatic genetic effects involved in the expression of grain yield were determined by the Hayman technique (1958) and were found significant in all three crosses. Dominance and dominance x dominance epistasis were predominant in two crosses whereas additive x additive epistasis was more involved in the other cross. Because of these epistatic effects, neither F_2 nor F_3 selection could

be effective but F_4 selection may be useful at the crosses where additive x additive epistasis was predominant.

All previously mentioned studies refuted the effectiveness of early generation selection for grain yield; however, many other investigations concluded otherwise. Among these investigations, good agreement has been lacking as to what is considered an early generation. Suggestions ranged from F_1 to the F_4 generations (Harlan, Martini, and Stevens, 1940; Frey, 1954; Charoenwatana, 1970). Yield of the \mathbf{F}_1 generation in barley was considered a means of identifying crosses from which high yielding segregates would be expected (Harlan, Martini and Stevens, 1940). Consequently, progeny could be selected on the basis of their F_1 performance. However, Briggs and Knowles (1967) explained that F_1 performance cannot be relied on for selection for two reasons: (1) heterotic effects in the F_1 generation may be misleading as to the true performance for grain yield of the cross, and (2) F_1 seeds are usually scarce and will not allow effective evaluations.

Evidences for reliable prediction of grain yield performance from F_2 generations in wheat and barley have been reported (Harrington, 1940; Harlan, Martini, and Stevens, 1940; Immer, 1941). Replicated bulk F_2 tests showed good indications of the yielding potentialities of wheat crosses (Harrington, 1940). Similar results were found on barley crosses by Harlan, Martini, and Stevens (1940).

Immer (1941), studying six barley crosses, reported that crosses producing high yielding segregates in F_2 and F_3 generations were among the highest yielding in the F_4 generation. Therefore, the discarding of low yielding segregates in F_2 and F_3 generations could be done effectively and without loss of valuable germ plasm.

Later investigations indicated, however, that effective selection for grain yield could be practiced only when started in the F_3 or F_4 generations (Frey, 1954; Rasmusson and Glass, 1967; McKenzie and Lambert, 1961; Smith and Lambert, 1968). According to Frey (1954), in contrast to simply inherited traits, complex traits, particularly grain yield, were the least accurately predicted in the F_2 generation. However, a certain level of accuracy was obtained for grain yield in the F_4 generation. Frey's suggestions were based on estimates of narrow-sense heritability by regression of F_5 and later generations on F_4 generation mean performance involving two barley crosses. Similar results were obtained in winter wheat populations having levels of genetic diversity (Charoenwatana, 1970).

Other investigators have concluded that selection for yield would be effective as early as the F_3 generation (Rasmusson and Glass, 1967; Smith and Lambert, 1968; McKenzie and Lambert, 1961; Jordaan and Laubscher, 1968; Daaloul, 1972). By measuring associations between F_3 and F_6 generation performances for grain yield in two barley crosses, significant associations were found and hence selections among and within F_3 families may be useful (McKenzie and Lambert, 1961). Rasmusson and Glass (1967) used two F_3 - derived populations of barley and multiplied them till the F_7 generation. Narrow-sense heritability estimates were calculated by standardized regression using F_5 on F_3 , F_6 on F_3 and F_7 on F_3 means. Estimates of heritability ranged from 31 to 33% and all were significant indicating that F_3 selections for grain yield were effective. F_3 generation performances gave good predictive values for the potentiality of different crosses in barley with respect to yield and kernel weight (Smith and Lambert, 1968). This latter conclusion was based on a study involving F_2 and F_3 generations grown as bulk populations from a 10-parent diallel cross of barley.

A recent extensive experiment using an 11-parent diallel cross was conducted by Jordaan and Laubscher (1968) to study the effectiveness of early generation selection in wheat. F_1 through F_5 generations were grown as bulk populations at three distinctive locations. By conducting an analysis of combining ability as outlined by Griffing (1956), there were significant general combining ability (G. C. A.) effects and specific combining ability (S. C. A.) effects for all generations in all locations. General combining ability variance to S. C. A. variance ratios in each generation indicated a decline in the S. C. A. effects after the F_3 generation. The remaining S. C. A.

between additive genetic effects. Finally significant S.C.A. effects x location interactions were observed in F_1 and F_2 generations and created a masking effect on G.C.A. effects in those generations. Therefore, selection for grain yield may start as early as the F_3 generation. A similar conclusion was made with a four-parent diallel cross of winter wheat grown at three locations (Daaloul, 1972). F₁ through F_5 generations derived from this diallel were used as bulk populations. The relative amounts of additive and non-additive gene action involved in the expression of grain yield were measured by narrow-sense heritability estimates and heterosis, respectively. Non-additive gene action was found to be predominant. In addition, combining ability analysis calculated for different generations at all locations indicated that there was a significant non-additive x location interaction which had a masking effect on the expression of additive gene action. By calculating inbreeding depression values for grain yield in F_2 , F_3 , F_4 and F_5 generations, the populations attained genetic stabilization in the F_3 generation.

Other studies conducted by McGinnis and Shebeski (1968), Briggs and Shebeski (1970) and Alcala (1973) were in agreement that the F_3 generation is the earliest time to start selection for grain yield <u>per se</u> in wheat; however, a certain selection pressure may be imposed on certain yield components in the F_2 generation. The choice of which yield component to select for the F_2 generation is important and may be decided by knowing the specific contributions of potential parents for each component of yield (Thomas and Grafius, 1971). Visual selection for tillering capacity in the F_2 generation, followed by selection for yield <u>per se</u> in the F_3 generation was suggested as the best procedure in certain populations of spring wheat (McGinnis and Shebeski, 1968; Briggs and Shebeski, 1970). Using two populations of winter wheat, Alcala (1973) reported that non-additive gene action was involved in grain yield <u>per se</u> and selection should be delayed until at least the F_3 generation. However, he suggested that F_2 single plant selections for large head size as a component of yield followed by F_3 selection for tillering capacity and yield <u>per se</u> would be advantageous in selecting for yield in early generations.

In evaluating the effectiveness of early generation selection, the main factor to be considered is the type of gene action involved in the expression of the trait under selection. However, because of the contradictory reports encountered in many investigations other possible causes may influence the effectiveness of early generation selection, i.e., genotype x environment interaction, the nature of the germ plasm utilized, experimental procedure and interpretation of results.

In general, most of the research against the effectiveness of early generation selection was conducted under a single environment; also, lack of correlations between early and later generations could be attributed to year to year variation (Mahmud and Kramer, 1951; Fowler and Heyne, 1955). Therefore, genotype x year interaction should be investigated. This is substantiated by results obtained by Jordaan and Laubscher (1969) and Daaloul (1972). In both studies genotype x environment interactions were important, particularly non-additive genetic effects x location interactions.

Narrowness of germ plasm used in the various studies may have influenced results and hence caused disagreement (Fowler and Heyne, 1955; Busch, Lucken, and Frohberg, 1971). Poor experimental procedure and misinterpretations of results were also considered as reasons for lack of agreement among different investigators concerning early generation selection (Fowler and Heyne, 1955; Rasmusson and Glass, 1967).

Finally, effective selection may start earlier than the F_3 generation when selection pressure is imposed upon a specific yield component such as tillers per plant (McGinnis and Shebeski, 1968; Briggs and Shebeski, 1970) or kernels per head (Alcala, 1973). Therefore, the third factor to be considered in evaluating the effectiveness of early generation selection is the combination of yield components contributed from potential parents as well as the specific contribution of these parents into the crosses where they are involved.

Genotype X Environment Interactions

Genotype x environment interactions are of major importance in early generation selection. Selection in early generations is based on phenotypic expression of the trait which is the product of an interaction between the genotype and the environment. In developing new well-adapted cultivars, the breeder faces two alternatives. He can develop varieties which are either adapted to a wide range of environments or provided with a high degree of immediate fitness to a specific environment (Frankel, 1958). A basic knowledge of genotype x environment interactions is necessary when pursuing both alternatives. If the plant breeder chooses the first alternative he must obtain fundamental information on adaptation and yield of different cultivars under a wide range of soil, climatological and biological conditions (Salmon, 1951; Reitz and Salmon, 1959). If he chooses the second alternative of breeding; i. e., fitness to a specific environment, genotype x environment interactions are still of considerable importance (Finlay and Wilkinson, 1963). Because of the marked fluctuations of climatic conditions from year to year, varieties that are bred for specific areas must possess a high degree of broad adaptability. To develop the most appropriate plant breeding scheme for evaluation of genotypes according to their response to environments, most cultivated crops have been studied in relation to genotype x environment interactions (Abou-El-Fittouh, 1969; Baker, 1968; Stroike and Johnson, 1972).

Allard and Bradshaw (1964) presented a detailed review of the implications of genotype x environment interactions in applied plant breeding. In their review, environmental variations were classified into two types: predictable and unpredictable. The first includes genotype x location interactions, while the latter contains genotype x year interactions. Comstock and Moll (1961) considered three types of genotype x environment interactions: genotype x location interaction, genotype x year interaction, and genotype x year x location interaction. In addition, a model was developed by which variances for these different interactions could be partitioned from analysis of variance tables.

Estimates of genotype x environment interactions using the Comstock and Moll model were reported by many researchers. Variety x environment interactions were calculated from yield trials of wheat, barley and oats (Liang, Heyne, and Walter, 1966). Variety x year interactions were small and non-significant, whereas variety x location and variety x year x location interactions were highly significant and of a considerable magnitude. When locations were grouped in sub-areas, there was a considerable reduction in the interactions with locations. The implications of the genotype x environment

interaction on the conduction of early generation selection in barley were evaluated from genotype x location interactions for two populations in the F_3 through F_7 generations (Rasmusson and Glass, 1967). Small but significant variances for genotype x location interactions were reported, but the variances associated with error components were very large. The reduction of the variance associated with genotype means was due to the variation within locations and not among locations and this variation could be corrected by increasing the number of replications within locations. Early generation testing, therefore, over a wide range of environments would not be of great value when the cost of adding locations was considered. Finlay (1968) argues against this last conclusion and showed that the success of testing and selecting early generation material under a wide range of environments was striking in the development of the semi-dwarf Mexican spring wheat varieties. To show the influence of genotype x environment interactions on the effectiveness of early generation selection, Jordaan and Laubscher (1968) extended the Comstock and Moll technique to combining ability analysis. The genotype x environment interaction was partitioned into G. C. A. x location interactions and S.C.A. x location interactions. Both G.C.A. and S.C.A. x location interactions were highly significant with the predominance of S. C. A. x location interaction.

Even though the variance technique in estimating genotype x environment interaction was used extensively, it has failed to measure the stability of a given cultivar over different environments for a given year. An attempt to estimate stability of a cultivar from genotype x environment interaction variances was made in a study of cereals in western Canada (Baker, 1968). The ratio of the genotype x location interaction variance to the variance associated with experimental error was considered a measure of stability of cultivars in certain geographic areas. In another study on wheat Baker (1969) concluded that stability of a given cultivar was proportional to the genotype x location variance. Analysis of variance by matrix is another approach by which the contribution of each cultivar to the various types of interactions can be calculated (Kaltsikes, 1971). The cultivar that has the lowest contribution to genotype x location variance was considered the most stable one and vice-versa.

A new technique based on linear regression was developed to measure variety adaptation and adaptability (Finlay and Wilkinson, 1963). The mean yield of an individual variety was regressed on the mean yield of all cultivars for each location and within each season. Average phenotypic stability was indicated by a regression coefficient of unity. A regression coefficient smaller than one was an indication that the cultivar in question had above average stability and viceversa. An ideal cultivar was described as possessing genetic potential

in the highest yielding environments with a maximum stability. The same procedure was followed by St. Pierre, Klinck, and Gauthier (1967) in studying early generation selection under different environments and its influence on adaptability of barley. Selections from the F_2 through F_5 generations were made from a segregating population under two distinctive locations. In each generation seed from the selected plants was divided into two parts and planted at two locations. This yearly exchange of material provided sixteen different selection pathways. The adaptability of the selected strains was estimated from yield trials conducted in the F_7 and F_8 generations at two locations. The widest adaptability was obtained in strains which were selected at alternate locations in successive years.

Finlay (1970) conducted a study involving a series of simple crosses between barley varieties with either similar or different adaptation type responses to a range of environments. Transgressive segregation was demonstrated for adaptability especially in crosses involving similarly adapted but genetically different parents. Also, high yielding segregates were obtained from crosses between a high yielding, widely adapted variety and one specifically adapted to a high yielding environment. Finally, research to discover morphological characters which are indicators of good adaptability was urged because adaptability is an inherited characteristic (Finlay, 1970; Syme, 1970, 1972).
To measure stability, a modification of Finlay and Wilkinson's model was proposed by Eberhart and Russell (1966). The means of each cultivar in different environments were regressed on the environmental indices instead of on the environmental means for all cultivars. The environmental index is primarily the deviation of each environmental mean from the grand mean over all environments. Two parameters were proposed to measure stability: the regression coefficient and the square deviation of each variety from the regression line; e.g. the deviation mean square value (Eberhart and Russell, 1966). A stable variety would have the smallest possible deviation mean square; hence, this second parameter of stability has become also a measure of predictability. In a study using a 10×10 diallel of single and double cross maize hybrids, Eberhart and Russell (1969) reported that the deviation mean square was a more important stability parameter because it reflected changes in varieties resulting from specific changes in environment. Therefore, the mean square of deviations from regression line has been called a measure of specific genotype x environment interaction (Joppa, Lebsock, and Busch, 1971; Eberhart and Russell, 1969). The use of these parameters could materially assist plant breeders in making decisions regarding selection of potential parents for crosses and also in evaluating these crosses in early generations for high yielding segregates with wide adaptability.

In examining, on a theoretical basis, Finlay and Wilkinson's model and Eberhart and Russell's model, Hardwick and Wood (1972) showed that these two models suffered a bias. In their application, environmental means or environmental indices were assumed to be measured without error which is not always true. This bias may be reduced, however, by increasing the number of genotypes. Hardwick and Wool (1972) have also proposed a new model in which varietal means are regressed on the environmental variables. Multiple regression and simulation techniques are used because most of the environmental variables are neither well defined nor well measured. The main restriction to this latter model is the lack of simplicity for use in practical breeding programs.

In conclusion, genotype x environment interactions are of great value in studying the effectiveness of early generation selection. The estimation of genotype x location, genotype x year, and genotype x year x location according to Comstock and Moll (1961) may assist the breeder in understanding the performances of the segregating progenies and, hence, in directing his program of selection. This was emphasized when the genotype x environment interaction was partitioned into C. C. A. x location and S. C. A. x location interactions (Jordaan and Laubscher, 1968). Finally, the testing of the parents for adaptability using either the Finlay and Wilkinson model (1963) or the Eberhart and Russell model (1966) is of great value in directing the

choice of potential parents and in determining the amount of selection pressure to be used in any cross.

Components of Yield

Successful selection is basic to all plant breeding programs. Its effectiveness in early generations is determined, to a large extent, by the nature of the gene action involved in the expression of a trait and its interactions with changing environments. The problem of effectiveness of early generation selection is more complex when the trait is a function of other traits (Grafius, 1956). Certain complex traits, in particular, grain yield, were observed to be composed of subsidiary characters usually called component traits (Grafius, 1956). An understanding of the components of grain yield, their variation and the inter-relationships among themselves as well as to yield <u>per se</u>, would clarify the variability encountered in the final product, grain yield. Consequently, this would contribute to the effectiveness of early generation selection.

The identification of the components of yield in cereals dates back to investigations conducted by Engledow and Wadham (1923); Frankel (1935) and Boyce, Copp, and Frankel (1947). These studies have pointed out that the average yield per plant may be represented as the product of number of tillers per plant, average number of grains per head, average weight of a single kernel, and the percent of

dry matter in the grain. No conclusions were made at that time on the practicality of yield components as experimental variables because they were extremely fluctuable and interrelated. Grafius (1956, 1964) proposed that yield is an artifact and that it is the end result of three components: number of ears (x), average number of kernels per ear (y), and the average kernel weight (z). These components x, y, and z were represented geometrically as the edges of a rectangular parallelipiped with a volume (xyz) representing the final yield (w). If yield is a product of these components, there is no way in which yield can be changed without changing one or more of the components (Grafius, 1964). Independent gene systems governing the different components have been demonstrated when correlations among yield components were found to tend toward zero under minimum interplant competition. In effect, x, y and z have been directly related to three stages of development of the plant: tillering, floral initiation and maturity, respectively. Similar results concerning independence among trait components were reported for leaf area in field beans which is also a complex trait composed of two components (Duarte and Adams, 1963). In addition, functional genes were primarily due to the components of leaf area and not to the complex trait itself. As a result, variability in the complex trait may be accounted for in terms of variation of the components. Duarte and Adams (1963), using bean crosses, demonstrated that the parents complemented mas

each other in components of leaf area, and that this complementation was combined with favorable dominance resulting in heterosis in excess of the better parent. Such heterosis resulting from multiplicative relationships among components is potentially fixable in true breeding genotypes (Adams and Duarte, 1961).

Many reports have evaluated the correlations of these yield components suggested by Grafius (1956). Components of yield were shown to be highly and positively correlated to yield in a study involving 10-parent diallel cross of winter wheat (Kronstad and Foote, 1964). Similar results were reported by Gandhi et al. (1964); Fonseca and Paterson (1968); Reddi, Heyne, and Liang (1969) and Knott and Talukdar (1971). Effects of yield components were partitioned by pathway coefficient analysis into direct and indirect effects (Kronstad and Foote, 1964; Fonseca and Paterson, 1968; Reddi, Heyne, and Liang, 1969). Yield components had, in general, high direct effects on yield; however, some components such as the number of tillers per plant and number of kernels per head also had an indirect effect on yield through the other components of yield. These indirect effects were substantiated by reports on negative yield components (Kronstad, 1963; Fonseca and Paterson, 1968; Reddi, Heyne, and Liang, 1969; Knott and Talukdar, 1971). Occurrence of negative correlations among yield components is in contrast with the hypothesis of genetic independence among yield components advanced by Grafius (1964) and

Duarte and Adams (1963). The biological origin and meaning of these negative correlations among yield components were investigated and discussed by Adams (1967), Rasmusson and Cannel (1970), Adams and Grafius (1971), Thomas, Grafius, and Hahn (1971), and Grafius and Thomas (1971). These correlations arose in response to the competitional forces operating on developmental rather than genetic correlations (Adams, 1967). This conclusion was made from a study on yield of field beans under different competitive conditions. Correlations were near zero under space-planted conditions and were negative under dense planting conditions due to inter-plant competition. Adams explained that the development of yield components in a sequential pattern varies in response to the input of metabolites that are limiting at critical stages in the sequence. This concept was referred to as the concept of sequential development of components. Based on this concept, a practical approach to early selection for genetic merit in grain yield was advanced by Adams (1967). Selections should be practiced under input conditions that favor the full expression of genes relevant to yield components. This concept of sequential development of components was argued by Rasmusson and Cannel (1970). They imposed selection on each of the three yield components in a population of barley. Both negative or positive responses in two of the components were observed. Because parental combinations of characters

were retained, these responses were attributed to a linkage of genes controlling the components. Rasmusson and Cannel concluded that effectiveness of selection for each component to increase yield per se will depend on the extent of compensatory effects in other components determined by both environment and genetic history of the populations. The same data of Rasmusson and Cannel were re-examined by Adams and Grafius (1971) and an alternative explanation was proposed. The existence of any linkage relationships among genes controlling individual components was denied. Instead, the negative associations among yield components were attributed to an oscillatory response of components caused by the sequential nature of component development and a limitation of environmental resources. A practical approach for breeding for higher yields was derived (Adams and Grafius, 1971). Increasing the flow of environmental resources throughout the period of needs by the components would allow the raising, through selection, of genetic ceilings which limit the capacity of a component under available resources. Convincing evidences for sequential effects among yield components were presented by Thomas, Grafius, and Hahn (1971) in a study using diallel analysis in wheat. Because components occur in sequence, resources used at one stage of development may not be available for later use. The component developed under the best available resources will be the most influential in the sequence. Under environmental stresses, however, the

genetic control of the last component to develop in the sequence would be replaced by indirect control of the most influential component. Grafius and Thomas (1971) substantiated these conclusions. Thirtysix experimental lines of oats from six crosses were grown in replicated trials at two locations and the components of yield were measured. The most influential component was the number of heads per plot followed by the number of kernels per head. Direct genetic control of kernel weight, the last component in the sequence, was very weak and was replaced by indirect effects of the two other components. However, in crosses between lines having the same tillering capacity, the most influential component became number of kernels per head. Therefore, depending on the environmental stress present, segregates in early generations follow a certain pattern in setting priorities for each component influence. This pattern is largely under genetic control resulting from parental combinations with regard to yield components. The increase in the flow of environmental resources throughout the developmental stages will allow the plant breeder to predict more accurately which yield component will be the most influential in early segregating populations.

In addition to the nature of the correlations among yield components, investigations on the type of genetic effects involved in the expression of each yield component were conducted. Diallel analysis following Griffing's model (1956) or Hayman's model (1958) and

heritability estimates were utilized. Reports using diallel analysis to estimate the type of gene action involved in the expression of yield components showed that additive gene action was controlling directly or indirectly the expressions of all yield components (Kronstad, 1963; Kronstad and Foote, 1964; Fonseca and Paterson, 1968; Chapman and McNeal, 1971; Lee and Kaltsikes, 1972; Sun, Shands, and Forsberg, 1972). Degrees of dominance were also detected in the expression of kernel weight (Chapman and McNeal, 1971; Lee and Kaltsikes, 1972; Sun, Shands, and Forsberg, 1972). Finally epistatic effects were reported to be involved in the expression of tiller number (Chapman and McNeal, 1971) and kernel weight (Sun, Shands, and Forsberg, 1972). There exists many contradictions when gene action is evaluated using narrow-sense heritability estimates. Heritability values for number of tillers per plant were found to be high (Gandhi et al., 1964; Fonseca and Paterson, 1968; Lee and Kaltsikes, 1972); however, other studies reported the opposite (Kronstad and Foote, 1964; Johnson et al., 1966; Reddi, Heyne, and Liang, 1959). The estimates of heritability for the number of kernels per head were reported high by most of the studies mentioned above except by Gandhi et al. (1964) who showed low heritability values for the number of kernels per head. Also, there is disagreement concerning heritability estimates for kernel weight. Kronstad and Foote (1964), Gandhi et al. (1964); Johnson (1966) and Reddi, Heyne, and Liang (1959) found

high heritability values for kernel weight, whereas Fonseca and Paterson (1968) and Lee and Kaltsikes (1972) reported otherwise. Many reasons were advanced to interpret these contradictions on heritability estimates for yield components. First, the kind of genetic material and the parental combinations were different (Kronstad and Foote, 1964; Gandhi et al., 1954; Lee and Kaltsikes, 1972). Second, the techniques used for estimating heritabilities were also different: F_1 on mid-parent, F_2 on mid-parent and F_4 on F_3 regression were used by Kronstad and Foote (1964), Fonseca and Paterson (1958) and Reddi, Heyne, and Liang (1969), respectively; while Johnson et al. used the variance component technique. The third cause of contradictory estimates of heritability was reported by Frey and Horner (1957) to be the failure to meet the theoretical assumptions underlying the use of each one of those techniques. The fourth and most important cause is that these different studies were conducted under a wide range of environmental stresses which could have affected the expression of the different components during their sequential development (Adams, 1967, Adams and Grafius, 1971; and Grafius and Thomas, 1971).

A new approach in studying yield components has been undertaken by Walton and associates (1971, 1972). The list of the components of yield has been extended to other developmental stages as well as morphological structures above the flag leaf node in wheat.

Walton (1971) investigated 14 different characteristics and their influence on yield of spring wheat. Additive genetic effects were found to be involved in the expression of all those characters. Therefore, consideration of all those traits in early generation selection would be of great value. Among those morphological traits studied, ear length, flag leaf sheath length and flag leaf breadth, all influenced the final yield as significantly as the standard yield components (Hsu and Walton, 1971). Factor analysis was used to classify those 14 characteristics in order of contribution to the final product in a 5×5 diallel cross of spring wheat (Walton, 1972). The characters studied were classified into four factors. The first factor which controls the photosynthetic area of the flag leaf and the duration of its activity would contribute up to 29.9% of the final yield. The second factor included those characteristics which control the development of the sink that receives photosynthate material; its contribution to the total yield was 29.2%. The third factor contained head size, number of heads, and kernel weight, whereas the fourth included the rest of the standard yield components. They contributed to the final yield by 23.2 and 16%, respectively.

In conclusion, components of yield and their genetic control have a direct control on yield <u>per se</u> (Grafius, 1956; Kronstad and Foote, 1964; Gandhi <u>et al</u>., 1964; Fonseca and Paterson, 1968; Reddi, Heyne, and Liang, 1969; Knott and Talukdar, 1971).

Therefore, parental combinations of crosses which complement each other should result in a large and rapid increase in yield due to fixable heterotic effects (Adams and Duarte, 1961; Duarte and Adams, 1963). However, the sequential nature in the development of these components and the environmental stresses imposed upon the sequence complicate the situation (Adams and Grafius, 1971). The following suggestions made by Grafius and Thomas (1971) and Thomas, Grafius, and Hahn (1971) may be of practical use in early generation selection: (1) knowledge of the parental characteristics and components that contribute to the yield; (2) study of environmental stress effects on the developmental sequence; (3) conduction of early generation selection under maximum flow of resources throughout the developmental sequence; and (4) selection for an increase in the genetic potential of the most influential component of yield. If this strategy of selection for yield through yield components could be improved by considering additional morphological or physiological characteristics, a major contribution to increased yields should be achieved (Thorne, 1968; Walton, 1971).

III. CHAPTER ONE: SOLID-SEEDED EXPERIMENTS

Materials and Methods

A diallel cross involving four agronomically and genetically diverse winter wheat cultivars was used. The four cultivars were: Sel. 101, Moro, Brevor, and Sel. 55-1744. Detailed pedigrees and descriptions of each line are given in the Appendix. Crosses were first made in 1966, and subsequently the F_1 through F_6 generations were grown as bulk populations from 1967 to 1972. Thus, in 1972 there were six possible crosses with six generations per cross.

The experimental material was grown in 1972 at three distinct environmental locations in Oregon. The experimental sites were North Willamette, Pendleton and Malheur Branch Experiment Stations at Aurora, Pendleton and Ontario, respectively.

The soil type at Aurora is a Willamette silt loam which consists of a very dark brown "A" horizon, and a dark silty clay "B" horizon. The experimental field contained 24 kg/ha of nitrogen as residue from a bean rotation grown the previous year. One hundred forty kg/ha of nitrogen (NH_4NO_3) were added as a split application during the growing season: 20 kg were applied before planting during seed-bed preparation, and 120 kg were added by top dressing at the tillering stage. The rainfall at Aurora during the 1971-72 season was 1088 mm. Diuron was sprayed at a rate of 1.6 kg/ha for weed control in early December 1971.

At Pendleton, the soil series is a Walla Walla silt loam which is characterized by a very deep, well drained, medium textured soil. Summer-fallow preceeded in the experimental plots in 1970-71. Prior to seeding, 60 kg/ha of nitrogen (NH_4NO_3) was applied. Dry-land conditions prevailed in this location with 439 mm of rainfall recorded during the growing season in 1971-72. Karmex was sprayed at a rate of 0.5 kg/ha before tillering for weed control.

The soil series at the Malheur Branch Experiment Station is a silty clay loam characterized by a deep, fine structured heavy soil. The experimental field was in barley in 1970-71. Sixty kg of nitrogen (NH_4NO_3) were applied per hectare prior to seeding in the fall of 1971. The experimental material was grown under irrigation to minimize the possibility of water stress. For weed control, Karmex was sprayed at a rate of 0.5 kg/ha.

At each location, the parents and F_1 through F_6 generations resulting from each of the six crosses were grown under commercial solid-seeded conditions. The experimental design was a split-plot with crosses the main plots and parents and F_1 through F_6 generations of each cross, the sub-plots. Therefore, there were 48 entries per replication and four replications per location. The data was analyzed as a randomized block design. Individual plots consisted of three rows with 30 cm between rows. Three hundred seeds were planted per row. However, the seeding rates differed from one location to another according to the commercial rates recommended for those environments. At North Willamette and Malheur stations, the rows were four meters long which corresponded to a seeding rate of 100 kg/ha, whereas at Pendleton, the rows were five meters long corresponding to a seeding rate of 80 kg/ha.

Because the production of large numbers of F_1 seeds was difficult, only 20 F_1 seeds were grown per plot. To simulate solid-seeding conditions, the blend method of seeding was used (Peterson, 1970). Twenty F_1 seeds were mixed with 280 seeds of a semi-dwarf, brownchaffed winter wheat (Selection 172-RR-69-214). Mixed seeds were planted in the central row of the F_1 plot with two border rows planted with the 172-RR-69-214 selection.

Data were collected from individual plots for the following six agronomic traits: grain yield, plant height, tillering, average number of spikelets per spike, kernel weight and average number of kernels per spike.

Grain yield was determined for the parents and the F_2 through F_6 bulk populations plots by harvesting 2.40 M from the central row of the plot. To determine grain yield for the F_1 plots, the F_1 plants

were harvested separately and the yield for 2.40 M was calculated on the basis of 300 seeds per row.

Plant height measurements were taken from the crown to the tip of the spike of the tallest culm at maturity. Three measurements were averaged for the parents and F_1 plots, whereas 10 measurements were taken and averaged for the segregating generation plots.

Tillering was recorded by counting the number of head-bearing tillers per 60 cm length of the central rows before harvest.

The average number of spikelets per spike was determined from a random sample of 10 heads per plot. From these same samples the average number of kernels per spike was determined for each plot.

Kernel weight was based on 1,000 kernels randomly taken from each plot harvested.

Plot measurements for each characteristic at each location were subjected to two different analyses of variance, i. e., (1) each parental line was included three times with their corresponding crosses and the total variation due to 48 entries was partitioned into among and within crosses; and (2) the parents were included only once reducing the number of entries to 40 and the variation among the 40 genotypes was partitioned into variations of the parents, and the F_1 through F_6 generations. A fixed model was assumed in both analyses because the four parents were a selected sample. Appropriate error terms were used to test differences due to each source of variation mentioned above.

Mean values for grain yield for parents, F_1 's and F_2 's through F_6 's of each cross were compared at each location using the Duncan Multiple Range Test (DMRT) at the five percent level.

To evaluate gene action, heterosis and inbreeding depression values were calculated for each cross at each location. Heterosis was expressed as percent increase of the F_1 means above the average of the two parents (Matzinger, Mann and Cockerham, 1962). Inbreeding depression values were calculated as percent F_2 reduction below F_1 performance (Matzinger, Mann and Cockerham, 1962). For later generations, inbreeding depression values were calculated as percent F_n reduction below F_{n-1} performance (Daaloul, 1972).

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

Heterobeltiosis values were calculated only for grain yield at each location and for each cross. Hybrid vigor was expressed as the percent increase of the F_1 performance above the better parent (Fonseca and Patterson, 1968).

Narrow-sense heritability estimates were calculated for each trait at each location by the regression of F_2 on F_1 , F_3 on F_2 , F_4 on F_3 , F_5 on F_4 , and F_6 on F_5 in standard units (Frey and Horner, 1957). Plot values for each trait were used.

Effects of G. C. A. and S. C. A. were tested for each trait at each location using Griffing's model for diallel analysis (1956). Because only the F_1 performances were included in the matrix, method IV of Griffing's model was used. Also a fixed model was followed because parents represented a selected population from which inferences could be made. Specific contributions of the parents due to G. C. A. and S. C. A. effects were also computed for each trait at each location (Griffing, 1956).

General and S. C. A. effects across the three locations were tested for each trait in each generation (F_1 through F_6) according to Schaffer and Usanis model (1969). This model is summarized in Table 1. Components of variance due to G. C. A., S. C. A., and G. C. A. x location interactions (G x L) were partitioned for each trait in each generation according to the same model (Table 2). Ratios of G. C. A. variances to S. C. A. variances (G/S) were computed to compare the relative magnitude of these variances in each generation.

These two models for G.C.A. and S.C.A. analysis from diallel crosses (Griffing, 1956; Schaffer and Usanis, 1969) have been adapted to computer programming and are available in the Computer Center Library at Washington State University, Pullman, Washington.

Data from three locations were combined and analyzed for each trait to test the effects of locations and genotype x location interactions

Source of Variation	d. f.	Mean Squares	Expected Mean Squares (Random Model) (2)	Expected Mean Squares (Fixed Model) (2)
Mean	1	м µ		
Location	lo - 1	M _{lo}	$\sigma_{e}^{2} + r[p(p-3)/2]\sigma_{glo}^{2} + [p(p-1)/2]\sigma_{r}^{2} + r[p(p-1)/2]\sigma_{lo}^{2}$	$\sigma_{e}^{2} + r[p(p-1)/2]\sigma_{lo}^{2}$
Replication within Location	lo(r -1)	M r	$\sigma_{e}^{2} + \log[p(p-3)/2]\sigma_{r}^{2}$	$\sigma_e^2 + \log[p(p-3)/2]\sigma_r^2$
General Combining Ability (G. C. A.)	p - 1	Mg	$\sigma_{e}^{2} + r \left[p(p-3)/2 \right] \sigma_{g \times lo}^{2} + lor \sigma_{s}^{2} + lor \left[p(p-3)/2 \right] \sigma_{g}^{2}$	$\sigma_e^2 + lor[p(p-3)/2]\sigma_g^2$
Specific Combining Ability (S.C.A.)	p(p-3)/2	M s	$\sigma_e^2 + \log \sigma_s^2$	$\sigma_e^2 + \log \sigma_s^2$
G.C.A. X Location	(lo - 1)(p - 1)	M gxlo	$\sigma_{e}^{2} + r [p(p-3)/2] \sigma_{gxlo}^{2}$	$\sigma_{e}^{2} + r[p(p-3)/2]\sigma_{gxlo}^{2}$
Error	N-1-[(lo-1)(p-1)]	M ¹ e (3)		
Total				

Table 1. Model used for partitioning variance components for G.C.A. and S.C.A. from combining ability analysis over many locations (1).

(1) Schaffer and Usanis, 1969

(2) p = Number of parents

lo = Number of locations

r = Number of replications

(3)
$$M_{e}^{1} = \frac{M_{e}}{12}$$
 (Griffing, 1956)

Source of Variation	d.f.	Mean Squares	Expected Mean Squares (Fixed Model) (2)	Components of Variance (Fixed Model) (2)
Mean	1	M µ	·	1
Location	2	M _{lo}	$\sigma \frac{2}{e} + 24\sigma \frac{2}{10}$	$\sigma \frac{2}{10} = \frac{M_{10} - M_{e}}{24}$
Replications	9	Mr	$\sigma \frac{2}{e} + 6\sigma \frac{2}{r}$	$\sigma_r^2 = \frac{M_r - M_r^2}{6}$
G. C. A.	3	Mg	$\sigma \frac{2}{e} + 24\sigma \frac{2}{g}$	$\sigma_{g}^{2} = \frac{M_{g} - M_{e}^{2}}{24}$
S.C.A.	2	M_{s}	$\sigma \frac{2}{e} + 12\sigma \frac{2}{s}$	$\sigma_{s}^{2} = \frac{M_{s} - M_{e}}{12}$
G.C.A. X Location	6	Mgxlo	$\sigma \frac{2}{e} + 8\sigma \frac{2}{g \times lo}$	$\sigma \frac{2}{g \times lo} = \frac{M_{g \times lo} - M_{e}}{8}$
Error	49	M ¹ e (3)	σ <mark>2</mark> e	
Total	72			

Table 2. Fixed model followed to partition the variance components for G.C.A., S.C.A., and G.C.A. X locations interaction from 4-parent diallel analysis over three locations (1).

(1) Schaffer and Usanis, 1969

(2) p = Number of parents, lo = Number of locations, r = Number of replications $(3) <math>M_e^1 = \frac{M_e}{12}$ (Griffing, 1956) according to Comstock and Moll's model (1961). The same analysis was performed for the parents separately.

Mean values for the parent performances for each trait over the three locations were compared using DMRT at the five percent level.

In 1970-71, the parents, F_1 's and F_2 's through F_6 's of the same diallel cross were grown in solid-seeded experiments at the same three locations (Daaloul, 1972). Those data from 1970-71 experiments were combined with the data from the 1971-72 experiments to test for different genotype x environment interactions; viz., genotype x location, genotype x year, and genotype x year x location interactions. The models described by Comstock and Moll (1962) and by Liang, Heyne and Walter (1966) were followed. These models are summarized in Table 3. Components of variances for each of these interactions were partitioned to compare their relative magnitude for each trait (Table 4).

Stability of yield for each of the four parents was estimated from data of two years and three locations by regression analysis (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). Logarithmic transformations were made to achieve better linearity. Regression coefficients were obtained to measure stability of each parent for yield (Finlay and Wilkinson, 1963). Mean squares of deviations from the regression line were used to measure the specific parent x environment interactions (Eberhart and Russell, 1966).

Source of Variation	d.f.	Mean Squares	Expected Mean Squares (Random Model) (2)	Expected Mean Squares (Fixed Model) (2)
Year	y-1	My	$\sigma_{e}^{2} + r\sigma_{ylog}^{2} + rglo\sigma_{y}^{2}$	$\sigma \frac{2}{e} + rglo\sigma \frac{2}{y}$
Location	lo -1	M _{lo}	$\sigma \frac{2}{e} + r\sigma \frac{2}{y \log} + rgy\sigma \frac{2}{lo}$	$\sigma e^{2} + rgy\sigma \frac{2}{lo}$
Genotypes	g - 1	Mg	$\sigma \frac{2}{e} + r\sigma \frac{2}{y \log} + r \log \sigma \frac{2}{g}$	$\sigma \frac{2}{e} + r \log \frac{2}{g}$
Year X Location	(y-1)(lo-1)	M _{ylo}	$\sigma \frac{2}{e} + r\sigma \frac{2}{y \log} + rg\sigma \frac{2}{y \log}$	$\sigma e^{2} + rg\sigma^{2}$ ylo
Year X Genotype	(y-1)(g-1)	M yg	$\sigma \frac{2}{e} + r\sigma \frac{2}{y\log} + r\log \frac{2}{yg}$	$\sigma \frac{2}{e} + r \log \frac{2}{yg}$
Location X Genotype	(lo-1)(g-1)	M _{log}	$\sigma \frac{2}{e} + r\sigma \frac{2}{y\log} + ry\sigma \frac{2}{\log}$	$\sigma \frac{2}{e} + ry\sigma \frac{2}{\log}$
Year X Location X Genotype	(y-1)(lo-1)(g-1)	Mylog	$\sigma \frac{2}{e} + r\sigma \frac{2}{y \log}$	$\sigma \frac{2}{e} + r\sigma \frac{2}{y \log}$
Error	ylog(r-l)	Me	2 ° e	2 و
Total	ylogr-l			

Table 3. Theoretical model used for partitioning the variance components for genotype by environment interactions (1).

(1) Comstock and Moll, 1961; Liang, Heyne, and Walter, 1966

(2) y = Number of years, lo = Number of locations, g = Number of genotypes, r = Number of replications

Source of Variation	d.f.	Mean Squares	Expected Mean Squares (1)	Components of Variance (1)
Year	1	M y	$\sigma e^2 + 408\sigma y^2$	$\sigma \frac{2}{y} = \frac{M_y - M_e}{408}$
Location	2	M _{lo}	$\sigma \frac{2}{e} + 272\sigma \frac{2}{lo}$	$\sigma \frac{2}{10} = \frac{M_{10} - M_{e}}{272}$
Genotypes	33	Mg	$\sigma \frac{2}{e} + 24\sigma \frac{2}{g}$	$\sigma_{g}^{2} = \frac{M_{g} - M_{e}}{24}$
Year X Location	2	Mylo	$\sigma \frac{2}{e} \pm 136\sigma \frac{2}{ylo}$	$\sigma \frac{2}{\text{ylo}} = \frac{\frac{M_{\text{ylo}} - M_{\text{e}}}{136}}{136}$
Year X Genotype	33	Myg	$\sigma \frac{2}{e} + 12\sigma \frac{2}{yg}$	$\sigma \frac{2}{yg} = \frac{\frac{M_{g} - M_{e}}{yg}}{12}$
Location X Genotype	66	M _{log}	$\sigma \frac{2}{e} + \frac{2}{8\sigma} \frac{2}{\log}$	$\sigma_{\log}^2 = \frac{M_{\log} - M_e}{8}$
Year X Location X Genotype	66	M _{ylog}	$\sigma \frac{2}{e} + 4\sigma \frac{2}{y \log}$	$\sigma \frac{2}{\text{ylog}} = \frac{M_{\text{ylog}} - M_{\text{e}}}{4}$
Error	612	M _e	σ e	
Total	815	-	,	

Table 4. Fixed model followed for partitioning the variance components for genotype x environment interaction in this study.

(1) y =Number of years

lo = Number of locations

g = Number of genotypes

r = Number of replications

Results and Discussion

The four parental lines, Sel. 101, Moro, Brevor and Sel. 55-1744 were selected for their genetic diversity for plant height as well as for differences in yield and yield components. Means for plant height, 1000 kernel weight and number of kernels per spike differed significantly across parental lines (Table 5). Sel. 101 and Sel. 55-1744 were the top yielders and differed significantly from Moro and Brevor. For tiller number per unit area Sel. 101 and Brevor ranked first and differed significantly from the two other parents. Finally Moro and Sel. 55-1744 had the highest number of spikelets per spike and were followed by Brevor and Sel. 101. These results substantiated the genetic diversity assumed among the four parents.

The parental lines and the F_1 's through F_6 's resulting from a diallel cross were grown under three locations representing diverse environments. Detailed per plot mean values for grain yield, plant height, tiller number per unit area, average number of spikelets per spike, 1000 kernel weight and average number of kernels per spike are given in the Appendix (Appendix Tables 1, 2, and 3) for the three locations. The location means varied for each trait indicating a broad diversity among the three environments (Table 6).

Parents	Yie	eld	He	eight	Tiller Ber 6	Number 0 cm	Nun Spil Per	nber of kelets Spike	1 Ko W	000 ernel eight	Num Ke Per	ber of rnels Spike
	Means gm	DMRT(*)	Means cm	DMRT(*)	Means	DMRT(*)	Means	DMRT(*)	Means gm	DMRT(*)	Means	DMRT(*)
Sel. 101	473.50	А	96.75	с	128.83	A	15.92	с	34.84	С	39. 36	c
Moro	292.92	с	125.42	А	108.00	В	19. 50	А	30. 90	D	53.64	Α
Brevor	390. 42	В	1 23 . 58	В	125.00	Α	16.83	В	37. 76	В	35.68	D
Sel. 55-1744	448.00	А	91.75	D	92.00	C	19. 33	\mathbf{A}^{\cdot}	39. 25	А	49.69	В

Table 5. Parental mean performances over three locations for six agronomic traits measured under solid-seeded conditions.

(*) DMRT = Duncan multiple range test, means followed by a different upper case letter differ significantly at the five percent level.

Locations	Yield (*) gm	Height (*) cm	Tiller Number Per 60cm (*)	Number of Spikelets Per Spike (*)	1000 Kernel Weight (*)	Number of Kernels Per Spike (*)
North Willamette	451.48 A	124.87 A	80.46 B	21.41 A	39.81 A	58.35 A
Pendleton	342.74 B	112.81 B	126.96 A	17.41 B	30.52 B	37.78 B
Malheur	421.02 A	107.49 B	129.08 A	15.86 C	38.01 A	34.14 B

Table 6. Location means for each trait across all genotypes grown under solid-seeded conditions.

(*) DMRT = Duncan multiple range test at the 5% level

<u>Analysis of Variance</u>

When parental lines were included three times in the analysis, the total variation among 48 entries was tested and subsequently partitioned into variations among and within sets of crosses (Tables 7, 8, 9). Highly significant differences among all entries and among and within crosses were found for grain yield, 1000 kernel weight and average number of kernels per spike at North Willamette (Table 7) and for all traits considered at Pendleton and Malheur locations (Tables 8 and 9). At North Willamette, lodging occurred in the plots prior to harvest, therefore errors in sampling and measuring would have been increased, which could explain the lack of significance for plant height, number of tillers per unit area and number of spikelets per spike. This was also reflected in the high coefficient of variation (C. V.) for these traits at North Willamette (Table 7) compared to the other C.V. values (Tables 7, 8, and 9). When each specific cross was tested for significant differences at each location some crosses showed significant differences; others did not depending on the trait and the location (Tables 7, 8, and 9). This lack of significant differences with some crosses could perhaps be attributed to sampling errors. Because of these significant genetic variations within populations, further statistical comparisons of mean performances within crosses were justified. Also, a sound basis was established for genetic

Source of Variation		d. f.		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernels Per Spike
Replications	3			11523. 21*	38104. 21*	17323.46*	1862. 19*	120.59**	145.72*
Entries	47			16514.62**	9459.02	5711.59	653.00	39.82*	262. 77**
Among crosses		5		49838.94**	4336.42	1975.32	504.55	81.19**	1225.86**
Within crosses (1)		42		12547.44**	10068.85	6156. 38	670. 68	34.90**	148.12**
Within P ₁ X P ₂			7	18088. 35**	335.07**	119.67	4.86**	7.70**	178.29**
Within P ₁ X P ₃			7	7660. 82	310.99**	111.64	1.14	7.34**	34.99*
Within $P_1 X P_4$			7	15833.50**	21703.85	12358.57	1388.27	39.65	122.43*
Within P ₂ X P ₃			7	7810.99	36. 92	309.28	3.84**	21.08**	239.25**
Within $P_2 X P_4$			7	19353.28*	18353.64	11884.39	286.93	63. 18	121.55*
Within P3 X P4			7	6537.71*	19672.64	12154.71	1339.03	70.43	192.23**
Replications X Entries	141			3952.74	11897.00	6021.70	606.57	26.41	40.18
Reps.X Within P ₁ X P ₂			21	3782. 23	16.61	154.15	0.87	1.81	48.71
Reps X Within $P_1 X P_3$			21	4548.71	19.70	359.95	1. 75	1.40	11.07
Reps X Within $P_1 X P_4$			21	3655.26	24952.15	11941.99	1269.21	50.93	47.46
Reps X Within P ₂ X P ₃			21	4295.94	28, 89	202.31	0.94	3.96	47.94
Reps X Within $P_2 X P_4$			21	6355.81	24715.70	12180.73	1263.26	55.63	46.92
Reps X Within $P_3 X P_4$			21	2079.02	24675.81	12363.67	1270. 48	50.94	28.94
Reps X Among crosses		15		2552.01	7659.43	4520.02	372.55	17.76	54.20
FOTAL	191					_		. .	
Coefficients of Variation				13. 92	87.34	96.44	115.03	12.90	10.86

 Table 7.
 Summary of observed mean squares from analysis of variance for six agronomic traits of six winter wheat crosses grown under solid-seeded conditions at North Willamette Experiment Station, Aurora, Oregon.

* Significant at the 5% level

** Significant at the 1% level

(1) P1 = Sel. 101

P2 = Moro

P3 = Brevor

P4 = Sel. 55 - 1744

Source of Variation	d. f.			Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernels Per Spike
Replications	3			21723.44**	11.08	1183.71**	2. 80**	30.84**	37.90
Entries	47			20073.51**	415.61**	908.53**	6. 76**	48.86**	167.38**
Among crosses		5		98310. 52**	1084. 28**	3665.61**	35.04**	142.93**	474. 1 4* *
Within crosses (1)		42		10759,58**	336.01**	580.31**	3.39**	37.66**	130.86**
Within $P_1 X P_2$			7	21181.92**	425.27**	814.78*	6.07**	30. 86**	205.01**
Within $P_1 X P_2$			7	11025.36**	345.60**	225.27	0. 93	27.75**	20. 47
Within $P_1 X P_4$			7	8197.67**	402.77**	782.07**	4.10**	15.10**	99.33**
Within $P_2 X P_2^{\dagger}$			7	5217.07**	35.85*	342.89	4.64**	56.72**	195.92**
Within $P_2 X P_4$			7	13327.21**	411.14**	396.92**	1.55	60.97**	169.77**
Within $P_3 X P_4$			7	5608.27**	395.43**	919.91**	3.03**	34.58**	94. 64*
Replications X Entries	141			1321.11	15.14	225.66	0.76	2.54	19.68
Reps X Within P ₁ X P ₂			21	1770.66	26.76	295.22	0.50	2.63	12. 12
Reps X Within $P_1 X P_3$			21	487.96	10.72	252.14	0.51	1.10	11.58
Reps X Within $P_1 X P_4$			21	858.36	10.77	189.27	0. 76	1.42	16. 19
Reps X Within P2 X P3	a.		21	843.98	10.44	226.94	0.63	2.89	33.33
Reps X Within P_2 X P_4	,		21	1516.02	13.54	84. 25	0.92	1.89	11.88
Reps X Within $P_3 X P_4$			21	1027.57	11.07	153.39	0.84	3.87	32.32
Reps X Among crosses		15		3312.06	25.68	439.53	1.30	3.87	21.06
TOTAL	191	_							
Coefficients of Variation				10.60	3.45	11.83	5.00	5.22	11.74

Table 8. Summary of observed mean squares from analysis of variance for six agronomic traits of six winter wheat crosses grown under solid-seeded conditions at Pendleton Experiment Station, Pendleton, Oregon.

* Significant at the 5% level

** Significant at the 1% level

(1) P1 = Sel. 101

P2 = Moro

P3 = Brevor

P4 = Sel. 55 - 1744

Source of Variation		d. f.		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernels Per Spike
Replications	3			22946.27**	85.39*	2690.01**	5. 18**	8. 15	35.98
Entries	47			8561.28**	425.54**	1072.40**	6.30**	48.87**	64.77**
Among crosses		5		27226. 89**	1428.92**	4821.14**	31.86**	276.89**	297.97**
Within crosses (1)		42		6339.18**	306.09**	626. 12	3. 26**	21.73**	37.01**
Within P ₁ X P ₂			7	8505.05*	376. 39**	620.10	4.27**	7.09	27.20
Within $P_1 X P_3$			7	6875.70	251.70**	561.82	2.03*	4.56	26.77
Within $P_1 X P_4$			7	8925.50**	250.29**	1029.07	5.20**	35.38**	26.87**
Within $P_2 X P_3$			7	5364.92*	158.71**	362.84	2. 79*	28.49**	42.41*
Within $P_{2} X P_{4}$			7	3668.27	453.55**	488.93	1.79*	43.85**	60.06*
Within $P_3 X P_4$			7	4695.63**	345.89**	693.96	3.50**	11.01**	38.77*
Replications X Entries	141			2662.70	29.09	514.76	0.73	3, 33	16.07
Reps X Within $P_1 X P_2$			21	2847.77	14.63	667.95	0.74	4.36	20.41
Reps X Within $P_1 X P_3$			21	3800.57	18.73	799.11	0.58	2.76	13.63
Reps X Within $P_1 X P_4$			21	2426.61	14.63	456.06	0. 43	3.07	5.92
Reps X Within P ₂ X P ₃	1		21	1801.60	15.64	292.45	1.02	4.12	15, 33
Reps X Within $P_2 X P_4$			21	2392.92	92.33	371.04	0.61	2.46	23, 50
Reps X Within $P_3 X P_4$			21	1037.76	24.53	662.42	0.67	2.13	14.67
Reps X Among crosses		15		4999.18	20.79	290.11	1. 21	4.85	20. 19
TOTAL	191								
Coefficients of Variation				12.26	5.02	17.58	5. 39	4.80	11.74

Table 9. Summary of observed mean squares from analysis of variance for six agronomic traits of six winter wheat crosses grown under solid-seeded conditions at Malheur Experiment Station, Ontario, Oregon.

* Significant at the 5% level

** Significant at the 1% level

(1) P1 = Sel. 101

P2 = Moro

P3 = Brevor

P4 = Sel. 55-1744

analysis, heterosis and inbreeding depression for each cross at each location.

When parental lines were included only once in the analysis, the total variation among genotypes was partitioned into variation among and within groups of genotypes for each location (Tables 10, 11, and 12). There were highly significant differences for each trait at all locations except for tiller number per unit area at North Willamette when all 40 genotypes were tested (Tables 10, 11, and 12). This lack of significance for number of tillers per unit area may be due to lodging and in turn may account for the high C.V. value (Table 10). Significant differences among groups were found for all traits at all locations except for the number of spikelets per spike and grain yield at North Willamette (Table 10) and tiller number per unit area and kernels per spike at Malheur (Table 12). When each group of genotypes was tested separately, highly significant differences were obtained for parents for all traits at all locations. However, in the F_1 's through F_6 's, consistency was not maintained.

From these analyses of variance, the following conclusions were drawn: (1) genetic variability within populations was great; (2) the parents were also genetically diverse and their performance as evaluated by the six agronomic traits differed across locations; and (3) an analysis of the gene action across groups of genotypes by

Source of Variation	·	d. f.	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernels Per Spike
Replications	3		6556.42	26.87	62.47	14.87**	3. 67	185.14**
Genotypes	39		13589.36**	328.40**	288.75	5.11**	27.25**	241.44**
Among groups		6	15588.99	302. 91**	1103.71**	3.12	58.04**	300, 22**
Within groups		33	13225.77**	333.03**	140.58	5.47**	21.66**	230.75**
Parents		3	37366.50**	1618. 25**	199.08*	12.06**	38. 43**	482.22**
F ₁ 's		5	19749. 20**	457.97**	63.48	9.30**	28.80**	565.26**
F ₂ 's		5	25159.18**	168.24**	88.14	2,80	21.50**	218.67**
F ₃ 's		5	6974.07	223.44**	370.64	5.70*	13, 18**	148.61
F ₄ 's		5	2298.74	190.10**	76.10	3.20	14.05**	141.68
F ₅ 's		5	2424.74	60.37	64.27	3.74*	22.70**	89.64
F ₆ 's		5	8264.24	126.94**	145.74	4.14*	19.65**	69.75
Replication X genotypes	117		4228.22	23.64	210.76	1.29	2.27	42.62
Reps X Parents		9	1715.78	1.81	47.69	0.45	0.85	25.33
Reps X F ₁ 's		15	2726.64	19.61	247.34	1.01	1.74	31.64
Reps X F2's		15	2373.35	32.49	144.65	1.11	1.57	34.49
Reps X F3's		15	4175.00	32.22	206.86	1.28	2,62	53.47
Reps X F ₄ 's		15	4608.28	22.37	358.12	2.56	2.36	57.31
Reps X F ₅ 's		15	3125.92	26.48	195.09	0.90	3.22	39.18
Reps X F ₆ 's		15	4923.82	25.25	252.72	1.14	1. 49	50.14
Reps X Among groups	18		8348.03	20.76	175.44	1.48	3.51	42.48
FOTAL	159							
Coefficients of Variation			14.40	3.89	18.04	5.30	3. 78	11. 19

Table 10. Summary of the observed mean squares from analysis of variance for six agronomic traits measured on parents and F_1 through F_6 generations of six winter wheat crosses grown under solid-seeded conditions at North Willamette Experiment Station, Aurora, Oregon.

** Significant at the 1% level

 $P_1 = Sel. 101$

 $P_2 = Moro$ $P_3 = Brevor$ $P_4 = Sel. 55-1744$

Source of Variation		d. f.		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernels Per Spike
Replications	3			23025. 11**	7.09	969.47*	1.82	24. 78**	17.46
Genotypes	39			18296.81**	288.66**	843.34**	5.59**	52.50**	137.16**
Among groups		6		30881.97**	577.55**	802.25*	2.80**	191.20**	383.33**
Within groups		33		16008.60**	236. 14**	850.82**	6.09**	27.29**	92. 41**
Parents			3	37834.25**	1229. 17**	1578.08**	16.40**	41.31**	390.01**
F ₁ 's			5	19385.17**	389. 24**	497.07	3.28*	19.93*	136.58**
F ₂ 's			5	12472.54*	117.97**	267.90	5.48**	20.88*	68.98**
F3's			5	14682.77**	133.77**	677.37	6.14**	40.23**	43.86
F ₄ 's			5	13872. 20**	46.57	597.30	7.14**	44.35**	35.27
F ₅ 's			5	11047.70**	37.70	1292.04**	5.57**	16.16**	27.74
F ₆ 's			5	11495.87**	95.78**	1336.87**	2. 77*	13.77*	63.51*
Replication X genotypes	117			1362.61	17.00	249.59	0.85	2.90	21.84
Reps X parents			9	1110.25	7.33	126.53	0.34	1.01	8.07
Reps X F ₁ 's			15	1528.26	18.20	323.49	0.85	4.43	21.57
Reps X F ₂ 's			15	2790.96	21.41	321.17	0. 99	5.15	15.15
Reps X F3's			15	1158.52	16.06	253.90	1. 23	1.87	47.92
Reps X F ₄ 's			15	899.36	18.72	225.41	0. 74	2,14	18.46
Reps X F5's			15	1197. 28	28.34	271.95	1.08	1.94	21.23
Reps X F ₆ 's			15	909.60	1 6.4 9	225.51	0.81	3.62	16.31
Reps X Among groups		18		1231.86	7.50	207.87	0. 60	2.37	20.74
TOTAL	159								
Coefficients of Variation				10. 77	3.65	12.44	5. 30	5.58	12. 37

Table 11. Summary of the observed mean squares from analysis of variance for six agronomic traits measured on parents and F_1 through F_6 generations of six winter wheat crosses grown under solid-seeded conditions at Pendleton Experiment Station, Pendleton, Oregon.

Sign ncant at 5% level

** Significant at the 1% level

 $P_1 = Sel. 101$

 $P_2 = Moro$

 $P_3 = Brevor$ $P_4 = Sel. 55-1744$

Source of Variation		d. f.		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Kernel s Per Spike
Replications	3			16306. 26**	74.67	2653.82**	4. 64**	8.65	32.46
Genotypes	39			8374.58**	335.71**	955.53*	5.68**	44.09**	60.91**
Among groups		6		21873. 16**	583.67**	730.76	2.95*	30.30*	27.21
Within groups		33		5920.29**	290.63**	996.40*	6.17**	46.54**	67.04**
Parents			3	12427.17**	963.83**	2160.75**	12.06**	95.49**	111.05**
F ₁ 's			5	7113.07	521.58**	625.88	8.74**	81.28**	160.67**
F ₂ 's			5	3111.64	287.54**	500.18	4.24	38.77**	31.40
F ₃ 's			5	5946.54**	265.54**	1130.68	6.70**	39.05**	6.46
$F_4's$			5	6002.34	105.34*	782.84	2.94*	27.61**	58.62*
F ₅ 's			5	6185,78	49.10	1501.87*	4.04**	31.54**	20.03
F ₆ 's			5	3258.28	110.74**	738.34	6.88**	31.58**	98.67*
Replication X genotype	117			3004.56	34.57	570.28	0.83	3.83	18.54
Reps X parents			9	1206.78	2.44	277.36	0.23	0.84	4.49
Reps X F ₁ 's			15	5595.80	104.95	440.01	0.81	6. 99	21.26
Reps X F ₂ 's			15	3524.69	20.63	576.09	1.49	4.36	34.38
Reps X F3's			15	1253.56	14.72	433.61	0.97	2.73	12.04
Reps X F ₄ 's			15	2522.99	3.00	970.66	0.74	3.29	20.07
Reps X F5's			15	2442.98	29.81	496.00	0.64	4.96	10.20
Reps X F ₆ 's			15	3829.34	30.96	785.65	0.72	2.27	26. 92
Reps X Among groups		18		2951.79	30.94	483.12	0.84	8.52	14.23
FOTAL	159								
Coefficients of Variation				13.02	5.47	18.50	5.74	5. 15	12.61

 $P_4 = Sel. 55 - 1744$

Table 12. Summary of the observed mean squares from analysis of variance for six agronomic traits measured on parents and F₁ through F₆ generations of six winter wheat crosses grown under solid-seeded conditions at Malheur Experiment Station, Ontario, Oregon.

Significant at the 5% level

** Significant at the 1% level

 $P_1 = Sel, 101$

 $P_2 = Moro$

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parent-progeny regression or within groups of genotypes by combining ability analysis would be valid.

Gene Action

The effectiveness of selection in early generations must be based on a sound evaluation of the type of gene action involved in the expression of a trait, particularly when breeding self-pollinated species (Elliot, 1959; Briggs and Knowles, 1967). Because non-additive gene action will be lost in later generations, breeders can be misled when selecting during early generations for traits governed largely by nonadditive gene action. However, for traits responding mainly to additive gene action, that portion of gene action which is fixed throughout segregating generations, reliable predictions on early generation performance can be made.

Heterosis, measured in percent of the mid-parent, is primarily due to non-additive genetic effects. In this study, small and negative amounts of heterosis were found for plant height in all crosses at all three locations except for the cross Moro X Sel. 55-1744 at Malheur (Table 13). Similar amounts of heterosis have been reported for plant height in winter wheat grown under solid-seeded conditions (Briggle, Cox and Hayes, 1967). When heterosis for plant height was reported, significant values were smaller for grain yield and yield components (Peterson, 1970; Bitzer and Fu, 1972). For grain yield

	HETEROSIS						
Locations	Crosses (2)	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Spike
	$P_1 \times P_2$	26.78	-0.41	. 9.20	10.98	8.09	24.63
North Willamette	$P_1 \times P_3$	20.65	0.41	10.32	-1.28	6.52	-8.56
	$P_1 \times P_4$	25.01	-4.13	23.69	2.99	6.13	2.57
	$P_2 \times P_3$	17.79	-4.74	13.55	11.90	11.90	21.24
	$P_2 \times P_4$	17.06	1.49	12.97	2.79	18.37	13.92
	$P_3 \times P_4$	3.24	-0.21	14.11	2.92	12.50	4.57
<u></u>	Average	18.42	-1.27	13.97	5.05	10.59	9.73
Pendleton	P ₁ x P ₂	28.34	-3.14	20.62	3.60	17.71	15.89
	$P_1 \times P_3$	26.46	0.23	2.44	6.45	22.79	16.36
	$P_1 \times P_4$	13.24	-5.85	11.35	8.95	12.96	16.58
	$P_2 \times P_3$	11.18	-4.61	5,14	4.96	28.71	7.46
	$P_2 \times P_4$	20.19	-0.71	14.88	1.99	24.73	13,71
	$P_3 \times P_4$	14.84	-4.10	23.08	7.35	21.90	12.87
	Average	19.04	-3.03	12.92	5.55	21.47	13.81

Table 13. Estimates of heterosis (1) for six agronomic traits for six winter wheat crosses grown at three locations under solid-seeded conditions.

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Locations	Crosses (2)	Yiel d	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Spike
	P ₁ x P ₂	18.56	-5.19	-2.62	3.28	-0.55	6.01
	P ₁ x P ₃	14.38	-6.77	6.89	-7.96	1.28	-9.86
Malheur	$P_1 \times P_4$	8.09	-2.99	2.30	9.83	14.71	9.23
	P ₂ x P ₃	12.39	-11.72	-0.56	3.94	10.76	1.33
	P ₂ x P ₄	8.00	16.63	14.32	0.00	8.32	16.92
	$P_3 \times P_4$	19.24	-3.18	1.50	-3.94	10.39	-8.47
• 	Average	13.44	-2.20	1.34	0.86	7.49	2.53
GENERAL AVERAG	E	16.97	-2.17	9.41	3.82	13.18	8.69

Table 13. Continued.

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

(2) P_1 = Sel. 101
 P_2 = Moro
 P_3 = Brevor
 P_4 = Sel. 55-1744

and yield components in this study, measurable amounts of heterosis were found at all locations (Table 13). Similar heterotic responses were reported for yield and yield components when measured under solid-seeded conditions (Livers and Heyne, 1966; Briggle, Cox and Hayes, 1967; Bitzer, Patterson and Nyquist, 1967; Briggle, Peterson and Hayes, 1967; Peterson, 1970; Bitzer and Fu, 1972). Because heterosis provides an estimate of the amounts of non-additive gene action, the six agronomic traits can be ranked in order of magnitude of non-additive genetic effects as follows: grain yield, 1000 kernel weight, number of tillers per unit area, number of kernels per spike, number of spikelets per head and plant height. Non-additive gene action is undesirable when selecting in early generations in selfpollinating species; therefore, effective selection for those traits would be made in the reverse order of importance in terms of nonadditive gene action.

Heterosis values for a specific trait varied from one location to another for the same cross (Table 13) indicating a possible interaction between non-additive gene action and the environment. Heterosis values also differed from one cross to another, especially for grain yield and yield components (Table 13). Crosses involving Sel. 101 had the highest heterosis values for grain yield at all locations. Hybrid vigor for grain yield may be the result of complementation between tillering capacity of Sel. 101 and one or two other yield components

contributed by the other parents of the cross. Increase in tillering, number of kernels and spikelets per head may account for the increased yield observed in the cross, Sel. 101 X Moro. In the cross, Sel. 101 X Brevor, tillering capacity of Sel. 101 was combined with kernel weight from Brevor. Finally, in the cross, Sel. 101 X Sel. 55-1744, the latter parent contributed to the increase in yield through number of kernels per head as well as kernel weight. These results on heterosis for grain yield support the concept developed by Adams (1963) and Grafius (1964) concerning the nature of heterosis of a complex trait such as grain yield in terms of its components.

In contrast to conventional breeding, non-additive genetic effects are essential in a hybrid wheat program. Only those effects which enhance the hybrid grain yield above the better parent are desirable. Such non-additive genetic effects are measured by heterobeltiosis values. For grain yield, heterobeltiosis values were lower than the heterotic values and in some cases negative in sign (Table 14). Crosses involving Sel. 101 showed measurable heterobeltiosis at all locations except Sel. 101 X Moro at Pendleton. Brevor X Sel. 55-1744 also had high heterobeltiosis under Pendleton and Malheur environments (Table 14). Other crosses did not show significant heterobeltiosis. Therefore, the success of a hybrid wheat program would depend primarily on the selection of the right combinations of parents and also on the choice of location under which such crosses would be grown.

	Н	ETEROBELTIOSIS	
Crosses (2)	North Willamette	Pendleton	Malheur
P ₁ X P ₂	7.55	-3.50	2.21
P ₁ X P ₃	11.16	8.63	9.05
P ₁ X P ₄	20.31	5.62	2.11
P ₂ X P ₃	2.30	-5.40	1.08
P ₂ X P ₄	-7.85	-4.92	-2.02
P ₃ X P ₄	-8.14	5.05	18.09
Average (1) Heterobeltiosis (2) $P_1 = Sel. \ 101$ $P_2 = Moro$ $P_3 = Brevor$ $P_4 = Sel. \ 55-17$	$\frac{4.22}{=\frac{F_1 - HP}{HP}} \times 100$	0.87	5.09

Table 14. Estimates of heterobeltiosis (1) for grain yield for six wheat crosses at three locations under solid-seeded conditions.

Assessment of the relative amounts of non-additive gene action involved in the expression of each trait was also determined by calculating inbreeding depression values for each generation after the F₁. These values indicate how fast the heterotic effects were lost and how soon genetic stabilization would be realized in the populations. Crosses with the highest heterosis values for grain yield and the yield components in the F₁ generation had the highest inbreeding depression values in the F₂ generation (Appendix Tables 4, 5, 6, 7, 8, and 9). Heterosis was, therefore, primarily due to non-additive genetic effects lost by selfing. Average inbreeding depression values for grain yield and tiller number per unit area decreased drastically by the F₃ generation in Pendleton and Malheur; however, at North Willamette, significant inbreeding depression values were found in the F_3 and F_4 generations for both grain yield and number of tillers per unit area (Table 15). Therefore genetic stabilization was not attained for grain yield and tiller number per unit area until after the F_3 generation. For the other yield components, i.e., number of spikelets per spike, 1000 kernel weight, and number of kernels per spike, significant inbreeding depression was not observed after the F₂ generation (Table 15). For plant height, negative inbreeding depressions were observed in the F_2 generation indicating that transgressive segregation was responsible for the increased height observed in the F₂ populations. Also, for plant height small amounts of

		Inbreeding Depression Values						
Locations	Traits	F ₂	F ₃	$^{ m F}_4$	F ₅	F ₆		
	Yield	11.50	1.31	4.62	-3.19	1.25		
	Height	-6.75	-0.38	1.99	-1.50	0.35		
North	Tiller number per 60 cm	26.90	-4.76	4.39	-5.34	4.78		
Willamette	Number of spikelets per spike	3.50	0.13	-1.20	2.26	1.02		
	1000 kernel weight	10.55	-1.02	2.32	-1.77	0.89		
	Number of kernels per spike	12.94	3.96	-3.02	4.13	-4.20		
	Yield	26.15	3.19	0.72	-0.01	1.40		
	Height	-10.10	-0.99	2.34	-0.43	0.83		
Pendleton	Tiller number per 60 cm	15.52	-1.23	-0.79	0.41	2.37		
	Number of spikelets per spike	5.99	-0.86	-0.89	0.22	1.43		
	1000 kernel weight	27.47	-1.65	3,77	-1.77	-0.12		
	Number of kernels per spike	22.75	0.96	7.63	-1.47	0.90		
4.	Yield	18.27	-3,71	1.80	0.32	4.16		
	Height	-9.03	-2.25	0.99	-0.80	0.13		
Malheur	Tiller number per 60 cm	13.30	-4.30	-1.49	-3.80	8.09		
	Number of spikelets per spike	-0.54	-4.06	6.65	-2.75	-1.92		
	1000 kernel weight	6.05	2,30	-0.45	0.63	-0.91		
	Number of kernels per spike	3.67	-3.82	8.74	-4, 45	-4.02		
	5	$-\frac{F_{n-1}-F}{F}$	<u>n</u>		:			

Table 15. Average inbreeding depression values (1) for six agronomic traits in five segregating generations of six single crosses grown at three locations under solid-seeded conditions.

(1) Average inbreeding depression

c=1n x 100 6

		Regression in Standard Units						
Locations	Traits	$F_2 \text{ on } F_1$	$F_3 \text{ on } F_2$	F_4 on F_3	$F_5 \text{ on } F_4$	F_6 on F_5		
	Yield	68.44	29.79	25.29	-15.67	-02.50		
	Height	64.53	42.89	58.55	57.58	79.00		
North	Tiller number per 60 cm	-18.57	0.63	-14.28	55.96	-3.80		
Willamette	Number of spikelets per spike	45.52	69.04	50.68	45.23	39.15		
	1000 kernel weight	65.73	61.40	58.88	74.17	72.55		
	Number of kernels per spike	73.39	74.03	29.52	39.31	35.97		
	Yield	58.59	55.64	47.83	32.54	42.46		
	Height	77.45	66.55	83.88	81.69	81.46		
Pendleton	Tiller number per 60 cm	62.62	68.72	39.19	11.69	39.84		
	Number of spikelets per spike	55.79	68.14	63.08	71.28	58.18		
	1000 kernel weight	6.91	58.56	86.83	84.22	62.06		
	Number of kernels per spike	39.02	51.50	-5.62	38.93	16.03		
	Yield	62.19	26.36	24.55	13.94	23.92		
	Height	24.45	76.27	63.44	31.61	42.33		
Malheur	Tiller number per 60 cm	28.81	20.36	23.74	11.48	-8.36		
	Number of spikelets per spike	46.41	54.83	56.39	37.78	70.08		
	1000 kernel weight	65.78	72.77	77.56	66.58	80.65		
	Number of kernels per spike	23.79	13.75	5.26	41.88	38.63		

Table 16. Narrow-sense heritability estimates, h^2 (1), for six agronomic traits obtained in solid-seeded experiments at three locations.

(1) $h^2 = F_n \text{ on } F_{n-1}$ regression in standard units x 100

inbreeding depression were found after the F_2 generation suggesting that genetic stabilization was obtained. Similar conclusions were made for grain yield and plant height when the same material was grown in 1970-71 (Daaloul, 1972). Genetic stabilization was attained in the F_2 and F_3 generations for plant height and grain yield, respectively (Daaloul, 1972).

Narrow-sense heritability estimates are a measure of the amounts of additive gene action involved in the expression of a given trait. Heritability values for plant height were consistently high from one location to another (Table 16). Values ranged from 42.9 to 79.0 percent at North Willamette, 66.6 to 83.9 percent at Pendleton, and from 24.5 to 76.3 percent at Malheur. Similar results have been reported on plant height heritability in winter wheat (McNeal, 1960; Kronstad and Foote, 1964; Anwar and Chowdhry, 1969; Bhatt, 1972; Daaloul, 1972; Solen, 1973; Alcala, 1973). Because additive gene action is predominant in controlling the expression of plant height, selection for this trait in early generations should be successful.

Heritability values for grain yield were generally lower than those for plant height (Table 16), except values obtained by the regression of F_2 on F_1 means at North Willamette and Malheur. Heritability values for grain yield ranged from -2.5 to 68.4 percent, 32.5 to 58.6 percent, and from 13.9 to 62.2 percent at North Willamette, Pendleton and Malheur stations, respectively. These

results parallel those from previous studies (Anwar and Chowdhry, 1969; Daaloul, 1972; Alcala, 1973). Because lesser amounts of additive gene action were involved in the expression of grain yield when compared to plant height, early generation selection for grain yield would be less effective.

Narrow-sense heritability estimates for tiller number per unit area were generally low at North Willamette (-18.6 to 56.0 percent) and Malheur (-8.4 to 28.8 percent) (Table 16). However, at Pendleton heritability values for the same trait were higher and ranged from 11.7 to 68.7 percent. Low as well as high heritability values for number of tillers per unit area were reported in previous studies on wheat (Johnson et al., 1966; Heyne and Liang, 1969; Gandhi et al., 1964; Fonseca and Patterson, 1968; Lee and Kaltsikes, 1972). These extreme ranges in heritability estimates for tiller number per unit area may be related to differences in genetic material, environments and statistical techniques utilized. Differences in heritability estimates for tillering capacity were observed among locations suggesting the existence of an interaction between the additive genetic effects controlling tillering capacity and the various environments. Nevertheless, a measurable amount of additive gene action was involved in the expression of the number of tillers per unit area but to a lesser extent than plant height.

Heritability estimates for the other yield components were high and ranged from 37.8 to 71.3 percent for number of spikelets per spike; from 6.9 to 86.8 percent for 1000 kernel weight and from -5.6 to 74.0 percent for number of kernels per spike (Table 16). Variation in heritability estimates for those yield components was also observed across locations. As with tillering capacity, the environment influenced the expression of additive gene action for those yield components. Similar interactions between additive gene action and environment have been observed when calculating heritability estimates for yield components (Heyne and Liang, 1969).

From the wide range of heritability estimates, additive gene action was involved to different extents in the expression of the six traits. These traits can be ranked according to the magnitude of additive gene action involved: plant height, kernel weight, number of spikelets per spike, number of kernels per spike, tiller number per unit area and grain yield. The effectiveness of early generation selection for these traits would follow the same order.

Combining ability analysis from diallel crosses has been used widely to estimate the relative magnitude of the types of gene action involved in the expression of a trait. General combining ability effects are a measure of additive gene action, whereas S.C.A. effects measure the gross gene system that deviates from the additive scheme, i. e., non-additive gene action. When G.C.A. effects were tested on

the F₁, highly significant G.C.A. effects were found for all traits at all locations except for tiller number per unit area at North Willamette (Table 17). Similar analysis on previous investigations usually reported high significant G.C.A. effects for plant height, grain yield and its components (Kronstad and Foote, 1964; Bitzer, Patterson and Nyquist, 1967; Gyawali, Qualset and Yamazaki, 1968; Wells and Lay, 1970; Walton, 1971; Bitzer and Fu, 1972). Because G.C.A. effects are a measure of additive gene action, the expression of the traits is influenced by additive genetic effects and as a result, progress by selection could be achieved for these traits. The extent of progress, however, depends on the amount of non-additive genetic action. Results from S.C.A. effects do not show the same consistency of significance across locations as did the G.C.A. effects (Table 17). Highly significant S. C. A. effects were detected across all three locations only for plant height; whereas for other traits, results differed from one location to another. Specific combining ability effects were highly significant for grain yield at Pendleton, for tiller number per unit area at Pendleton and Malheur, for number of spikelets per spike and 1000 kernel weight at North Willamette and Malheur, and for number of kernels per spike at North Willamette (Table 17). The lack of significance for S.C.A. effects could be related to the large error terms (Table 17) associated with variations within each environment. Environmental effects masked the

Table 17.	Observed mean squares for General Combining Ability (G.C.A.), and Specific Combining
	Ability (S. C. A.) from Combining Ability Analysis for six agronomic traits measured in F1
	generation grown in solid-seeded experiments at three locations (1).

Location	Traits	G.C.A.	S.C.A.	Error
	Yield	32233.96**	1022.00	681.66
	Height	701.50**	92.63**	4.90
North Willamette	Tiller number per 60 cm	49.54	84.63	61.84
	Number of spikelets per spike	12,42**	4.65**	0.33
	1000 kernel weight	45.57**	3.63**	0.44
	Number of kernels per spike	887.12**	82.60**	7.91
	Yield	29951.02**	3536.00**	543.44
	Height	610.21**	57.75**	4.55
Dondloton	Tiller number per 60 cm	314.58*	771.00**	80.87
i endreton	Number of spikelets per spike	5.12**	0.51	0.21
	1000 kernel weight	31.14**	3.09	1.11
	Number of kernels per spike	225.22**	3.62	5.39
	Yield	9654.52**	3300.00	1398.95
	Height	625.54**	365.75**	26.24
Malhour	Tiller number per 60 cm	731.54**	467.88*	110.00
	Number of spikelets per spike	10.87**	5.55**	0.20
	1000 kernel weight	120.38**	22.63**	1.33
	Number of kernels per spike	259.75**	12.04	5.32

(1) Using Griffing's Model (1956)
* Significant at the 5% level
** Significant at the 1% level

expression of non-additive genetic effects. Wide variation for S. C. A. effects was also found across environments in other studies (Bitzer, Patterson and Nyquist, 1967; Gyawali, Qualset and Yamazaki, 1968; Wells and Lay, 1970; Peterson, 1970; Bitzer and Fu, 1972). Despite the lack of significant S. C. A. effects at certain locations, a comparison of the S. C. A. mean squares for the six traits would permit the ranking of these traits in terms of magnitude of non-additive gene action. Non-additive gene action was found to be more involved in grain yield, tiller number per unit area, and plant height than in the other yield components. Hence, some problems might be encountered when selecting for those traits in early generations.

When G. C. A. and S. C. A. effects for each trait were pooled across the three locations for the F_1 through F_6 generations, the G. C. A. S. C. A. effects and G. C. A. X locations interactions (G X L) were highly significant for all traits in all generations except S. C. A. effects for number of tillers per unit area in the F_1 and F_6 generations, number of spikelets per spike in the F_4 generation and 1000 kernel weight in the F_2 , F_3 and F_4 generations (Table 18). Because of this wide range of significance of both G. C. A. and S. C. A. effects, the expression of all traits was considered as the result of different degrees of both types of gene action, i. e., additive and non-additive. Also consistent significant G X L interactions for all traits in all

Table 18. Observed mean squares for General Combining Ability (G.C.A.), Specific Combining Ability (S.C.A.) and General Combining Ability X location interaction (G X L) from combining ability analysis for six agronomic characters measured in F₁ through F₆ generations grown in solid-seeded experiments across three locations (1).

Traits	Source	F ₁	F ₂	F ₃	F ₄	F ₅	F ₆
	G. C. A.	59613.611**	34569.569**	14897. 264**	11434. 944**	20280.028**	29163.250**
	S. C. A.	15446.670**	9322.638**	11286. 167**	4920.667**	3536,014**	4208.597**
Yield	GXL	6113.111**	12901.528**	11132. 181**	6697.236**	2739.986**	2747.677**
	Error	272, 770	256.921	174.772	249. 993	196.312	251.089
	G. C. A.	1434.083**	665.083**	731.528**	380. 403**	172.250**	413.740**
	S.C.A.	416.292**	253.597**	191.792**	9.597**	13. 763**	70. 847**
Height	GXL	251.583**	49.917**	37.111**	72. 986**	27.333**	29.486**
	Error	3. 981	2,015	2. 139	2.004	2. 206	2.037
	G.C.A.	769,500**	858.694**	2554.583**	1357. 153**	2463.375**	1982.556**
Tiller Number	S. C. A.	59.389	373.264**	330. 125**	378.389**	561.167**	9.056
Per 60 cm	GXL	163.083**	103.069**	356. 708**	288.736**	574. 250**	718.513**
	Error	30.083	27.158	23. 545	40.873	28.535	33.650
	G. C. A.	25.611**	15.028**	27.736**	19.528**	16.111**	17.972**
Number of	S.C.A.	8. 222**	5.097**	0.347*	0. 264	0.667**	0.292*
Spikelets	GXL	1.403**	0.819**	0.236*	0.986**	2.361**	0.639**
<u>Per</u> Spike	Error	0.076	0.095	0, 101	0. 105	0.072	0.086
1000 17 1	G.C.A.	153.225**	112. 921**	114.527**	117. 787**	105.827**	94.525**
1000 Kernel	S. C. A.	3.860**	0.467	0.617	0. 433	3.732**	2.290**
Weight	GXL	21.886**	8.312**	15.398**	11.026**	2.166**	5.734**
·	Error	0. 423	0.095	0.227	0. 215	0. 282	0, 192
	G.C.A.	1213.344**	420.309**	168.344**	312. 109**	157.525**	301.701**
Number of	S. C. A.	11.813**	25.938**	22.780**	17.536**	41.522**	42.558**
Kernels Per Spike	GXL	79.368**	45.588**	69.379**	28.650**	20.619**	5.368
_	Error	2. 194	2. 159	2. 941	2,503	1.814	2.615

(1) Using Schaffer and Usanis Computer Program, 1969

* Significant at the 5% probability level

** Significant at the 1% probability level

generations suggest that the expression of additive genetic effects was highly influenced by the environment.

To measure the relative amounts of each type of gene action involved in each trait at each generation, components of variance for G.C.A., S.C.A. as well as G X L interactions were calculated (Table 19). General combining ability and S. C. A. variance for grain yield were higher than for the other traits indicating great genetic variability in this trait. General combining ability variance to S.C.A. variance ratios (G/S) were calculated in each generation (Table 19). For grain yield the G/S ratios did not increase uniformity until after the F_3 generation indicating that non-additive genetic effects were important in controlling grain yield only through the F_3 generation. Jordaan and Laubscher (1968) reported in a similar study that the S.C.A. effects detected in the F_3 and later generations were primarily a result of additive x additive epistasis. Because additive x additive epistatic effects are desirable, non-additive genetic action was considered at its lowest rate in the F_3 generation.

For plant height G.C.A. variances were always higher than S.C.A. variances confirming that additive gene action contributed strongly in the expression of this trait. The significant increase in G/S ratios after the F_2 generation indicated that the genetic effects in the populations after the F_2 generation were mainly of additive nature.

F_1 F2 F₃ F₄ F₅ F₆ Traits Source G.C.A. 2472.54 1429.69 613.44 466.04 836.82 1204.67 S.C.A. 1264.49 755.48 925.95 389.22 278.31 329.79 Yield G/S 1.96 1.89 0.66 1.20 3.01 3.65 GXL 730.04 1580.58 1396.68 805.91 317.96 312.08 G. C. A. 59.59 27.63 30.39 15.77 7.09 17.15 S. C. A. 34.36 20.97 15,80 0.63 0.96 5.73 Height G/S 1.73 1.32 1.92 24.91 7.36 2.99 GXL 30.95 5.99 4.37 8.87 3.14 3.43 G.C.A. 30.81 34.65 105.46 55.50 101.45 81.20 Tiller Number S. C. A. N.S. 28.84 25.55 28.13 44.39 N. S. Per 60 cm G/S 1.20 4.13 1.97 Large 2.29 Large GΧL 16.63 9.49 41.65 30.98 68.21 85.61 G. C. A. 1.06 0.62 1,15 0.81 0.67 0.75 Number of S.C.A. 0.68 0.42 0.02 N. S. 0.05 0.02 Spikelets Per G/S 1.57 1.49 54.81 Large 13.36 4.34 Spike GXL 0.17 0.09 0.02 0.11 0.29 0.07 G. C. A. 6.37 4.69 4.76 4.90 4.40 3.93 1000 Kernel S.C.A. 0.29 N. S. N.S. N. S. 0.29 0.18 Weight G/S 22.46 22.28 Large Large Large 15.27 G.X L 2.68 1,00 1.90 1.35 0.24 0.69 G.C. A. 50.47 17.42 6.89 12,90 6.49 12.46 Number of 0.80 S.C.A. 1.98 1.65 1.25 3.31 3.33 Kernels Per Ġ/S 62.92 8.79 4.17 10.30 1.96 3.74 Spike GΧL 9.65 5.43 8.31 3.27 2.35 0.34

Table 19. Components of variance for General Combining Ability (G.C.A.), Specific Combining Ability (S.C.A.), and General Combining Ability X locations interaction (G X L) and ratios of G.C.A. variances to S.C.A. variances (G/S) for six agronomic traits measured in F₁ through F₆ generations grown in solid-seeded experiments across three locations (1).

(1) Using Schaffer and Usanis Computer Program, 1969

For tiller number per unit area, G.C.A. variances were higher than S.C.A. variances. Additive gene action was important in the expression of this trait. Because no significant S.C.A. effects were detected in the F_1 generation, the G/S ratio was large. In the F_2 generation, the G/S ratio declined sharply indicating that S.C.A. effects were important. It is also possible that the S.C.A. effects were important in the F_1 generation but the error term was so great that no significance was detected. There was a consistent increase of the G/S ratios in the F_3 and subsequent generations; therefore, additive gene action was the most important in the expression of tillering in F_3 and following generations.

For the three other components of yield studied, i.e., number of spikelets per spike, 1000 kernel weight, and number of kernels per head, S.C.A. variances were low and sometimes non-significant (Table 19). Therefore high G/S ratios were obtained indicating the large amounts of additive gene action for those traits in all generations.

Genotype X Environment Interactions

Most of the studies that refuted the effectiveness of early generation selection for grain yield were conducted under a single environment; therefore, differences in estimates of gene action across environments were not detected. Estimates of gene action in the current investigation varied in relation to environmental effects (Tables

13, 14, 16, 17, and 18). When genotype x location interactions were tested, significant effects were found for grain yield, plant height, 1000 kernel weight, number of kernels per spike and number of spikelets per spike (Table 20). Similar results were found when parent x location interactions were tested (Table 21). Differences observed in estimates of gene action from one location to another were mainly caused by genotypic environmental interactions. Also, testing early generation material under a wide range of environments could be important in evaluating progeny performance. These results support the conclusions of Finlay (1968) who emphasized the benefits of testing segregating material under a wide range of environmental conditions. But, these results contradict the conclusions of Rasmusson and Glass (1967) who refuted the value of testing early generation material of barley under many locations. Rasmusson and Glass (1967) concluded that if error terms were larger than genotype x location interactions variation within environments would be more dangerous than among environments. Certainly their conclusions may be sound for their own objectives, but they cannot be generalized.

Year to year variations have also been an important factor in the misinterpretation of results on the effectiveness of early generation selection (Mahmud and Kramer, 1951; Fowler and Heyne, 1955). Field data for the parents, F_1 through F_5 generations were combined with field data from the same genetic material grown in 1970-71 (Daaloul,

Source of Variation	d. f.	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Spike
Locations	2	503387.83**	12680.88**	120799.13**	1309.77**		27252. 87**
Genotypes	39	29801. 27**	844.62**	1444. 16**	13.69**	103. 36**	346.34**
Location X Genotypes	78	5229.74**	54.07**	321.73	1. 34*	10. 2 4**	46.59**
Error	360	3175.90	25.35	365.67	1.14	3. 23	28.93
TOTAL	479	7766.74	149, 57	949. 18	7.66	28.73	171. 32

Table 20. Observed mean squares attributed to genotype x location interactions for six agronomic traits measured under solid-seeded conditions.

* Significant at the 5% level

** Significant at the 1% level

Source of Variation	d. f.	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernels Weight	Number of Kernels Per Spike
Locations	2	27844.08**	1530.75**	10774.33**	121.58**	352.10**	2867.73**
Parents	3	77036.36**	3716. 97**	3097.42**	38.74**	162.58**	858.63**
Locations X Parents	6	5295.78*	47.14**	420.25*	0.89	6.32**	62.32**
Error	36	2004. 28	3.94	143.60	0.49	1.22	1.32
TOTAL	47	8313.30	311.43	819.81	8.14	27, 10	194.88

Table 21. Observed mean squares attributed to parents x location interactions for six agronomic traits measured under solid-seeded conditions.

* Significant at the 5% level

** Significant at the 1% level

1972). Genotype x environment interactions were then partitioned and tested from the combined data (Table 22). Year x genotype interactions were highly significant for grain yield, plant height, tiller number per unit area and kernel weight, but not for the component traits related to head size and fertility, i.e., number of spikelets per spike and number of kernels per spike, respectively. Location x genotype interactions were highly significant for all traits except for number of spikelets per spike. Thus, variations among locations influenced all traits except head size. When year x location x genotype interactions were tested, highly significant effects were found for all traits except tiller number per unit area. When considering all three types of interactions, namely: genotype x location, genotype x year, and genotype x year x location interactions, all of them affected the six traits. However, neither variation among locations nor between years has affected head size. Therefore, head size was considered the least vulnerable yield component to change across environments and should be considered when selecting for grain yield in early generations.

Variance components attributed to these genotype x environment interactions were calculated for each one of the six traits to compare the relative magnitude of each interaction (Table 23). Year x genotype variances for grain yield and plant height were much higher than location x genotype variances. Thus, year to year variation should be

Source of Variation	d. f.	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernela Weight	Number of Kernels Per Spike
Year	1	566061.36**	1181.77**	58905.01**	32. 96**	4190.89**	1661.55**
Location	2	828965.47**	48683. 42**	122991.20**	1931.77**	3342.75**	37919.84**
Genotypes	33	61364.01**	2193.93**	2128.91**	26.75**	156.11**	667.29**
Year X Location	2	114881.05**	8412.06**	16043.83**	209.93**	768.29**	2629.06**
Year X Genotype	33	11161.96**	185.02**	688.83**	1.28	14.04**	39.78
Location X Genotype	66	8345.28**	57.88**	705. 42**	1. 17	15.05**	65.03**
Year X Location X Genotype	66	5115.09**	91.55**	300.82	1. 66**	5.26**	42.22**
Error	612	3811.35	34. 36	284. 22	1.03	3. 03	28.95
TOTAL	815	9899. 43	275.68	822. 47	7.43	26.04	160.60

Table 22. Summary of observed mean squares attributed to genotype x environment interactions for six agronomic traits measured under solid-seeded conditions in two years at three locations.

* Significant at the 5% level

** Significant at the 1% level

Source of Variation	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Spike
Year	1378.06	1.10	143. 68	0.08	10. 26	4.00
Location	3033.65	178.86	451.13	7.10	12.27	139. 30
Genotypes	2398.03	89.98	76.86	1.07	6. 38	26. 60
Year X Location	816.69	61.60	115.88	1.54	5.63	19. 12
Year X Genotype	990. 38	12.56	33.72	0.02	0.92	0.90
Location X Genotype	476. 42	2,94	52.65	0.02	1.50	4.51
Year X Location X Genotype	325.94	14.30	4. 15	0.16	0.56	3. 32

Table 23. Components of variances attributed to genotype x environment interactions for six agronomic traits measured under solid-seeded conditions in two years at three locations.

considered when selecting for these two traits in early generations. Year to year variation is one of the main factors involved in the controversial reports on validity of early generation selection for grain yield (Mahmud and Kramer, 1951). In contrast, year x genotype variances for number of kernels per spike were much smaller than those of location x genotype and year x location x genotype variances (Table 23). Therefore, location had a marked effect on head fertility. For the number of tillers per unit area, variances for both year x genotype and locations x genotype were similarly large (Table 23). Tillering capacity was the most vulnerable trait and varied considerably with locations and years. Finally, for number of spikelets per spike as well as 1000 kernel weight, variances for all interactions were small even though significant (Table 23). Hence, these yield components were considered the least susceptible to location or year effects.

Parental Evaluation

The success of early generation selection also depends largely on the knowledge of the contribution of each parent to the resulting progeny. Such knowledge would indicate which parents are good combiners for a given trait, thereby identifying crosses with good parental combinations to intensify selection in the superior populations. When G. C. A. effects for each parent were calculated for grain yield at each location (Table 24) Sel. 101 had the largest G. C. A. effects at the three locations. Sel. 55-1744 had high G. C. A. effects at North Willamette and Pendleton Stations, and Brevor had high G. C. A. effects at Malheur locations (Table 24). Sel. 101 was, therefore, the best combiner for grain yield among the four parents and was the most widely adapted parent for grain yield. Sel. 55-1744 was also a good combiner for grain yield even though it was specifically adapted to certain environments.

For plant height, Moro had the highest G.C.A. effects across the three locations followed by Brevor which had high G.C.A. effects at North Willamette and Pendleton (Table 24). Moro and Brevor were good combiners for tall straw while Sel. 101 and Sel. 55-1744 were good combiners for short straw. Similar conclusions on both plant height and grain yield were found in 1970-71 growing season under solid-seeded conditions using average combining ability values (Daaloul, 1972).

When the other yield components were considered, Sel. 101 and Brevor were found to have high G.C.A. effects for tillering capacity. Moro and Sel. 55-1744 were good combiners for number of spikelets and number of kernels per spike; and finally Sel. 55-1744 and Brevor were good combiners for kernel weight (Table 24).

	cations (1).			
Traits	Parents	North Willamette	Pendleton	Malheur
	Sel. 101	75.87	79.62	33.38
V: 14	Moro	-56.25	-66.87	-45.25
riela	Brevor	-48.38	-19.38	19.88
	Sel. 55-1744	28.75	6.63	-8.00
	Sel. 101	-6.12	-6.19	-9.69
TT -: ~1.4	Moro	8.13	7.06	11.19
Height	Brevor	7.88	7.94	-3.44
	Sel. 55-1744	-9.87	-8.81	1.94
	Sel. 101	0.06	6.38	10.19
liller	Moro	-2.31	-0.12	-6.44
Number Per	Brevor	3.44	2.25	5.94
60 cm	Sel. 55-1744	-1.19	-8.50	-9.69
Number	Sel. 101	-1.25	-0.81	-0.81
Number of	Moro	1.62	0.69	1.06
Spikelets	Brevor	-0.63	-0.56	-1.19
Fer Spike	Sel. 55-1744	0.25	0.69	0.94
1000	Sel. 101	-2.93	-1.42	-2.01
1000	Moro	-0.74	-1.77	-3.99
Kernel	Brevor	1.05	2,43	1.11
weight	Sel. 55-1744	2.62	0.77	4.89
N	Sel. 101	-5.42	-2.80	-2.12
Number of	Moro	13.66	6.48	5.63
Nernels	Brevor	-10.56	-5.57	-7.00
Per Spike	Sel. 55-1744	2.32	1.90	3.50

Table 24. Estimates of General Combining Ability (G.C.A.) effects for six agronomic traits for each parent involved in the diallel cross grown under solid-seeded conditions in three locations (1).

(1) Using Griffing's Model (1956).

Parental adaptation for grain yield can be evaluated when stability parameters are calculated (Table 25). Parental means for grain yield were used from field data of three locations for two years. Sel. 101 had a regression coefficient of 0.443 indicating its great resistance to environmental changes (Finlay and Wilkinson Model, 1963). Because the deviations mean square was small, there was little environmental interactions with this parent (Eberhart and Russell Model, 1966). Sel. 101 was confirmed to be a widely adapted, good combiner for grain yield. Sel. 55-1744 had a stability coefficient between 0.5 and unity (0.774) suggesting an above average stability for grain yield, but not as good as for Sel. 101 (Finlay and Wilkinson, 1963). Because the mean square of deviations from the regression line was rather high (Table 25), a specific genetic factor of Sel. 55-1744 may make this parental line more sensitive to certain environments. Sel. 55-1744 shatters under dry land conditions and this shattering characteristic is under genetic control. Consequently, Sel. 55-1744 was considered as a good combiner for grain yield, but less widely adapted than Sel. 101. Brevor had a stability coefficient close to unity (1.037) indicating average stability. Deviation mean square for Brevor was also intermediate reflecting an average stability (Eberhart and Russell, 1966). Because average stability was associated with low yielding ability, Brevor was considered a poorly adapted variety (Finlay and Wilkinson, 1963). In contrast to the other

Table 25.	Stability parameters calculated for the parents when	grown
	at three locations for two years.	

Parents	Regression Coefficients <u>+</u> Standard Error (1)	Mean Squares for Deviation From Regression Lines (2)		
Sel. 101	0.443 ± 0.099	136 X 10 ⁻⁶		
Moro	2.081 ± 0.282	1084×10^{-6}		
Brevor	1.037 ± 0.209	601 X 10 ⁻⁶		
Sel. 55-1744	0.774 ± 0.267	976 x 10 ⁻⁶		

(1) Using Finlay and Wilkinson Model (1963) with logarithmic transformations of the data.

(2) Using Eberhart and Russell Model (1966)

three parents, the b value for Moro was the highest (2.081) reflecting its sensitivity to environmental changes. This regression coefficient was also associated with a high mean square for deviations suggesting that the sensitivity to environmental changes of Moro was due to a specific genetic x environment interaction. Lodging of Moro under high yielding environments could be attributed to that genetic factor. Therefore, Moro was considered to have below average stability.

Early Generation Selection

The effectiveness of early generation selection for different traits should be based on evaluations of the type of gene action, genotype x environmental interactions and parental contributions. Results from such evaluations would indicate if and when early generation selection can be practiced. In this study, the evaluations of these factors may be summarized in terms of early generation selection. First, for plant height, average number of spikelets per head, 1000 kernel weight and number of kernels per spike, additive gene action is predominant (Tables 13, 14, 16 and 17). Because inbreeding depression values were low, genetic stabilization was largely attained in the F_2 population for these traits (Table 15). Also S. C. A. variances for those traits declined sharply after the F_2 generation (Table 19). Because genetic stabilization was attained in the F_2 generation and S. C. A. variances declined sharply, early generation selection

for these traits should be effective and could be initiated as early as the F_2 generation. Other studies have drawn similar conclusions for plant height (Daaloul, 1972; Solen, 1973). Second, for tiller number per unit area both additive and non-additive genetic effects were involved to different extents depending upon the location as well as the year (Tables 13, 16, 17, and 23). Inbreeding depression values (Table 15) and S.C.A. variances (Table 19) indicated that the non-additive genetic effects became less important by the F3 generation. Selection for tillering capacity may be, therefore, practiced safely as early as the F₂ generation. Third, because of the high heterosis and heterobeltiosis values (Tables 13 and 14) and the low heritability estimates (Table 16), grain yield was considered greatly influenced by non-additive genetic effects. However, the large G.C.A. variances for this same trait indicated that additive gene action was also important. Inbreeding depression values were low in the F3 generation for grain yield. Also G/S ratios indicated that G.C.A. variances were more important than S.C.A. variances after the F_3 generation (Tables 15 and 19). Specific combining ability variances at the F_3 generation were attributed to additive x additive epistasis (Jordaan and Laubscher, 1968). Therefore, selection for grain yield can be practiced effectively in early generations and may start as early as the F_3 generation. Comparisons of the mean performances for grain yield within each cross in the F_1 through the F_6 generations

substantiated the conclusion about selection as early as the F_3 generation. In effect no significant differences in grain yield were found among F_3 , F_4 , F_5 and F_6 generations for all crosses at all locations except for Brevor X Sel. 55-1744 at Pendleton (Table 26). Fourth, genotype x environmental interactions are an important aspect for success of early generation selection. Selections should be practiced under the environment where the potential varieties will be grown. The number of spikelets per spike, commonly referred to as head size, was not strongly affected by environmental changes, whereas grain yield and other yield components were. Thus, when handling F_2 material, selection emphasis should be on head size rather than on the other yield components. The F_3 material should be tested under different environments and selection should be emphasized on yield per se and tillering capacity. Finally, information on parental contributions to progeny performances is important for effective early generation selection. Sel. 101 was identified as a good combiner for grain yield and tillering capacity and as a widely adapted parental line. Sel. 55-1744 was a good combiner for grain yield, kernel weight, head size and head fertility. Therefore, the cross Sel. 101 X Sel. 55-1744 should produce good progeny and early generation selection within these progenies should be effective. Brevor was also identified as a good combiner for kernel weight and Moro as a good combiner for number of kernels per spike. The crosses, Sel. 101 X Brevor and

Pedigrees	North V	North Willamette		Pendleton		Malheur	
	Means gm	DMRT (1)	Means gm	DMRT (1)	Means gm	DMRT (1)	
P_1	477.00	A-B	457.50	A	486.00	A-B	
P_2	296.25	с	230, 50	С	352.00	С	
$P_1 X P_2 F_1$	513.00	А	441.50	А	496.75	Α	
P ₁ XP ₂ F ₂	470.00	A-B	321.00	В	420. 25	A-B-C	
$P_1 X P_2 F_3$	477.00	A-B	344.50	В	442.75	A-B	
P ₁ XP ₂ F ₄	399.50	В	309. 50	В	432.25	A-B-C	
PXPF 1 2 5	419.25	A-B	347.75	В	442.75	A-B	
$P_1 X P_2 F_6$	458.75	A-B	330, 50	В	399.75	B-C	
P 1	477, 00	А-В	457.50	В	486.00	A-B	
P ₃	402.00	В	328.50	D	440. 75	A-B	
P ₁ XP ₃ F ₁	530.25	А	497.00	А	530.00	Α	
P ₁ X P ₃ F ₂	400, 50	В	371.75	С	400.75	В	
P ₁ XP ₃ F ₃	413.50	A-B	397.50	С	469.75	A-B	
P ₁ XP ₃ F ₄	451.50	A-B	397.75	С	430.75	A-B	
PXP F ₅	429.25	A-B	399, 75	С	426.50	В	
$P_1 X P_3 F_6$	448.25	A-B	383.25	C	427.00	В	
P_1	477.00	В	457.50	А	486.00	A	
P ₄	515.75	В	39 6 . 00	B-C	432.25	A-B	
P ₁ X P ₄ F ₁	620.50	Α	483.25	А	496.25	Α	
PXP4F2	591.50	А	405.00	В	383.25	В	
P ₁ X P ₄ F ₃	472.25	В	374.25	B-C	383.00	В	
PXP4F4	439.50	В	381.75	B-C	371.00	В	
PXPF 145	483.00	В	353.50	C	442.25	A-B	
$P X P F_{1} 4 6$	485.25	В	369.00	B-C	417.00	A-B	
P.2	296.25	В	230. 50	В	352.00	с	
P ₃	402.00	Α	328.50	А	440.75	A-B	
P ₂ X P ₃ F ₁	411.25	А	310.75	А	445.50	A	
P ₂ XP ₃ F ₂	372.25	A-B	246, 50	В	366.75	C	

Table 26. Mean values for grain yield obtained in solid-seeded experiments at three locations $(P_1 = Sel. 101; P_2 = Moro; P_3 = Brevor; P_4 = Sel. 55-1744).$

Pedigrees		North Willamette		Pendleton		Malheur	
		Means gm	DMRT (1)	Means gm	DMRT (1)	Means gm	DMRT (1)
PXP3	F ₃	388.25	А	244.50	В	374.00	B-C
P ₂ X P ₃	F4	422.75	Α	236.50	В	379.00	A-B-C
P ₂ X P ₃	F ₅	436.00	А	258.75	В	370, 75	С
P ₂ X P ₃	F ₆	360.00	А-В	250.00	В	356.00	С
P2		296.25	В	230.50	С	352.00	А
P 4		515.75	А	396.00	А	432,25	Α
P ₂ XP ₄	F ₁	475.25	А	376.50	А	423.50	Α
$P_2 X P_4$	F_2	487.50	А	305.25	В	391.25	Α
$P_2 X P_4$	F ₃	498.00	А	263.50	B-C	397.00	Α
$P_2 X P_4$	F ₄	458.25	А	279.75	B-C	397.00	А
$P_2 X P_4$	F ₅	414.00	А	278.00	B-C	352.75	Α
$P_2 X P_4$	F_6	434.25	А	265.75	B-C	364.25	Α
P_3		402.00	В	328.50	с	440.75	B-C
P_4		515.75	А	396.00	A-B	432.25	B-C
P ₃ XP ₄	F 1	473.75	A-B	416.00	А	520, 50	
P ₃ XP ₄	F ₂	413.50	В	355.75	В	445.00	B-C
P ₃ XP ₄	F ₃	442.50	A-B	330.75	с	441. 25	B-C
P ₃ XP ₄	F ₄	406.75	В	356.75	В	468.75	В
PXP 34	F ₅	461.75	A-B	307.75	С	433.25	B-C
P ₃ XP ₄	F 6	479.25	А	324. QO	С	403.75	С

Table 26. Continued.

 DMRT = Duncan Multiple Range Test; Means followed by the same upper case letter do not differ significantly at the 5% level. Sel. 101 X Moro were demonstrated to be good crosses. They produced superior progeny under many environments due to the wide adaptation of Sel. 101. Finally, crosses with specific adaptation to high yielding environments such as Brevor X Sel. 55-1744 at the North Willamette location could be identified.

In conclusion, based on these results from solid-seeded experiments of bulked populations, early generation selection was found to be feasible for all traits studied. The timing of these early generation selections is dependent upon the amount of additive gene action involved in the trait as well as the sensitivity of the trait to environmental changes. For simply inherited traits controlled mainly by additive genetic effects and less influenced by environments, selection should start in the F_2 generation. For complex traits, especially grain yield per se, selection may start as early as the F_3 generation and a strategy of selection may be adopted in terms of yield components based on parental combinations.

IV. CHAPTER TWO: SPACE-PLANTED EXPERIMENTS

Materials and Methods

For each single cross resulting from the same four-parent diallel cross (Chapter I), F_2 and F_5 -derived random selections were made. The F_3 and F_6 seeds resulting from these random selections were planted along with the parents and F_1 seeds for each cross under space-planted conditions at three locations: North Willamette, Pendleton and Malheur Experiment Stations (Chapter I).

The experiments were planted in a split-plot design with crosses the main plots and the parents, the F_1 's, F_3 's and F_6 's of each cross, the sub-plots. With each set of crosses, the corresponding parents were planted. Thus, each parent was planted in three different plots per replication resulting in a total of 30 individual plots per replication. There were four replications at each location.

Individual plots consisted of one, two and four rows for the F_1 's, parents, and F_3 's and F_6 's, respectively. Each row consisted of 15 plants spaced 30 cm apart with 30 cm spacing between rows. Where missing plants occurred, barley was planted in the spring to provide uniform inter-plant competition.

Five agronomic traits were measured: grain yield per plant, plant height, number of tillers per plant, kernel weight and average number of kernels per spike. Grain yield per plant was determined by the weight of grains per plant. Plant height was measured from the crown to the tip of the spike of the tallest culm of the plant at maturity. Number of tillers per plant was measured by counting the number of head-bearing culms at harvest. Kernel weight was obtained from 500 kernels randomly selected from the harvest of each individual plant. Finally, the average number of kernels per spike was calculated indirectly from data on yield per plant, 500 kernel weight and number of tillers per plant according to the following equation:

Average number of kernels per spike =

500 (yield per plant/500 kernel weight) Number of tillers per plant

The plot mean values for each characteristic were subjected to analysis of variance to determine significant differences. Two kinds of analysis of variance were used: (1) parents were included in each cross and the total genotypic variation was partitioned into variations among and within crosses, and (2) the three values of each parent were averaged in each replication, reducing the number of genotypes to 22 instead of 30. The variation was partitioned into variation due to parents, F_1 's, F_3 's, and F_6 's. A fixed model was assumed and appropriate error terms were used. Mean values for grain yield per plant for the parents, F_1 's, F_3 's, and F_6 's were compared for each cross at each location using DMRT at the five percent level.
Heterosis values were calculated for each trait at each location as percent of increase of the F_1 means above the mid-parent (Matzinger, Mann and Cockerham, 1962). Heterobeltiosis values were determined only for grain yield at each location following the Fonseca and Patterson formula (1968).

Narrow-sense heritability values were estimated by the regression of F_1 plot values on mid-parent plot values in standard units across the six crosses (Frey and Horner, 1957).

Using plot means, correlations between F_3 and F_6 performances were calculated and tested for significance for each trait at each location.

Associations among the five agronomic traits were calculated in terms of correlation coefficients at each location using mean plots across the six crosses.

General Combining Ability and S.C.A. effects were calculated for each of the five characters at each location using F_1 data. Method IV and Model I of Griffing's technique were used (1956). Parental contributions to G.C.A. and S.C.A. effects were calculated for each trait at each location.

The G.C.A. and S.C.A. effects were pooled over the three locations using Schaffer and Usanis' model (1969). Significance of these pooled effects were tested along with the G.C.A. x location interactions (G X L) for each trait in the F_1 , F_3 and F_6 generations (Chapter I, Tables 1 and 2). The components of variance for G.C.A., S.C.A., and G X L were calculated and the G/S ratios computed as explained in Chapter I.

Genotype x location interactions as well as parents x location interactions were tested for significance from analysis of variance across location (Comstock and Moll, 1961). Each character was considered separately. Means of the four parents for each trait across the three locations were compared using DMRT at the five percent level.

<u>Results</u> and Discussion

Genetic diversity among the four parental lines was also substantiated under space-planted conditions (Table 27). Mean values for plant height, number of tillers per plant and number of kernels per spike differed significantly from one parent to another. For grain yield, a significantly higher yield was noted for Moro when contrasted with other parents. For 500 kernel weight, Brevor was the highest, followed by Sel. 101 and Sel. 55-1744 in a second group while Moro was in the third group (Table 27). When the parental performances were compared to those under solid-seeded conditions (Chapter I), similar rankings were found for all the traits except grain yield. In fact Moro, was the highest yielding under space-planted conditions but the lowest under solid-seeded conditions. In contrast, Sel. 101

Parents (2)	Yield		Height		Number of Tillers P e r Plant		500 Kernel Weight		Number of Kernels Per Spike	
	Means (gm)	DMRT (1)	Means (gm)	DMRT (1)	Means (gm)	DMRT (1)	Means (gm)	DMR T (1)	Means (gm)	DMR T (1)
Pl	53,18	В	85.60	С	33.52	A	18.85	В	41.79	С
P ₂	57.80	А	110.41	А	28.08	С	17.81	С	57.18	А
P ₃	51.51	В	107.27	в	30.98	В	21.93	Α	37.73	D
P ₄	51.44	B	80.10	D	25.82	D	19.22	В	50.88	В

Table 27. Parents mean-performances over three locations for five agronomic traits measured under space-planted conditions.

(1) DMRT = Duncan's Multiple Range Test, means followed by a different upper case letter differ significantly at the five percent level.

(2) $P_1 = Sel. 101$ $P_2 = Moro$ $P_3 = Brevor$ $P_4 = Sel. 55-1744$

which was the best yielder under solid-seeded conditions ranked second in the space-planted experiments. These differences in parental ranking for grain yield from solid-seeded to space-planted conditions may be explained by examining the four parental lines in terms of the yield components. Means for tiller number per plant differed significantly across parents under space planted conditions. These differences however, were small when compared to differences reported under solid-seeded conditions (Chapter I). Tillering capacity was enhanced for Sel. 101 as well as Moro, Brevor and Sel. 55-1744 under space-planted conditions. For the later developing components and particularly for number of kernels per spike differences from one parent to another were significant and very large. Tiller number, which was the most important trait with regard to grain yield under competitive conditions, became less influential and was replaced by kernel number per spike under less competitive conditions. Consequently, under space-planted conditions, Moro having the highest number of kernels per spike had the highest grain yield per plant; whereas under solid-seeded conditions, Sel. 101 which had the highest tillering capacity and competitive ability was the top yielder. This substantiates the concept of sequential development of yield components and its relationship to stresses on environmental resources (Grafius and Thomas, 1971).

The broad diversity among the three environments found under solid-seeded conditions (Chapter I) was also substantiated for spaceplanted conditions (Table 28). The location means for grain yield differed significantly. For plant height, North Willamette ranked first. North Willamette and Pendleton differed significantly from Malheur for number of tillers per plant. Pendleton was significantly lower for 500 kernel weight. For number of kernels per spike, North Willamette ranked first, followed by Pendleton and Malheur (Table 28). Plot mean values for each one of the five agronomic traits studied are presented in the appendix for each location (Appendix Tables 10, 11, and 12, respectively).

Location	Yield Per Plant (*)	Plant Height (*)	No. of Tillers/ Plant (*)	500 Kernel Weight (*)	No. of Kernels/ Spikelet (*)
North Willamette	75.57 A	114.34 A	32.70 A	21.61 A	52.76 A
Pendleton	47.55 C	94.07 B	31.14 A	17.30 B	44.52 B
Malheur	53.62 B	90.93 B	28.47 B	20.41 A	46.08 B

Table 28. Location means for each trait across all genotypes grown under space-planted conditions.

(*) DMRT at the five percent level.

Analysis of Variance

When parental lines were included three times in each replication, the variation for the 30 entries was highly significant for all traits at the three locations (Tables 29, 30 and 31). This variation among entries was partitioned into variation among and within crosses and significant differences were detected for all traits at each location except for grain yield at the Pendleton station. This lack of significance was associated with a high C.V. value and may be attributed to the sampling error. In turn, these errors might be related to lodging and shattering which occurred prior to harvest. In general, when variations within each specfic cross were tested separately, significant differences were also found for most traits at each location (Tables 29, 30 and 31).

Similar significant differences were found among all 22 genotypes when parental lines were included only once in each replication. These significant differences were consistent for all traits at the three locations (Tables 32, 33 and 34). The total variation among the 22 genotypes was partitioned into variations among and within groups of genotypes. Significant differences were found among and within groups of genotypes for all five traits at all locations except for grain yield at Pendleton (Tables 32, 33 and 34). Differences were also generally significant within each specific group, i. e. parents, F_1 's, F_3 's and

Table 29. Summary of observed mean squares from analysis of variance for five agronomic traits of six winter wheat crosses grown in a space-planted experiment at North Willamette Experiment Station, Aurora, Oregon.

Source of Variation	d.	f.	Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Replications	3		332.78**	62.64**	142.33**	3.68**	5.22
Entries	29		669.34**	687,44**	40.82**	3.64**	163.60**
Among crosses	5		248.13*	1987.65**	57.52**	9.87**	427.99**
Within crosses (1)	24		757.09**	416.57**	37.34**	2.34**	108.51**
Within P ₁ X P ₂		4	383.21**	585.42**	25.25	0.83	97.01**
Within $P_1 X P_3$		4	226.67*	472.98**	12.08	2.67**	21.90*
Within $P_1 X P_4$		- 4	1115.33**	73.08**	88.02**	0.96	93.13**
Within $P_2 X P_3$		4	688.91**	31.57**	37.96*	3.38**	156.96**
Within $P_2 X P_4$		4	1448.46**	702.05**	26.92**	4.40*	147.65**
Within $P_3 X P_4$		4	679.95**	634.31**	33.83**	1.79**	134.41**
Replications X Entries	87		61.31	6.42	7.73	0.49	5.96
Reps X Within $P_1 X P_2$		12	46.26	3.30	9.31	0.40	4.60
Reps X Within $P_1 X P_2$		12	65.34	5.13	9.45	0.24	6.54
Reps X Within $P_1 X P_4$		12	36.59	4.55	4.73	0.42	3.78
Reps X Within $P_2 X P_3^{\dagger}$		12	53.14	4.62	8.46	0.23	2.92
Reps X Within $P_2 X P_4$		12	61.99	6.29	4.09	0.82	7.03
Reps X Within $P_3 X P_4$		12	82.28	6.03	3.38	0.32	5,54
Reps X Among crosses	15		79.20	13.30	8.77	0.88	10.23
TOTAL	119		-	-	- - -		
Coefficients of Variation		-	10.36	2.22	8.50	3.24	4.63
* Significant at the 5% level ** Significant at the 1% level	· · · · ·	(1) P P	9 ₁ = Sel. 101 9 ₂ = Moro	P ₃ P ₄	= Brevor = Sel. 55-1	744	

Table 30. Summary of observed mean squares from analysis of variance for five agronomic traits of six winter wheat crosses grown in a space-planted experiment at Pendleton Experiment Station, Pendleton, Oregon.

Source of Variation	d.f.		Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Replications	3		321.33**	185.98**	24.54*	12.60**	92.18**
Entries	29		225.03**	569.12**	41.58**	9.89**	213.23**
Among crosses	5		40.16	1791.86**	58.25*	28.15**	601.30**
Within crosses (1)	24		263.55**	314.38**	38.11**	6.09**	132.38**
Within P ₁ X P ₂		4	285.94**	414.70**	62.12**	0.96	185.03**
Within $P_1 X P_3$		4	103.50*	244.01**	16.44	8.07**	23.66**
Within $P_1 X P_4$		4	117.02**	78.89**	38.27*	1.19*	33.43**
Within $P_2 X P_3$		4	246.11**	51.00*	26.82**	13.47**	304.88**
Within $P_2 X P_4$		4	524.90**	661.10**	42.68**	0.31	151.89**
Within $P_3 X P_4$		4	303.81**	436.59**	42.31*	12.51**	95.38**
Replications X Entries	87		30.56	9.28	8.42	0.48	3.37
Reps X Within $P_1 X P_2$		12	13.93	7.75	2.70	0.52	1.90
Reps X Within $P_1 X P_3$		12	26.67	9.07	9.91	0.21	1.56
Reps X Within $P_1 X P_4$		12	21.23	5.06	10.10	0.33	2.78
Reps X Within $P_2 X P_3$		12	22.96	10.07	4.03	0.28	3.60
Reps X Within $P_2 X P_4$		12	14.05	3.07	2.55	0.31	5.08
Reps X Within $P_3 X P_4$		12	40.36	5.15	9.79	0.22	1.55
Reps X Among crosses	15		65.89	21.68	17.60	1.30	6.39
TOTAL	119						-
Coefficients of Variation		<u>.</u>	11.63	3.24	9.32	4.00	4.12
* Significant at the 5% level ** Significant at the 1% level			(1) $P_1 = Sel. 101$ $P_2 = Moro$		$P_3 = Brevor$ $P_4 = Sel. 55-1744$		

Table 31. Summary of observed mean squares from analysis of variance for five agronomic traits of six winter wheat crosses grown in a space-planted experiment at Malheur Experiment Station, Ontario, Oregon.

Source of Variation	d,f.		Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Replications	3		44.24	23.30**	31.78**	1.98**	44.39**
Entries	29		186.62**	258.48 * *	45.35**	8.98**	164.95**
Among crosses	. 5		91.37*	723.95**	126.76**	25.35**	421.94**
Within crosses (1)	24		206.46**	161.51**	28.39**	5.58**	111.41**
Within $P_1 X P_2$		4	99.48	197.20**	22.90	1.62**	173.27**
Within $P_1 X P_3$		4	194.17**	176.53**	31.82*	6.62**	10.25*
Within $P_1 X P_4$		4	208.05**	45.23**	55.39**	2.14	83.97**
Within $P_2 X P_3$		4	288.81**	7.19	14.44	14.13**	229.21**
Within $P_2 X P_4$		4	362.74**	309.22**	26.51**	5.35**	70.73**
Within $P_3 X P_4$		4	85.54*	233.68**	19.29*	3.59	101.03**
Replications X Entries	87		25.47	5.51	5.17	0.37	5.13
Reps X Within $P_1 X P_2$		12	56.69	2.93	7.13	0.27	8.99
Reps X Within $P_1 X P_3$		12	26.39	5.56	7.02	0.24	2.82
Reps X Within $P_1 X P_4$		12	8.40	4.47	2.62	0.71	5.64
Reps X Within $P_2 X P_3$		12	13.59	11.18	5.64	0.29	2.75
Reps X Within $P_2 X P_4$		12	16.42	4.82	2.00	0.11	8.03
Reps X Within $P_3 X P_4$		12	16.81	3.54	4.12	0.26	1.34
Reps X Among crosses	15		37.09	5.97	7.14	0.67	6.11
TOTAL	119						
Coefficients of Variation			9.41	2.58	7.99	2.98	4.92
* Significant at the 5% level		- (1) $P_1 = Se1$.	101	P ₃ = B	revor	· · · · · · · · · · · · · · · · · · ·
** Significant at the 1% level			$P_2 = More$	o	$P_4 = S$	el. 55-174	4

Table 32. Summary of the observed mean squares from analysis of variance for five agronomic traits measured on Parents, F_1 , F_3 and F_6 generations of six winter wheat crosses grown in a space-planted experiment at North Willamette Experiment Station, Aurora, Oregon.

					Tillers	500	Number of
Source of Variation	d. f	•	Yield	Height	Per	Kernel	Kernels
			<u> </u>		Plant	Weight	Per Spike
Replications	3		282.61*	43.95**	104.17**	2.18*	4.86
Genotypes	21		842.36**	534.64**	46.22**	3.73**	158.27**
Among groups	. 3		4658.18*	218.19**	171.55**	6.42**	294.56**
Within groups	18		206.40**	587.38**	25.33**	3.28**	135.56**
Parents		3	39.19	1372.59**	30.60*	4.29**	215.02**
Fl's		5	498.43*	577.68**	16.89	2.91	200.50**
F ₃ 's		5	209.78*	441.08**	28.74**	3.40**	103.11**
F ₆ 's		5	11.31	272.27**	27.20	2.91**	55.39**
Replications X Genotypes	63		75.38	7.94	8.53	0.56	7.65
Reps X Parents		9	30.17	3.07	7.33	0.36	1.79
Reps X F _l 's		15	147.16	10.69	12.38	1.26	11.84
Reps X F ₃ 's		15	63.19	12.13	5.75	0.39	5.82
Reps X F ₆ 's		15	53.07	5.23	10.84	0.38	7.88
Reps X Among groups	9		58.43	5.76	4.11	0.16	9.23
TOTAL	87						
Coefficients of Variation			11.49	2.46	8.93	3.46	5.24
· · · · · · · · · · · · · · · · · · ·					· · · · · · · · · · · · · · · · · · ·		

** Significant at the 1% level

Table 33. Summary of the observed mean squares from analysis of variance for five agronomic traits measured on Parents, F_1 , F_3 , and F_6 generations of six winter wheat crosses grown in a space-planted experiment at Pendleton Experiment Station, Pendleton, Oregon.

	d.f.		Yield	Height	Tillers Per	500 Kernel	Number of Kernels Per Spike	
					Plant	Weight		
3			261.74**	134.83**	19.74	9.91**	63.49**	
21			275.09**	478.08 * *	39.77**	7.72**	178.04**	
	3		1652.16**	173.61**	155.41**	4.36**	178.57**	
	18		45.58	528.83**	20.50*	8.28**	177.96**	
		3	61.87*	1005.08 * *	50.88**	20.54**	407.13**	
		5	102.51	558.02**	8.67	8.35**	199.73**	
		5	15.86	516.00**	12.84	4.77**	137.66**	
		5	8.60	226,70**	21.75*	4.37**	58.99**	
63			39.32	11.89	10.51	0.58	4.16	
		9	9.63	2.60	3.70	0.23	1.30	
		15	93.15	18.91	22.87	0.77	7.09	
		15	32.63	13.26	8.29	0.73	4.30	
		15	20.34	8.33	4.96	0.97	3.27	
	9		22.04	13.10	9.66	0.32	3.42	
87					· ·			
			13.19	3.67	10.41	4.40	4.58	
	3 21 63 87	d.f. 321 318 63 9 87	d.f. 3 21 3 18 3 5 5 63 9 15 15 15 9 87	d.f. Yield 3 261.74** 21 275.09** 3 1652.16** 18 45.58 3 61.87* 5 102.51 5 15.86 5 8.60 63 39.32 9 9.63 15 93.15 15 32.63 15 20.34 9 22.04 87 13.19	d. f.YieldHeight 3 $261.74**$ $134.83**$ 21 $275.09**$ $478.08**$ 3 $1652.16**$ $173.61**$ 18 45.58 $528.83**$ 3 $61.87*$ $1005.08**$ 5 102.51 $558.02**$ 5 15.86 $516.00**$ 5 8.60 $226.70**$ 63 99.63 2.60 15 93.15 18.91 15 32.63 13.26 15 20.34 8.33 9 22.04 13.10 87 13.19 3.67	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	

** Significant at the 1% level

Table 34. Summary of the observed mean squares from an analysis of variance for five agronomic traits measured on Parents, F_1 , F_3 , and F_6 generations of six winter wheat crosses grown in a space-planted experiment at Malheur Experiment Station, Ontario, Oregon.

Source of Variation		d.f.	Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Replications	. 3	<u> </u>	45.33	11.75	34.92**	1.82**	27.58**
Genotypes	21		220.24**	197.71**	43.85**	6.77**	127.91**
Among groups		3	1123.82**	74.58**	55.92**	2.70**	150.65**
Within groups		18	69.64**	218.23**	41.84**	7.45**	124.12**
Parents		3	58,20*	521.82**	63.67**	18.91**	348.19**
F _l 's		5	97.80	152.36**	38.81**	6.61**	112.51**
F ['] ₃ 's		5	36.95	193.40**	21.50	3.12**	85.76**
F ₆ 's		5	81.04**	126.76**	52.11*	3.74**	39.67**
Replications X Genotypes	63		30.45	7.08	5.94	0.45	5.81
Reps X Parents		9	9.14	1.30	2.37	0.19	3.90
Reps X F _l 's		15	60.68	8.22	10.99	0.71	8.64
Reps X F ₃ 's		15	27.71	7.33	7.80	0.30	3.98
Reps X F ₆ 's		15	10.48	11.33	2.06	0.49	3.88
Reps X Among groups		9	39.24	3.47	4.45	0.49	9.28
TOTAL	87						
Coefficients of Variation			10.29	2.93	8.56	3.29	5.23
			· · · · · · · · · · · · · · · · · · ·	· · · · · ·			

** Significant at the 1% level

 F_6 's with some exceptions. Based on these analyses of variance (Tables 29, 30, 31, 32, 33 and 34), genetic variation in the parental lines, the F_1 's, as well as in the randomly selected populations of F_3 's and F_6 's was considered significant for the three locations. A sound basis was established for further statistical and genetic analyses, namely: comparisons and correlations of performances of F_3 and F_6 randomly selected populations, computations of heterosis, heterobeltiosis, narrow-sense heritability and both G.C.A. and S.C.A. estimates.

Gene Action

Measurable amounts of heterosis in percent of the mid-parent were found for all five traits at all locations (Table 35). Non-additive gene action was therefore involved in the expression of these traits. When all traits were compared in terms of heterosis values, grain yield ranked first and was followed by number of tillers per plant, number of kernels per spike, plant height and 500 kernel weight (Table 35). The same ranking was reported under solid-seeded experiments (Chapter I) except for plant height. When the amounts of heterosis were compared to those from solid-seeded experiments (Chapter I) they were generally higher under space-planted conditions (Table 35), especially for grain yield and plant height. The higher amounts of hybrid vigor for grain yield could be due to the full expression of the

			HEI	EROSIS		<u> </u>	
Locations	Crosses	Yield	Height	Tillers	500 Kernel Weight	Number of Kernels Per Spike	
	P ₁ X P ₂	26.76	8.86	5,83	3.09	14.66	
	$P_1 X P_3$	26.05	7.88	11.75	1.66	7.80	
North Willamette	$P_1 X P_4$	53.27	1.61	24.65	3.56	16.81	
	$P_2 X P_3$	39.04	5.05	16.19	3.05	13.37	
	$P_2 X P_4$	59 .22	7.71	18.70	10.61	21.02	
	$P_3 X P_4$	34.78	9.75	12.96	5.70	7.32	
	Average	39.85	6.81	15.01	4.61	13.50	
	P ₁ X P ₂	36.74	12.58	11.15	4.11	6.18	
	$P_1 X P_3$	26.12	9.08	4.77	3.41	7.94	
	$P_1 X P_4$	27.25	-1.40	2.05	5.72	5.24	
Pendleton	$P_2 X P_3$	30.08	6.16	15.82	5.63	0.94	
	$P_2 X P_4$	55.07	10.72	29.14	2.98	14.63	
	$P_3 X P_4$	48.63	9.45	23.44	7.96	7.06	
	Average	37.32	7.77	14.40	4.97	7.00	

Table 35.	Estimates of heterosis (1) for five agronomic traits for six winter wheat crosses grown at
	three locations under space-planted conditions.

Τ	ab]	e	35	•	Cont	inued.

			HE	I ER OSIS		
Locations	Crosses	Yield	Height	Tillers	500 Kernel Weight	Number of Kernels Per Spike
	P ₁ X P ₂	16.19	4.25	4.14	0.68	5.37
Malheur	$P_1 X P_3$	34.33	8.84	17.58	2.64	9.48
	$P_1 X P_4$	35.54	2.19	11.54	6.03	12.36
	$P_2 X P_3$	29.96	-1.44	10.69	4.96	8.25
	P ₂ X P ₄	38.68	7.36	18,55	8.48	8.48
	$P_3 X P_4$	19.61	4.97	1.91	3.65	8.55
	Average	29.05	4.36	10.73	4.41	8.75
General Average	2	35.41	6.31	13.38	4.66	9.75
(1) Heterosis = $\frac{F_1 - MP}{MP} \times 100$		$P_1 = P_2 =$	= Sel. 101 = Moro	P ₃ = P ₄ =	Brevor Sel. 55-1744	

different yield components under less competitive conditions. Each component had a small amount of hybrid vigor, but when these small heterotic effects were combined into yield, they became multiplied and yield ended up with a large hybrid vigor. This is further evidence for the complementarity of yield components as a source of heterosis (Adams, 1963; Grafius, 1964). The presence of hybrid vigor under space-planted conditions for plant height indicated that a certain amount of non-additive gene action was involved in plant height. The expression of these non-additive genetic effects was masked under competitive conditions yielding small and negative heterosis values (Chapter I). This hybrid vigor for plant height under space-planted conditions confirms the results on S. C. A. variances from the solidseeded experiments where certain amounts of non-additive gene action were suggested to be involved in plant height expression (Chapter I).

Heterobeltiosis values for grain yield were also higher under space-planted conditions than under solid-seeded conditions. Values ranged from 9.38 to 57.87 percent under space-planted conditions and from -8.14 to 20.31 percent under solid-seeded conditions (Tables 36 and 14, respectively). These differences between heterotic values under different seeding conditions become important when the feasibility of a hybrid wheat program is considered. In general, most heterosis measurements in wheat have been done under either spaceplanted or hill-planted conditions (Briggle, 1963; Kronstad and Foote,

	HETE	HETEROBELTIOSIS					
Crosses	North Willamette	Pendleton	Malheur				
P ₁ X P ₂	22.85	32,38	9.38				
P ₁ X P ₃	23.63	24.10	32.89				
P ₁ X P ₄	49.78	18.18	32.18				
P ₂ X P ₃	32.24	23.98	21.12				
P ₂ X P ₄	57.87	39.77	28.02				
P ₃ X P ₄	29.24	40.14	18.39				
Average	35.94	29.76	23.66				
(1) Heterobe	$Itiosis = \frac{F_1 - HP}{HP} \times 100$						

Table 36. Estimates of heterobeltiosis (1) for grain yield for six winter wheat crosses at three locations under spaceplanted conditions (P_1 = Sel. 101, P_2 = Moro, P_3 = Brevor, P_4 = Sel. 55-1744).

Table 37.	Narrow-sense heritability estimates, h^2 (1), for five
	agronomic traits obtained in space-planted experiments
	at three locations.

Traits Yield	LOCATIONS					
	North Willamette	Pendleton	Malheur			
	30.43	28.22	10.30			
Height	94.88	90.57	77.89			
Tillers per Plant	42.08	26.21	48.88			
500 Kernel Weight	43.89	89.53	73.21			
Number of Kernels per Spike	86.96	91.24	84.14			

(1) $h^2 = Regression of F_1$ on mid-parent in standard units X 100.

1964; Johnson <u>et al.</u>, 1966; Fonseca and Patterson, 1968; Knott and Talukdar, 1971; Zeven, 1972; Alcala, 1973). However, because of the differences between values of heterobeltiosis obtained under solidseeded and space-planted conditions, heterosis estimates should be made under solid-seeded conditions. This conclusion is in agreement with previous studies (Peterson, 1970; Solen, 1973).

The amounts of additive gene action involved in each trait were evaluated using narrow-sense heritability estimates (Table 37). High heritability values were found for plant height, 500 kernel weight and number of kernels per spike and ranged from 77.8 to 94.9 percent, 43.9 to 89.5 percent and 84.1 to 91.2 percent, respectively. Heritability estimates for grain yield and tiller number per plant were lower and ranged from 10.3 to 30.4 percent and 26.2 to 48.9 percent, respectively (Table 37). These results are in agreement with those reported under solid-seeded conditions (Chapter I). Additive gene action was more involved in the expression of plant height, kernel weight and number of kernels per spike than in tillers per plant and grain yield. Therefore, early generation selection could be effective for the first three traits while some problems might be encountered for the latter two.

Combining ability analyses were used to test for significance of both additive and non-additive gene action through G.C.A. and S.C.A. effects, respectively. From the F_1 data there were highly significant G.C.A. and S.C.A. effects for plant height (Table 38). However,

Table 38. Observed mean squares for General Combining Ability (G.C.A.) and Specific Combining Ability (S.C.A.) from combining ability analysis for five agronomic traits measured in the F_1 generation grown in space-planted experiments at three locations (1).

Location	Traits	G. C. A.	S. C. A.	Error
	Yield	666.03**	246.25**	36.79
	Height	906.25**	82.63**	2.67
North Willamette	Number of tillers per plant	11,82*	24.48**	3,10
	500 kernel weight	4.39**	0.62	0.32
	Number of kernels per spike	326.71**	11.28*	2.96
	Yield	116.18*	82.05	23.29
	Height	846.01**	125.50**	4.73
Pendleton	Number of tillers per plant	4.59	14.80	5.72
	500 kernel weight	13.54*	0.52	0.19
	Number of kernels per spike	311.77**	31.67**	1.77
	Yield	36.25	190.30**	15.17
	Height	188.82**	97.38**	1.59
Location North Willamette Pendleton Malheur	Number of tillers per plant	41.84**	34.20**	2.75
	500 kernel weight	10.31**	1.00*	0.18
	Number of kernels per spike	184.34**	4.80	2.16

(1) Using Griffing's Model (1956)

* Significant at the 5% level

** Significant at the 1% level

for grain yield and the components, results differed across locations (Table 38). At North Willamette, both G.C.A. and S.C.A. effects were significant for grain yield, number of tillers per plant and number of kernels per spike, and only G.C.A. effects were significant for 500 kernel weight. At Pendleton, both G.C.A. and S.C.A. were significant for 500 kernel weight whereas only G.C.A. effects were significant for grain yield and kernel weight. No significant G.C.A. and S.C.A. were found for number of tillers per plant. Finally, at Malheur both G.C.A. and S.C.A. effects were significant for tiller number per plant and 500 kernel weight. General combining ability effects were significant for number of kernels per spike and S. C. A. effects were highly significant for grain yield. Both additive and nonadditive gene action were involved in the expression of these traits and confirms the conclusions made from heterosis estimates. However, the differences observed in grain yield and yield components across locations indicated that the degree of expression of each type of gene action depended mainly on the extent of environmental interactions. Because similar conclusions were made under solid-seeded conditions (Chapter I) environmental factors other than seeding rate could be involved in these interactions. Peterson (1970) noted that the environments interacted with both additive and non-additive gene action and changed their relative expression, especially in relation to moisture and fertility levels. In this study, such factors as

moisture stress and fertility conditions may have influenced these interactions. At the Malheur location, good fertility and adequate moisture permitted a better expression of non-additive gene action for grain yield in terms of hybrid vigor. At North Willamette, excellent soil fertility along with adequate rainfall raised the expressions of both types of gene action for grain yield. Finally, at Pendleton water stress prior to maturity might have suppressed nonadditive genetic effects controlling grain yield.

General combining ability and S.C.A. effects were pooled across locations and tested along with G X L interactions for all traits in the F_1 , F_3 and F_6 generations (Table 39). Highly significant G.C.A., S.C.A. and G X L effects were found for all five traits in all generations except S.C.A. effects for 500 kernel weight in the F_1 and F_3 generations. These significant G.C.A. and S.C.A. effects support the results from combining ability analyses in the solid-seeded experiments (Chapter I) indicating that both additive and non-additive genetic effects were involved in the expression of all traits measured.

The ratios between G. C. A. and S. C. A. variance were also calculated from components of variance (Table 40). The G/S ratio for grain yield in the F_3 generation was 2.09 indicating that the G. C. A. effects were twice as high as the S. C. A. effects. The high G/S ratio for grain yield almost doubled from the F_1 to F_3 generations supporting the predominance of additive gene action for grain yield in the F_2

Trait	Source	F ₁	F ₃	^F 6
	G. C. A.	489. 728 **	166. 177**	57.660**
Yield	S.C.A.	200.670**	42.525**	6.259**
	GXL	16 4. 369**	82. 306**	21.555**
	Error	8, 762	3.552	2. 288
	G. C. A.	1745.840**	1777. 305**	960. 131**
Jeight	S. C. A.	278. 440**	74.883**	26.651**
	GXL	97.625**	42. 739**	30.723**
	Error	1. 067	0.859	0. 653
	G. C. A.	36.609**	77.661**	112.500**
Fillers Per Plant	S.C.A.	19.887**	8.103**	54.992**
illers ber flaht	G X L	10.824**	5.197**	7.554**
	Error	1. 362	0.617	0. 477
	G.C.A.	20. 192**	17.189**	14. 563**
00 Kernel Weight	S. C. A.	0. 155	0.065	0.608**
oo Keinel Weight	G X L	4.024**	1.927**	1. 426**
	Error	0.077	0.042	0. 040
	G.C.A.	796. 828**	485. 988**	243.758**
Number of Kernels Per Spike	S.C.A.	19.557**	28.475**	2 . 019**
······································	GXL	1 2. 997**	1 8. 4 57**	4. 328**
	Error	0.779	0. 372	0. 399

Table 39. Observed mean squares for General Combining Ability (G.C.A.), Specific Combining Ability (S.C.A.) and General Combining Ability X Location interaction (G X L) from Combining Ability Analysis for five agronomic characters measured in F₁, F₃, and F₆ generations grown in space-planted experiments across three locations (1).

(1) Using Schaffer and Usanis Computer Program, 1969.

* Significant at the 5% level

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

Traits	Source	F ₁	F ₃	F6
	G.C.A.	20.040	6. 776	2.308
7.13	S.C.A.	15.992	3.248	0.332
lield	G/S	1.253	2.086	6.946
· · · · · · · · · · · · · · · · · · ·	GXL	19. 451	9.844	2. 410
	G. C. A.	72. 699	74.019	39.978
T	S.C.A.	23.114	6. 169	2. 167
neight	G/S	3.145	12.000	18.449
	GXL	12.069	5.235	3. 759
	G. C. A.	1. 469	3. 210	4. 668
	S. C. A.	1.544	0.624	4.543
illers per Plant	G/S	0.951	5.144	1.028
	GXL	1.183	0. 573	0.885
	G.C.A.	0.838	0.715	0.605
	S.C.A.	NS	NS	0.047
00 Kernel Weight	G/S	Large	Large	12,872
	GXL	0. 493	0.236	0. 173
	G.C.A.	33. 168	20.234	10. 140
	S. C. A.	1. 563	2.342	0.135
number of Kernels per Spike	G/S	21.221	8.640	75.111
	GXL	1.525	2, 261	0.491

Table 40. Components of variance for General Combining Ability (G.C.A.), Specific Combining Ability (S.C.A.), and General Combining Ability x Location interactions (G X L) and ratios of G.C.A. variance to S.C.A. variances (C/S) for five agronomic traits measured in F₁, F₃, and F₆ generations grown in space-planted experiments across three locations (1).

(1) Using Schaffer and Usanis Computer Program, 1969.

* Significant at the 5% level

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

generation and the effectiveness of selection for grain yield in that generation (Chapter I). For plant height, 500 kernel weight and number of kernels per spike, G/S ratios were high in all generations. Thus, additive genetic effects were important for effective selection for those traits in early generations (Chapter I). Finally, for number of tillers per plant, a large G/S ratio was obtained in the F_3 generation but not in the F_6 generation (Table 40). This small G/S ratio for tillering in the F_6 generation is in contradiction to the ratio obtained under solid-seeded conditions for the same generation (Chapter I). Tillering was an unstable trait and had a strong interaction with the environment. Because additive genetic effects were highly significant in both the F_3 and F_6 generations for tillering, early generation selection may be effective.

Genotype X Location Interactions

Genotype x location interactions were calculated for all traits to compare their relative sensitivity to environmental changes. All traits exhibited highly significant genotype x location interaction except number of tillers per plant (Table 41). This lack of significance for genotype x location interaction for tillering could be attributed to a large error term which was inflated by the sampling error within environments. In general, all five traits were influenced differently from one environment to another. This emphasizes again the

Source of Variation	d.f.	Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Locations	2	19115.14**	14213.82**	404.32**	435.63**	1684.42**
Genotypes	21	1096.24**	1134.89**	109.44**	14.44	439.73**
Location X Genotype	42	120.73**	37.77**	10.20	1.89**	12.25**
Error	198	55.12	11.45	10.36	0.72	7.06
TOTAL	263	293.67	213.36	21.24	5.31	55.19

Table 41. Observed mean squares attributed to genotype x location interactions for five agronomic traits measured in space-planted experiments.

* Significant at the 5% level

** Significant at the 1% level

importance of genotype x location interactions in the expression of trait performances and its consequence on the effectiveness of early generation selection (Chapter I). Testing early generation material under a wide range of environments would therefore provide a more reliable criteria for success.

When parent x location interactions were tested for each trait, highly significant values were found for plant height, 500 kernel weight and number of kernels per spike, but not for grain yield and tiller number per plant (Table 42). This lack of significance of parent x location interaction for grain yield and tiller number per plant could not be attributed to sampling error because error terms were not large. Therefore, the parental lines responded in the same manner in terms of tillering capacity and grain yield at the three different locations. This is in contrast to the results obtained under solidseeded conditions. Under competitive conditions, the location effect was important on the performance of parental lines.

Parental Evaluation

To evaluate parental contributions to progeny performances under space-planted conditions, parental G.C.A. effects were calculated for each trait at each location (Table 43). Results on G.C.A. effects of parental lines for plant height, number of tillers per plant, 500 kernel weight and number of kernels per spike were similar to

Source of Variation	d.f.	Yield	Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Locations	2	2527.31**	2368.69**	59.34**	77.16**	149.13**
Parents	3	107.11**	2782.32**	135.56**	36.95**	927.01**
Location X Parents	6	26.07	59.59**	4.79	3.39**	21.66**
Error	36	19.33	5.48	5.56	0.41	3.96
TOTAL	47	132.51	290.06	16.04	6.60	71.31

Table 42. Observed mean squares attributed to parents x location interactions for five agronomic traits measured in space-planted experiments.

* Significant at the 5% level

** Significant at the 1% level

Traits	Parents	North Willamette	Pendleton	Malheur
	Sel. 101	-5.49	-3.77	-1.03
Yield	Moro	4.01	5.05	· 2.98
	Brevor	-9.32	-1.87	-1.90
	Sel. 55-1744	10.80	0.58	-0.05
,	Sel. 101	-8.41	-5.98	-2.62
Height	Moro	9.51	11.12	4.05
	Brevor	8.89	5.94	4.11
	Sel. 55-1744	-9.98	-11.07	-5.54
Number of Tillers Per Plant	Sel. 101	1.17	0.79	2.71
	Moro	-1.69	-0.11	-0.22
	Brevor	0.41	0.32	0.36
<u></u>	Sel. 55-1744	0.11	-0.99	-2.85
500	Sel. 101	-0.91	-0.39	-0.76
Kernel	Moro	-0.22	-0.98	-1.14
Weight	Brevor	0.31	1.91	1.26
	Sel. 55-1744	0.82	-0.54	0.64
Number of	Sel. 101	-2.44	-3.12	-3.50
Willamette Sel. 101 -5.49 Yield Moro 4.01 Brevor -9.32 Sel. 55-1744 Height Moro 9.51 Brevor 8.89 Sel. 55-1744 Height Moro 9.51 Brevor 8.89 Sel. 55-1744 Number of Sel. 101 1.17 Tillers Moro -1.69 Per Plant Brevor 0.41 Sel. 55-1744 0.11 500 Sel. 101 -0.91 Kernel Moro -0.22 Weight Brevor 0.31 Sel. 55-1744 0.82 Sel. 55-1744 Number of Sel. 101 -2.44 Moro 6.01 Per Spike Brevor -7.87 Sel. 55-1744	6.01	7.25	5.09	
Per Spike	Brevor	-7.87	-6.86	-4.65
	Sel. 55-1744	4.30	2.73	3.06

Table 43. Estimates of General Combining Ability Effects for five agronomic traits for each parent involved in the diallel cross grown under space-planted conditions across three locations (1).

(1) Using Griffing's Model (1956).

those from the solid-seeded experiments (Chapter I): Moro and Brevor were good combiners for plant height; Sel. 101 had the highest G.C.A. effects for number of tillers per plant; Brevor was a good combiner for kernel weight and Moro had the highest G.C.A. effects for number of kernels per spike followed by Sel. 55-1744 (Table 43). However, for grain yield, results from the space-planted experiments differed from those of the solid-seeded study. Moro had the highest G.C.A. effects for grain yield at all locations followed by Sel. 55-1744 which had high G.C.A. effects at North Willamette. Sel. 101 which was identified as the best combiner under solid-seeded conditions had a negative G.C.A. effect under space-planted conditions for this trait. Similar differences were found when parental mean values for grain yield were compared (Table 27). Grain yield is the product of the yield components (Adams, 1963; Grafius, 1964) and the complexity of this character may account for the differences in parental mean values and G.C.A. effects from solid-seeded to spaceplanted conditions. Under solid-seeded experiments, tillering was the most influential yield component in terms of final yield because it was the first component to develop under available environmental resources. But when moisture and fertility stresses were imposed upon these populations in later stages of development, the other yield components did not attain their maximum genetic potential; instead they were indirectly influenced by tillering, hence they did not

contribute as much as tillering in grain yield per se. Under spaceplanted conditions, the tillering component was developed first and was fully expressed. All plants responded similarly in producing more tillers. The second component to develop was the number of kernels per spike and was also fully expressed because of the availability of environmental resources and made the greatest contribution to the final yield. These conclusions also support the concept of sequential development of yield components in relation to environmental stresses (Grafius and Thomas, 1971). To obtain an over-all increase in yielding ability, the genetic potential of each component must be raised. Because the raising of genetic ceilings for yield components through selection necessitates their full expression, the progeny must be grown under less competitive conditions where there is a constant flow of environmental resources. To be effective, selections for grain yield through increased head size and fertility in the F_2 generation should be practiced under space-planted conditions with adequate soil moisture and fertility. However, selection practiced under space-planted conditions may result in the loss of the most competitive genotypes and the discarding of segregating lines which may become superior in commercial production. As a result, the F_3 generations should be planted under commercial seeding conditions with selection pressure placed primarily on tillering and grain yield.

Associations Among Yield and the Other Traits

Phenotypic correlations were calculated among the five traits for the parents, F_1 's, F_3 's, and F_6 's at all locations (Tables 44, 45, and 46). For the parents, grain yield per plant was significantly correlated with number of kernels per spike at North Willamette, with plant height at Pendleton and for plant height and number of kernels per spike at Malheur. The number of kernels per spike contributed the most to grain yield at all locations. Also the highly significant positive correlation between grain yield and plant height under dry-land conditions at Pendleton indicated that grain yield is not always negatively correlated to tall straw. Under dry-land conditions, plant height may be an important yield component.

Grain yield in the F_1 generation was highly significantly correlated with number of tillers per plant and number of kernels per spike at all three locations (Tables 44, 45, and 46). Both of these yield components were important in F_1 grain yield and together resulted in hybrid vigor. The correlation coefficients between grain yield and number of kernels per spike were generally higher than between grain yield and number of tillers per plant except at the Malheur location, confirming that under space-planted conditions, the number of kernels per spike had the greatest contribution to grain yield. This explains why Moro was a better combiner than Sel. 101 under space-planted conditions.

Table 44. Phenotypic correlation coefficients among five agronomic traits obtained from Parents, F_1 , F_3 , and F_6 generations of six single crosses grown in a space-planted experiment at North Willamette Experiment Station, Aurora, Oregon.

Generations		Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Parents	Yield	035	. 313	316	.505**
	Height		.061	.059	136
	Tillers per Plant			110	596**
	500 Kernel Weight				452**
F ₁ 's	Yield	198	. 614**	. 195	. 731**
	Height		143	.032	161
	Tillers per Plant			213	.011
	500 Kernel Weight				.067
F ₃ 's	Yield	442*	.559**	. 620**	. 469*
-	Height		332	329	106
	Tillers per Plant			.169	393
	500 Kernel Weight				.190
F ₆ 's	Yield	103	. 621**	.169	. 097
	Height		.043	280	084
	Tillers per Plant		×	208	643**
	500 Kernel Weight				.016

** Significant at the 1% level

Table 45. Phenotypic correlation coefficients among five agronomic
traits obtained from Parents, F_1 , F_3 , and F_6 generation
of six single crosses grown in a space-planted experiment
at Pendleton Experiment Station, Pendleton, Oregon.

Generations		Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Parents	Yield	.553**	. 302	.151	. 339
	Height		.020	.303	.202
	Tillers per Plant			.367	633**
- <u></u>	500 Kernel Weight				699**
F ₁ 's	Yield	.252	.564**	. 127	.567**
	Height		. 285	.059	.103
	Tillers per Plant			049	095
· · · · · · · · · · · · · · · · · · ·	500 Kernel Weight				477**
F ₃ 's	Yield -	.103	.657**	. 410*	. 415*
- · · · ·	Height		062	143	.105
	Tillers per Plant			. 360	225
	500 Kernel Weight				446*
F ₆ 's	Yield	.165	. 683**	.536**	.124
	Height		.130	121	.243
	Tillers per Plant			.271	451*
	500 Kernel Weight				367

* Significant at the 5% level ** Significant at the 1% level Table 46. Phenotypic correlation coefficients among five agronomic traits obtained from Parents, F₁, F₃, and F₆ generations of six single crosses grown in a space-planted experiment at Malheur Experiment Station, Ontario, Oregon.

Generations		Height	Tillers Per Plant	500 Kernel Weight	Number of Kernels Per Spike
Parents	Yield	. 495*	. 297	496*	.552**
	H e ight		.240	.012	.108
	Tillers per Plant			073	053
	500 Kernel Weight				664**
F ₁ 's	Yield	.180	. 662**	.119	. 474*
	Height		.293	.072	111
	Tillers per Plant		·	042	227
	500 Kernel Weight				297
F ₃ 's	Yield	187	. 723**	.092	. 181
	Height		.000	351	.042
	Tillers per Plant			.058	446*
	500 Kernel Weight				433*
F ₆ 's	Yield	.044	.878**	.133	134
	Height		.172	323	030
	Tillers per Plant			.058	476*
	500 Kernel Weight				530**

* Significant at the 5% level ** Significant at the 1% level In the F_3 generation, grain yield was significantly correlated with all three yield components at North Willamette and Pendleton and only with tillering at the Malheur location. However, the highest correlation coefficients were between grain yield and tiller number per plant. These high correlations reflect the importance of number of tillers per plant in the F_3 and later generations. These conclusions support those made under solid-seeded conditions (Chapter I) and those from other studies (Alcala, 1973). Similar results were obtained in the F_6 generation under space-planted conditions. Highly significant correlations of grain yield with tiller number per plant were found at all locations.

Early Generation Selection

From the results obtained from estimates of gene action and genotype x environment interaction, some conclusions can be made as to if and when early generation selection could be practiced. First from analysis of heritability estimates and G. C. A. variances, additive gene action was found to be predominant in the expression of plant height, kernel weight, and number of kernels per spike. Therefore, early generation selection for these traits would be effective. Because G/S ratios were high in all generations considered, selection would start effectively in the F_2 generation. Second heterosis values, narrow-sense heritability estimates and S. C. A. variances indicated

that non-additive genetic effects were important in the expression of both grain yield and plant tillering; however, because G.C.A. appeared to be more important than S.C.A. variances in the F_3 generation, effective selection could be practiced in the F₃ generation for those traits. These results were in agreement with those from solid-seeded experiments. Significant positive associations between ${\rm F}_3$ and ${\rm F}_6$ generation performances were observed for all traits at all locations except for yield at Malheur, which further confirmed the conclusion on the feasibility of selecting in F_2 and F_3 generations for the traits studied (Table 47). Also the effectiveness of selection in the F₃ generation for grain yield was substantiated when no significant differences between F_3 and F_6 generations were detected in 12 of 16 crosses (Table 48). Third, because of the significance of genotype x location and $G \ge L$ interactions, locations also had a very important effect on progeny performances. Therefore, selection should be practiced under environments where potential varieties would be released. Fourth, the differences in the relative G.C.A. effects of parental lines for grain yield under solid-seeded and spaceplanted conditions indicated that the space-planting of segregating material in early generations as it is used in the pedigree method of breeding may be hazardous. Good competitive high yielding progenies such as those involving Sel. 101 in this study may be misevaluated and discarded under space-planted conditions. The breeder should
Table 47.	Correlations between performances of random selections
	in F_3 and F_6 generations for five agronomic traits ob-
	served in six winter wheat crosses grown at three
	locations under space-planted conditions.

	LOCATIONS						
Traits	North Willamette	Pendleton	Malheur				
Yield	0.405*	0.635**	0.255				
Height	0.912**	0.898**	0.761**				
Number of Tillers per Plant	0.637**	0.743**	0.675**				
500 Kernel Weight	0.830**	0.852**	0.848**				
Number of Kernels per Spike	0.574**	0.888**	0.660**				

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

Pedigrees	North Wil	lamette	Pendle	ton	Malh	eur
(2)	Means	DMRT	Means	DMRT	Means	DMRT
	(gm)	(1)	(gm)	(1)	(gm)	(1)
P ₁	66.36	В	44.73	В	48.46	A
P	70.73	В	47.78	В	54.89	A
P ₁ XP ₂ F ₁	86.89	А	63.25	А	60.04	Α
$P_1 X P_2 F_1$	70.88	В	45.21	В	50.06	Α
$\frac{P_1^T X P_2^T F_3^T}{1 2 6}$	60.55	В	41.96	В	48.68	Α
P	66. 36	B	44. 73	В	48.46	с
P	63.81	В	43.30	В	47.42	C
P ³ XP ₂ F ₁	82,04	Α	55.51	А	64.40	А
$P_1^{T} X P_2^{T} F_2^{T}$	71.64	A-B	44.84	В	52.05	B-C
$\frac{P_1^{T} X P_3^{5} F_6^{5}}{1 3 6}$	64. 71	В	44.00	В	56.89	А-В
P_	66.36	B-C	44. 73	В	48.46	С
P	69.53	B-C	38.35	В	46.45	С
P ⁴ XP ₄ F ₁	104.14	А	52.86	А	64.32	Α
$P_1 X P_4 F_1$	76.01	В	45.35	В	55.78	В
$\underline{P_1^{1} X P_4^{4}} \underline{F_6^{3}}$	62.25	С	41.59	В	50.07	С
P	70.73	В	47.78	В	54.89	В
P_2^2	63.81	В	43.30	B	47.42	С
P ₂ XP ₂ F ₁	93.53	Α	59.24	Α	66.48	А
$P_2 X P_2 F_1$	65.77	В	40.20	В	48.15	° °C
$\frac{P_2^{T} \times P_3^{T} + F_6^{T}}{2 - 3 - 6}$	60.88	В	40.80	В	45.95	С
P	70.73	B-C	47.78	В	54.89	В
P	69.53	B-C	38.35	с	46.45	D
P ⁴ XP ₄ F ₁	111.66	А	66.78	А	70.27	А
$P_{2}^{2} X P_{4}^{4} F_{2}^{1}$	78.93	В	44.90	В	53.51	B-C
$\frac{P^2 X P^4}{2 4 6}$	64.04	С	39,58	с	47.58	C-D
P_2	63.81	В	43, 30	В	47.42	В
P	69.53	В	38.35	В	46.45	В
P ₂ [™] XP ₄ F ₁	89.86	А	60.68	А	56.14	A
$P_2 X P_4 F_2$	86.50	А	43.22	В	48.27	В
$P_3 X P_4^T F_6^3$	61.79	В	42.00	В	43.84	В

Table 48. Mean values for grain yield per plant obtained in space-planted experiments at three locations.

 DMRT = Duncan Multiple Range Test, means followed by the same upper case letter do not differ significantly at the 5% level.

(2) P = Sel. 101 $P_{1}^{1} = Moro$ $P_{2}^{2} = Brevor$ $P_{4}^{3} = Sel. 55-1744$

be aware of this hazard and should develop a system where progenies could be evaluated under solid-seeded conditions or a combination of both types of planting in time. Space-planting should be limited to the F_2 generation to allow selection for disease resistance and for raising the genetic potential of yield components. Selection for grain yield under space-planted conditions would be based primarily on head size and fertility because all plants would have enhanced tillering. Adequate soil moisture and fertility should be provided to ensure full expression of all yield components and to eliminate possible compensatory effects among them. The F_2 selected plants should be solid-seeded in the F_3 and later generations and selection for grain yield per se and tillering capacity should be initiated. Finally, crosses which produced the best promising progenies for grain yield were those which brought together parental lines which were good combiners for one or two of the yield components. Sel. 101 x Moro combined tillering capacity with head fertility, Sel. 101 x Brevor brought together tillering capacity with kernel weight and Sel. 101 x Sel. 55-1744 combined tillering capacity with head size, fertility and kernel weight. Thus, the choice of parental lines should be aimed at increasing grain yield and should be based on the relative contribution of the parents in terms of the yield components.

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APPENDIX

PEDIGREES AND DESCRIPTIONS OF THE FOUR PARENTS

<u>Sel. 101</u> (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. <u>Moro</u> is a variety developed at the Pendleton Experiment Station in Oregon from the Cross P. I. 178383 X Omar². 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. This variety is tall with weak straw and tends to lodge in high rainfall areas, particularly under heavy nitrogen fertilization.

3. <u>Brevor</u> was a selection made at Washington State University from the cross between (Turkey X Florence) with (Forty fold-Federation). It is a white chaffed, soft white winter wheat. The variety is of standard height, stiff and resistant to lodging straw.

4. <u>Sel. 55-1744</u> was selected from a cross between Norin 10 with 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.

				-		0	
Genotypes		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
Sel. 101	(P ₁)	477.00	107.50	82.50	19.00	37.72	54.73
Moro	(\mathbf{P}_{2})	296.25	137.00	83.25	22.00	35.44	68.40
Brevor	(P_2^{2})	402.00	137.50	92.00	20.00	41.31	46.38
Sel. 55-1744	(P ₄)	515.75	98.50	74.75	22.75	42.03	68.85
P, XP, F,		513.00	121.75	90.50	22.75	39.54	76.73
$P_1^{\downarrow} X P_2^{\downarrow} F_2^{\downarrow}$		470.00	135.50	75.75	20.50	35.70	65.00
$P_1^1 X P_2^2 F_2^2$		477.00	125.25	82.25	21.00	36.51	61.30
$P_1^1 X P_2^2 F_1^2$		399.50	126.50	74.25	21.00	35.90	59.73
$P_1^1 X P_2^2 F_5^4$		449.25	128.75	78.00	21.25	35.89	61.23
$P_1^1 X P_2^2 F_6^5$		453.75	128.75	75.25	21.50	35.98	60.40
P, XP, F,		530.25	123.00	96.25	19.25	42.09	46.23
$P_1^{\dagger} X P_2^{\dagger} F_2^{\dagger}$		400.50	128.00	82.50	20.00	39.52	46.98
$P_1^1 X P_2^3 F_2^4$		413.50	133.25	91.75	19.75	39.48	47.73
$P_1^{\downarrow} X P_2^{\flat} F_1^{\flat}$		451,50	125.25	83.50	20.50	39.20	50.63
$P_1^{\downarrow} X P_2^{\prime} F_2^{\prime}$		429.25	126.75	86.75	20.50	39.20	50.43
$P_1^1 X P_3^3 F_6^5$		448.25	124.00	83.75	20.00	39.50	51.00
P, XP, F,		620.50	98.75	97.25	21.50	42.32	63.38
$P_1 X P_4 F_2$		591.50	116.00	69.00	21.25	39.88	60.05
$P_1^{I} X P_4^{4} F_3^{2}$		472.25	119.25	65.75	20.50	40.97	52.40

Appendix Table 1. Plot means for six agronomic traits measured on 40 genotypes under solid-seeded conditions at North Willamette Experiment Station, Aurora, Oregon.

Genotypes	Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
$\begin{array}{ccc} P & X P & F \\ P_1 & X P_4 & F_5 \end{array}$	439.50 483.00	115.25 121.75	73.25 76.50	20.75 20.00	39.28 40.80	54.45 55.03
$P_1 X P_4 F_6$	485.25	119.50	77.50	21.25	39.44	59.53
$\begin{array}{ccc} P & X P & F_1 \\ P_2 & X P_3 & F_2 \end{array}$	411.25 372.25	130.75 128.50	99.50 76.75	23.50 22.00	42.94 37.69	69.58 58.10
$\begin{array}{ccc} P^2 \times P^3 & F^2 \\ P^2 \times P^3 & F^3 \\ P^2 \times P^3 & F^4 \end{array}$	388.25 422.75	133.25 135.00	85.75	21.25 21.75	38.74 38.33	59.00 58.70
$\begin{array}{c} P & X P & F \\ P_2^2 X P_3^3 & F_6^5 \end{array}$	436.00 360.00	132.50 134.25	82.50 82.25	21.75 22.25	40.03 38.58	51.83 56.05
$P_{2} X P_{4} F_{1}$	475.25	119.50	89.25	23.00	45.85	78.18
$\begin{array}{ccc} P & X P & F \\ P & X P & F \\ P & X P & F \\ \end{array}$	487.50 498.00	129.75 136.00	73.00 78.00	21.75 23.25	39.53 40.05	65.58 62.50
$\begin{array}{ccc} P^{2} \times P^{4} & F^{3} \\ P^{2} \times P^{4} & F^{4} \\ P^{2} \times P^{4} & F^{5} \\ \end{array}$	458.95 414.00	12 9. 25 129.00	77.00 76.50	22.75 22.50	37.79 37.77	67.25 60.55
$P_2 X P_4 F_6$	434.25	131.25	74.50	22.50	39.34	62.65
P ₃ XP ₄ F ₁	473.75	117.75	95.00	22.00	46.88	60.25
$P^{3}XP^{4}F^{2}$ $P^{3}XP^{4}F^{2}$	413.50 442.50	124.50 119.50	71.75 70.75	22.00 21.75	42.61 41.62	51.58
$P^3 X P^4 F^3$ $P^3 Y P^4 F^4$	406.75	120.25	75.75	22.25	41.56	53.35
$ \begin{array}{c} F_3 \\ F_3 \\ F_3 \\ F_4 \\ F_6 \end{array} \right) \begin{array}{c} F_5 \\ F_6 \\ F_$	479.25	122.50	67.00	20.25	42.71 42.90	51.60
Averages	451.48	124.87	80.46	21.41	39.81	58.35

Appendix Table 1. Continued.

Genotypes		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
Sel. 101	(P,)	457.50	93.50	139.25	15.25	30,69	32.85
Moro	(\mathbf{P}_2^1)	230,50	121.25	120.25	19.50	25.72	53.23
Brevor	(P_2^2)	328.50	123.00	137.50	15.75	32,10	32,38
Sel. 55-1744	(P_4^3)	396.00	90.25	96.50	18.25	32.87	42.98
P, XP, F,		441.50	104.00	156.50	18.00	33.20	49.88
$P_1^1 X P_2^2 F_2^1$		321.00	121.25	132.00	17.25	26.58	40.08
$P_1^1 X P_2^2 F_2^2$		344.50	119.50	132.00	16.50	27.06	38.45
$P_1^{\prime} X P_2^{\prime} F_4^{\prime}$		309.50	117.50	131.50	16.75	24.95	37.58
$P_1^1 X P_2^2 F_5^4$		347.75	119.25	139.75	17.25	26.38	38.00
$P_1 X P_2^2 F_6^3$		330.50	121.25	108.00	16.75	27.70	34.90
P, XP, F,		497.00	108.50	141.75	16.50	38.55	37,95
$P_1 X P_2 F_2$		371,75	117.50	128.00	15.00	30.44	30.58
$P_1^{\prime} X P_2^{\prime} F_2^{\prime}$		397.50	115.75	146.25	15.25	32.42	30.85
$P_1^{T}XP_2^{T}F_1^{T}$		379.75	113.25	143.50	15.50	31.99	32,85
$P_1 X P_2 F_1^{\dagger}$		399.75	119.50	151.50	15.75	30.72	32,55
$P_1^1 X P_3^3 F_6^3$		383.25	119.25	149.75	16.00	31.43	32.25
P ₁ X P ₄ F ₁		483.25	86.50	131.25	18.25	35.90	44.20
$P_1 X P_{\lambda} = F_2$		405.00	105.50	112.25	17.00	32.54	38.65
$P_1 X P_4 T_2$		374.25	107.00	118.25	18.00	32.51	38.95
$P_1 X P_4 F_4^3$		381.75	111.50	134.50	17.25	32.13	30.90

Appendix Table 2. Plot means for six agronomic traits measured on 40 genotypes under solid-seeded conditions at Pendleton Experiment Station, Pendleton, Oregon.

Genotypes		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
$\begin{array}{c} P & X & P \\ P_1^1 & X & P_4^4 \end{array}$	F5 F6	353.50 369.00	112.00 107.25	119.00 130.00	16.50 17.25	30.66 29.46	32.43 34.90
$\begin{array}{c} P_2 & X & P_3 \\ P_2 & X & P^3 \end{array}$	$F_1 F_2 F_3 F_4 F_5 F_6$	310.75 246.50 244.50 236.50 258.75 250.00	116.50 118.50 121.75 114.25 119.25 116.75	135.50 113.75 120.00 112.75 128.50 122.00	18.50 18.50 17.75 17.75 17.75 17.50	37.21 27.02 28.13 26.60 27.91 28.69	46.00 38.48 35.63 35.88 35.03 35.78
$\begin{array}{c} P_2 X P_4 \\ P_2 X P^4 \end{array}$	F_1 F_2 F_3 F_4 F_5 F_6	376.50 305.25 263.50 279.75 278.00 265.75	105.00 114.50 120.00 115.00 115.25 116.75	124.50 114.75 108.50 113.50 99.00 103.75	19.25 17.75 18.75 19.50 19.00 18.50	36.54 27.83 25.30 26.36 29.11 27.58	54.70 41.98 39.33 37.98 38.48 42.03
$\begin{array}{c} P_{3} X P_{4} \\ P_{3} X P_{4} \end{array}$	F_{1} F_{2} F_{3} F_{4} F_{5} F_{6}	416.00 355.75 330.75 356.75 307.75 324.00	102.25 114.75 111.00 107.50 115.25 114.00	144.00 120.75 127.00 123.25 125.50 142.00	18.25 17.25 17.50 18.00 18.25 17.00	36.90 29.57 32.20 31.75 31.74 31.93	42.53 34.43 38.95 32.28 34.00 30.33
Averages		342.74	112.81	126.96	97.41	30.52	37.78

Appendix Table 2. Continued.

Genotypes		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
Sel. 101	(P.)	486.00	89.25	155.75	13.50	36.13	30 50
Moro	(P_{a}^{-1})	352.00	118.00	120.50	17,00	31.54	39.30
Brevor	(\mathbf{P}_{2}^{2})	440.75	110.25	145.50	14.75	39.86	28.30
Sel. 55-1744	(P_4^3)	432.75	86.50	104.75	17.00	42.85	37.25
P, XP, F,		496.75	98.25	134.50	15.75	33,65	37.00
$P_1^1 X P_2^2 F_2^1$		420.25	115.25	130.00	15,25	34.48	34.90
$P_1^1 X P_2^2 F_2^2$		442.75	113,25	118.50	16,25	32.81	36.13
$P_1^1 X P_2^2 F_4^3$		432.25	111.50	135.75	15.75	33.77	38,00
$P_1^1 X P_2^2 = F_r^4$		442.75	108.25	118.50	15.00	33.20	36.18
$P_1 X P_2^2 F_6^3$		399.75	112.50	134.75	15.00	34.12	36.48
P, XP, F,		530.00	93.00	161.00	13.00	38.48	26.50
$P_1^{T} X P_2^{T} F_2^{T}$		400.75	103.00	136.50	14.50	38.77	29.48
$P_1^1 X P_2^2 F_2^2$		469.75	104.50	153.25	14.25	38.58	33.68
$P_1^{\prime} X P_2^{\prime} F_1^{\prime}$		430.75	106.50	145.00	14.00	37.64	28.28
$P_1 X P_2 F_2^{\dagger}$		426,50	109.25	172.00	14.50	37.96	33.20
$P_1^T X P_3^T F_6^T$		427.00	109.75	139.25	15.25	38.14	32.25
P, XP, F,		496.25	85.25	133,25	16.75	45.30	37.00
$P_1 X P_4 F_2$		383.25	94.75	112.00	15.25	40.25	32.53
$P_1 X P_1 F_2$		383.00	100.25	114.00	16.50	37.99	34.75
$P_1 X P_4 F_4$		371.00	101.25	122.75	15.00	37.86	30.43

Appendix Table 3. Plot means for six agronomic traits measured on 40 genotypes under solid-seeded conditions at Malheur Experiment Station, Ontario, Oregon.

Genotypes		Yield	Height	Tiller Number Per 60 cm	Number of Spikelets Per Spike	1000 Kernel Weight	Number of Kernels Per Head
$\begin{array}{c} P_1 \times P_1 \\ P_1^1 \times P_4^4 \end{array}$	F F ₆	442.25 417.00	106.75 101.00	130.00 116.50	16.00 15.50	38.89 38.91	33.48 33.53
$\begin{array}{c} P_2 & X & P_3 \\ P_2 & X & P^3 \\ \end{array}$	$ F_1 F_2 F_3 F_4 F_5 F_6 $	445.50 366.75 374.00 379.00 370.75 356.00	100.75 117.75 121.00 115.75 115.50 116.25	132.25 120.00 137.50 121.25 121.75 132.75	16.50 17.25 16.50 15.75 15.50 15.75	39.54 35.29 34.72 35.68 36.71 36.25	34.25 35.95 33.05 32.55 31.20 32.70
$\begin{array}{c} P_2 X P_4 \\ P_2 X P_4 \end{array}$	$ \begin{array}{c} F_1 \\ F_2 \\ F_3 \\ F_4 \\ F_5 \\ F_6 \end{array} $	423.50 391.25 397.00 384.50 352.75 364.25	119.25 111.50 118.75 111.25 114.50 113.75	128.75 106.50 107.75 107.75 130.00 103.00	17.00 16.75 18.00 16.50 17.25 18.50	40.29 37.27 37.98 38.09 35.83 36.35	$\begin{array}{r} 44.75\\36.70\\35.90\\35.73\\36.88\\45.23\end{array}$
$\begin{array}{c} P_{3} \times P\\ P_{3}^{3} \times P_{4}^{4}\\ P_{3}^{3} \times P_{4}^{4}\end{array}$	$ \begin{array}{c} F_1 \\ F_2 \\ F_3 \\ F_4 \\ F_5 \\ F_6 \end{array} $	520.50 445.00 441.25 468.75 433.25 403.75	95.25 108.50 108.00 112.50 110.25 111.00	127.00 117.25 128.75 140.25 138.25 128.50	15.25 15.75 17.50 15.75 16.50 16.75	45.65 42.76 41.71 41.60 41.44 42.29	30.00 31.53 35.70 29.25 32.15 33.15
Averages		421.02	107.49	129.08	15.86	38.01	34.14

Appendix Table 3. Continued.

	see	aea cona	1tions.	-			
Locations	Crosses	IN	INBREEDING DEPRESSION VALUES				
	(2)	F ₂	F ₃	$^{ m F}4$	F ₅	F ₆	
	P ₁ X P ₂	9.15	-1.47	19.40	-11.07	-0.21	
North	$P_1 X P_3$	32.40	-3.14	-8.42	5.18	-4.24	
Willamette	$P_1 X P_4$	4.90	25.25	7.45	-9.00	-4.64	
W IIIamette	$P_2^T X P_3^T$	10.48	-4.12	-8.16	-3.04	21.11	
	$P_2 X P_4$	-2.51	-2.11	8.67	10.69	-4.66	
	$P_3^{\prime} X P_4^{\prime}$	14.57	-6.55	8.79	-11.91	-3.65	
	Average	11.50	1,31	4.62	-3.19	1.25	
	P, XP,	37.54	-6.82	11.31	-11.00	5.22	
	$P_1^1 X P_2^2$	33.69	-6.48	4.67	-5.00	4.31	
Pendleton	$P'_1 X P'_2$	19.32	8.22	-1.96	7.99	-4.20	
	$P_2 X P_2^{\dagger}$	26.06	0.82	3.38	-8.60	3.50	
	$P_2^{\prime} X P_2^{\prime}$	23.34	15.84	-5.81	0.63	4.61	
	$P_3^2 X P_4^4$	16.94	7.56	-7.29	15.92	-5.02	
• ··· · ·	Average	26.15	3.19	0.72	-0.01	1.40	
	$P_1 X P_2$	18.20	-5.08	2.43	-2,37	10.76	
	$P_1^1 X P_2^2$	32.25	-14.69	9.05	1.00	-0.12	
Malheur	$P_1 X P_2$	29.48	0.07	3.23	-16.11	6.06	
	$P_2^{\dagger} X P_2^{\dagger}$	21.47	-1.94	-1.32	2,23	4.14	
	$P_2^{\prime} X P_1^{\prime}$	8.24	-1.45	3.25	9.00	-3.16	
	$P_3^2 \times P_4^4$	16.97	0.85	-5.87	8.19	7.31	
	Average	18.27	-3.71	1.80	0.32	4.16	
General Ave	erage	18.64	0.26	1.54	-0.96	2.27	

Appendix Table 4. Inbreeding depression values (1) for grain yield in five segregating generations of six single crosses grown at three locations under solidseeded conditions.

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

(2)
$$P = Sel. 101$$

 $P_{2}^{1} = Moro$
 $P_{3}^{2} = Brevor$
 $P_{4}^{3} = Sel. 55-1744$

Locations	Crosses	INBREEDING DEPRESSION VALUES					
	(2)	^F 2	F ₃	$^{ m F}4$	F ₅	F ₆	
North Willamette	$\begin{array}{c} P_1 & X & P_2 \\ P_1 & X & P^3 \\ P_1 & X & P^4 \\ P_2 & X & P^4 \\ P_2 & X & P^4 \\ P_3 & X & P_4 \end{array}$	-10.15 -3.91 -14.87 1.75 -7.90 -5.40	8.18 -3.94 -2.73 -3.56 -4.60 4.40	-0.99 6.39 3.47 -1.30 5.22 -0.83	-1.75 -1.18 -5.34 1.89 0.19 -2.83	0.00 2.22 1.88 -1.30 -1.71 1.02	
	Average	-6.75	-0.38	1.99	-1.50	0.35	
Pendleton	$\begin{array}{c} P & X & P \\ P_1 & X & P^2 \\ P_1 & X & P^3 \\ P_1 & X & P^4 \\ P_2 & X & P^4 \\ P_2 & X & P^4 \\ P_3 & X & P^4 \\ P_3 & X & P^4 \end{array}$	-14.05 -7.66 -18.01 -1.69 -8.30 -10.89	1.46 1.51 -5.07 -2.67 -4.58 3.38	1.70 2.21 -4.04 6.56 4.35 3.26	9.85 -5.23 -0.45 -4.19 4.12 -6.72	-1.65 0.21 4.43 2.14 -1.28 1.10	
	Average	-10.10	-0.99	2.34	-0.43	0.83	
Malheur	$\begin{array}{c} P_1 & X & P_2 \\ P_1 & X & P_3 \\ P_1 & X & P_4 \\ P_2 & X & P_4 \\ P_2 & X & P_4 \\ P_3 & X & P_4 \\ \hline \end{array}$	-14.75 -9.71 -10.03 -14.44 6.95 -12.21	1.77 -1.44 -5.49 -2.69 -6.11 0.46	$ \begin{array}{r} 1.57 \\ -1.88 \\ -0.99 \\ 4.54 \\ 6.74 \\ -4.00 \end{array} $	3.00 -2.52 -5.15 0.65 -2.84 2.04	-3.78 -0.46 5.69 -0.65 0.66 -0.68	
	Average	-9.03	-2.25	0.99	-0.80	0.13	
General Ave	erage	-8.63	-1.21	1.78	-0.91	0.44	

Appendix Table 5. Inbreeding depression values (1) for plant height in five segregating generations of six single crosses grown at three locations under solidseeded conditions.

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

(2) $P_1 = Sel. 101$ $P_1^2 = Moro$ $P_2^2 = Brevor$ $P_4^3 = Sel. 55-1744$

Locations	Crosses	INBREEDING DEPRESSION VALUES					
	(2)	F ₂	F ₃	F ₄	F ₅	F ₆	
	P, X P	19.47	-7.90	10.77	-4.81	3.65	
	$P_1^1 X P_2^2$	16.67	-10.08	9.88	-3.75	3.58	
North	$P_1^1 X P_2^3$	40.94	4.94	-10.24	-4.25	-1.29	
Willamette	$P_2^1 X P_2^4$	29.64	-10.50	21.20	-14,24	0.30	
	$P_2^{\prime} X P_1^{\prime}$	22.26	-6.41	1.30	0.65	2.68	
	$P_3^2 \times P_4^4$	32.40	1.41	-6.60	-5.61	19.78	
	Average	26.90	-4.76	4,39	-5.34	4.78	
	P, XP,	18.56	0.00	0.38	-5,90	29.40	
	$P_1^1 X P_2^2$	10.74	-12.48	1.92	-5.28	1.17	
D 11 ($P_1^1 X P_2^3$	16.93	9.49	-12.08	13.03	-8.46	
Pendleton	$P_{2}^{1} X P_{2}^{4}$	19.12	-5.21	6.43	-12.26	5.33	
	$P_2 X P_2$	8,50	5.76	-4.41	14.65	-4.58	
	$P_3^2 \times P_4^4$	19.25	-4.92	3.04	-1.79	-11.62	
	Average	15.52	-1.23	-0.79	0.41	2.37	
	P, XP	3,46	9.70	-12.71	14.56	-12.06	
	$P_1^1 X P_2^2$	17.95	-10.93	5.69	-15.70	23.52	
Malheur	$P_1^{\prime} X P_2^{\prime}$	18.97	-1.75	-7.13	-5,58	11.59	
	$P_2^{\dagger} X P_2^{\dagger}$	10.21	-12.73	13.40	-0.41	-8.29	
	$P_2^{4} \times P_2^{3}$	20.89	-1.16	0.00	-17.12	26.21	
	$P_3^2 \times P_4^4$	8.32	-8.93	-8.20	1.45	7.59	
	Average	13.30	-4.30	-1.49	-3.80	8.09	
General Ave	erage	18.57	-3.43	0.70	-2.91	5.08	
		F _{n-}	$-F_n$	• • • • • • •	-,,; <u>-</u>		

Appendix Table 6. Inbreeding depression values (1) for tiller number per unit area in five segregating generations of six single crosses grown at three locations under solid-seeded conditions.

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

(2)
$$P_1 = Sel. 101$$

 $P_2^1 = Moro$
 $P_3^2 = Brevor$
 $P_4^3 = Sel. 55-1744$

Locations	Crosses	INI	INBREEDING DEPRESSION VALUES				
	(2)	F ₂	F ₃	F_4	F ₅	F ₆	
<u> </u>	P ₁ X P ₂	10.98	-2.38	0.00	-1.18	-1.16	
N- ++	$P_1^1 X P_2^2$	-3.75	1.27	-3.66	0,00	2.50	
Willemette	$P_1 X P_2$	1.18	3.66	-1.20	3.75	9.41	
willamette	$P_2 X P_2^4$	6.82	3.53	-2.30	0.00	-2.25	
	$P_{2}^{4} \times P_{2}^{3}$	5,75	-6.45	2.20	1.11	0.00	
	$P_3^2 X P_4^4$	0.00	1.15	-2.25	9.88	-2.41	
	Average	3,50	0.13	-1.20	2.26	1.02	
	P, XP,	4.35	4.55	-1.49	-2.90	2.99	
	$P_1^1 X P_2^2$	10.00	-1.64	-1.61	-1.59	-1.56	
Pendleton	$P_1^1 X P_2^3$	7.35	-5.56	4.35	4.55	-4.35	
	$P_{2}^{1} X P_{2}^{4}$	0.00	4.23	0.00	0.00	1.43	
	$P_{2}^{4} \times P_{2}^{3}$	8.45	-5.33	-3.85	2.63	2.70	
	$P_3^2 X P_4^4$	5.80	-1.43	-2.78	-1.37	7.35	
	Average	5.99	-0,86	-0.89	0.22	1.43	
	P, XP,	3.28	-6.15	3.17	0.50	0.00	
	$P_1^1 X P_2^2$	-10.34	1.75	1,79	-3.45	-4.92	
Malheur	$P_1^{1} X P_2^{3}$	9.84	-7.58	10.00	-6.25	3,23	
	$P_{2}^{1} X P_{2}^{4}$	-4.35	4.55	4.76	1.61	-1.59	
	$P_{2}^{4} \times P_{4}^{3}$	1.49	-6.94	9.09	-4.35	-6.76	
	$P_3^4 X P_4^4$	-3.17	-10.00	11.11	-4.55	-1.49	
	Average	-0.54	-4.06	6.65	-2.75	-1.92	
General Average		1.49	-1.59	1.52	-0.23	0.18	
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Appendix Table 7.	Inbreeding depression values (1) for number of
	spikelets per spike in five segregating generations
	of six single crosses grown at three locations
	under solid-seeded conditions

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

(2)
$$P = Sel. 101$$

 $P_{2}^{1} = Moro$
 $P_{3}^{2} = Brevor$
 $P_{4}^{3} = Sel. 55-1744$

Locations	Crosses	INBREEDING DEPRESSION VALUES					
	(2)	F ₂	F ₃	\mathbf{F}_{4}	F ₅	F ₆	
	P, X P,	10.76	-2.22	1.70	0.03	-0.25	
No #th	$P_1^1 X P_2^2$	6.50	0.10	0.70	0.00	-0.76	
Willamette	$P_1^{\prime} X P_2^{\prime}$	6.12	-2.66	4.30	-3.73	3.45	
WIIIamette	$P_2 X P_2^4$	13.93	-2.46	1.07	-4.25	3.76	
	$P_2^{\prime} \times P_3^{\prime}$	15.99	-1.30	5.98	0.05	-3.99	
	$P_3^2 \times P_4^4$	10.02	2.38	0.14	-2.69	-0.44	
<u></u>	Average	10.55	-1.02	2.32	-1.77	0.89	
	P, X P	24.91	-1.77	8.46	-5.42	-4.77	
	$P_1^1 \times P_2^2$	26.64	-6.11	1.34	4.13	-2.26	
Pendleton	$P_1 X P_2^3$	10,33	0.09	1.18	4.79	4.07	
	$P_{2}^{1} \times P_{2}^{4}$	37.71	-3.95	5.75	-4.69	-2.72	
	$P_{2}^{2} \times P_{2}^{3}$	31.30	10.00	-4.02	-9.45	5.55	
	$P_3^2 \times P_4^4$	33.92	-8.17	1.42	0.03	-0.60	
	Average	27.47	-1.65	3.77	-1.77	-0.12	
	P, XP	-2.41	5.09	-2.84	1.72	-2.70	
	$P_1^1 X P_2^2$	-0.75	0.49	2.50	0.79	-0.52	
Malheur	$P_1 X P_2$	12.55	5.95	0.34	-2.65	-0.05	
	$P_{2}^{1} \times P_{2}^{4}$	12.04	1.64	-2.69	-2.81	1.27	
	$P_2^{\prime} \times P_4^{\prime}$	8.10	-1.87	-0.29	6.31	-1.43	
	$P_3^2 X P_4^4$	6.76	2.52	0.26	0.39	-2.01	
	Average	6.05	2.30	-0.45	0.63	-0.91	
General Average		14.69	-0,12	1.88	-0.97	-0.05	

Appendix Table 8. Inbreeding depression values (1) for 1000 kernel weight in five segregating generations of six single crosses grown at three locations under solidseeded conditions.

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

(2) $P_1 = Sel. 101$ $P_2^1 = Moro$ $P_3^2 = Brevor$ $P_4^3 = Sel. 55-1744$

Locations	Crosses	INBREEDING DEPRESSION VALUES					
	(2)	F ₂	F ₃	F_4	F ₅	F ₆	
	P, XP	18.05	6.04	2.63	-2.45	1.37	
	$P_1^{\prime} \times P_2^{\prime}$	-1.60	-1.57	-5.73	0,40	-1.12	
North	$\mathbf{P}_{1}^{I} \mathbf{X} \mathbf{P}_{2}^{S}$	5,55	14.60	-3.76	-1.05	-7.56	
Willamette	$P_{2}^{1} \times P_{2}^{4}$	19.64	-1.53	0.51	13.25	-7.53	
	$P_2^{\prime} \times P_2^{\prime}$	19.21	4.93	-7.20	11,23	-3.35	
	$P_3^2 X P_4^4$	16.81	1.28	-4.54	3.39	-7.03	
	Average	12.94	3.96	-3.02	4.13	-4.20	
	P, XP,	24.45	4.24	2.32	-1.11	8.88	
	$P_1 X P_2^2$	24.10	-0.88	-6.09	0.92	0.93	
Pendleton	$\mathbf{P}_{1}^{L} \mathbf{X} \mathbf{P}_{2}^{S}$	14.63	-0.77	26.05	-4.72	-7.08	
	$P_{2}^{1} \times P_{2}^{2}$	19.54	8.00	-0.70	2.43	-2.10	
	$P_2^{\prime} \times P_2^{\prime}$	30.30	6.74	3.55	-1.30	-8.45	
	$P_3^2 \times P_4^4$	23.53	-11.60	20.66	-5.06	13.19	
	Average	22.75	0.96	7.63	-1.47	0.90	
	P, XP,	6.02	-3.40	-4.92	5.03	-0.82	
	$P_1 X P_2^2$	-10.11	-12.47	19.09	-14,82	2.95	
Malhour	$P_1 X P_4$	13,74	-6.39	14.20	-9.11	-0.15	
Maineur	$P_2 X P_3^{\dagger}$	-4.73	8.77	1.54	4.33	-4.59	
	$P_2 X P_4$	21,93	2.23	0.48	-3.12	-18.46	
	$P_3^2 X P_4^2$	-4.85	-11.68	22.05	-9.02	-3,02	
	Average	3.67	-3.82	8.74	-4.45	-4.02	
General Ave	erage	13.12	0.37	4.45	-0.59	-2.44	
		F _n .	$-F_{n}$	- <u> </u>	• • • • • • • • • • • • • • • • • • •		

Appendix Table 9.

Inbreeding depression values (1) for number of kernels per spike in five segregating generations of six single crosses grown at three locations under solid-seeded conditions.

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

(2) $P_1 = Sel. 101$ $P_2^1 = Moro$ $P_3^2 = Brevor$ $P_4^3 = Sel. 55-1744$

		<u> </u>		Number of	Yield	500	Number of
Genotypes			Height	Tillers	Per	Kernel	Kernels
				Per Plant	Plant	Weight	Per Spike
Sel. 101		(P,)	95.69	34.42	66.36	20.73	46.73
Moro		(\mathbf{P}_2^1)	126.91	29.85	70.73	20.34	57.18
Brevor		(P_2^2)	124.75	33.41	63.81	22.65	41.88
Sel. 55-1744		(P_4^3)	92.07	28.65	69.53	21.70	55.81
P, XP	F,		121.16	34.01	86.89	21.17	59.57
$P_1^1 X P_2^2$	F_2^{\perp}		120.39	32.23	70.88	20.39	53.19
$P_1^1 X P_2^2$	F ₆		119.22	28.71	60.55	19.96	* 52.44
P, XP	F,		118.90	37.90	89.04	22.05	47.76
$P_1^1 X P_2^2$	F_2^{\perp}		112.28	36.26	71.64	21.37	46.14
$P_1^1 X P_3^3$	F_6^3		112.55	34.96	64.71	20.84	44.10
P, XP	F,		95.39	39.31	104.14	21.97	59.89
$P_1^{\uparrow} X P_4^{\uparrow}$	F_{2}		96.57	33.32	76.01	21.22	53.29
$P_1 X P_4^{\star}$	\mathbf{F}_{6}^{J}		103.69	27.74	62.25	21.14	52.42
P ₂ X P ₃	F,		132.18	36.75	93.53	22.15	56.16
$P_2' X P_3'$	F_2		126.20	30.01	65.77	21,23	50.67
$P_2^2 X P_3^3$	F_6^3		127.39	29.79	60.88	21.04	47.97
P, X P	F,		117.94	34.72	111.66	23.25	68.37
$P_2^2 X P_4^4$	F ¹		115.36	29.35	78.93	21.62	61.70
$P_2^2 X P_4^4$	F_6^3		120.20	28.39	64.04	21.28	52.75
PXP	F,		118.98	35.05	89.86	23.44	52.42
$P_{2}^{2} X P_{4}^{4}$	F_{2}^{\perp}		106.16	34.76	86.50	23.18	53,91
$P_3' X P_4^{\dagger}$	F ₆		111.58	29.92	61.79	22.60	46.30
Averages			114.34	32.70	75.57	21.61	52.76

Appendix Table 10. Plot means for five agronomic traits measured on 22 genotypes under spaceplanted conditions at North Willamette Experiment Station, Aurora, Oregon.

	pranted_co	nuttions at F	endieton Experin	ient Station,	Fendleton, Or	egon
			Number of	Yield	500	Number of
Genotypes		Height	Tillers	Per	Kernel	Kernels
			<u>Per Plant</u>	Plant	Weight	Per Spike
Sel. 101	(P ₁)	80.46	38.81	44.73	16.63	39.93
Moro	(\mathbf{P}_{2}^{1})	105.79	27.01	47.78	15,51	57.79
Brevor	(P_2^{L})	100.33	30.94	43.30	20.37	34.42
Sel. 55-1744	(P ₄)	72.48	26.14	38.35	15.70	46.05
P ₁ XP ₂ F ₁		104.84	36.58	63.25	16.73	51.88
$P_1 X P_2 F_3$		98.50	29.27	45.21	16.09	49.41
$P_1 X P_2^2 F_6^3$		98.27	28.95	41.96	16.39	44.84
P ₁ X P ₂ F ₁		98.60	36.54	55.51	19.13	40.13
$P_1 X P_2 F_3$		94.62	33.00	44.84	18.13	37.21
$P_1 X P_3 F_6$		93.61	34.24	44.00	17.74	36.35
P ₁ X P ₄ F ₁		75.30	33.14	52.86	17.09	45.77
$P_1 X P_4 F_3$		74.63	30.62	45.35	16.86	43.26
$P_1 X P_4 F_6$		83.19	29.33	41.59	16.87	41.79
P ₂ XP ₃ F ₁		109.41	33.56	59.24	18.95	46.54
$P_2 X P_3 F_2$		108.22	28.25	40.20	17.18	41.56
$P_2^2 X P_3^2 F_6^2$,	104.27	28.68	40.80	17.72	40.74
P, XP ₄ F ₁		98.69	34.32	66.78	16.07	60.09
$P_2 X P_4 F_3$	1	96.3 2	28,23	44.90	15.35	52.56
$P_2 X P_4 F_6$,	99.80	27.50	39.58	15.82	46.43
P ₃ XP ₄ F ₁		94.57	35.23	60.68	19.47	43.61
$P_3 X P_4 F_2$		87.31	30.08	43.22	18.05	39.89
$P_3 X P_4 F_6$		90.28	29.76	42.00	18.70	38.15
Averages	· · ·	94.07	31.14	47.55	17.30	44.52

Appendix Table 11.	Plot means for five agronomic traits measured on 22 genotypes under space-
	planted conditions at Pendleton Experiment Station, Pendleton, Oregon

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	planted_c	onditions at N	laineur Experime	ent Station, C	ontario, Orego	<u>n.</u>
			Number of	Yield	500	Number of
Genotypes		Height	Tillers	Per	Kernel	Kernels
			Per Plant	Plant	Weight	Per Spike
Sel. 101	(P,)	80.64	32.34	48.46	19.20	38.72
Moro	(P_2^1)	98.53	27.37	54.89	17.59	56.58
Brevor	(P_{2}^{2})	96.74	28.57	47.42	22.77	36.89
Sel. 55-1744	(P ₄)	75.75	22.67	46.45	20.28	49.78
P ₁ X P ₂ F	1	93.37	31.09	60,04	18.52	50.21
$P_1 X P_2 F$	3	93.23	27.23	50.06	18.38	48.84
$P_1 X P_2 F$	6	96.85	27.71	48.68	19.05	45.17
P, X P, F	2	96.53	35.81	64.40	21.54	41.39
$P_1^1 X P_2^3 F$	1	92.08	31.33	52.05	20.98	38.94
$P_1^1 X P_3^3 F$	6	94.12	34.51	56.89	21.20	38.85
P, XP, F	1	79.91	30.68	64.32	20.93	49.72
$P_1^{I} X P_4^{4} F$,L 2	78.80	29.20	55.78	20.87	45.53
$P_1 X P_4^4 F$	6	85.03	27.33	50.07	20.81	44.12
P ₂ XP ₃ F	1	96.23	30.96	66.48	21.18	50.59
$P_2 X P_3 F$	3	98.88	26.78	48.15	20.26	44.06
$P_2^2 X P_3^2 F$	6	99.20	26.14	45.95	20.30	42.89
P ₂ XP ₄ F	1	93.55	29.66	70.27	20.54	57.69
$P_2^{\prime} X P_4^{\prime} F$	2 	93.75	26.18	53.51	19.62	52.66
$P_2^2 X P_4^4 F$	6	93.44	25.35	47.58	19.61	47.96
P ₃ XP ₄ F	,]	90.53	26.11	56.14	22.31	47.04
$P_3 X P_4 T$	3	86.73	24.85	48.27	21.51	44.91
$P_3 X P_4^{\star} F$	6	86.55	24.41	43.84	21.59	41.34
Averages		90.93	28.47	53.62	20.41	46.08

Appendix Table 12. Plot means for five agronomic traits measured on 22 genotypes under spaceplanted conditions at Malheur Experiment Station. Ontario. Oregon