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Title: Influence of Competition on Combining Ability Estimates and Subsequent Prediction of Progeny Performance in Wheat (Triticum aestivum L. em Thell).

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Concerns regarding the influence of planting densities and years on estimates of genetic effects for selected traits in winter wheat prompted this investigation.

Four wheat parents and their F_1, F_2 and F_3 generations of single crosses and F_2 and F_3 generations of three-way and four-way crosses were planted in 1980-81. Generations were advanced by taking a random seed sample of 200 grams from the bulked seed of 30 unselected plants for each population. The experimental material was planted at high and low competition levels during both growing seasons. Data were collected on an individual plant basis for grain yield, yield components, biological yield, plant height and harvest index.

Estimates of general combining ability (GCA) were significant for most traits, including grain yield in both growing seasons. Interactions between GCA and competition level were detected indicating that genetic estimates obtained under two planting densities were different with the magnitude depending on the trait measured.

Estimates of specific combining ability (SCA) were also significant. The large contribution of SCA to the genetic variation among crosses in F_3 and F_4 generations was attributed to the presence of intergenomic epistasis. Interactions between SCA and competition level were not significant for most traits measured.

Correlation coefficients for GCA effects between generations in the same growing season were high. When the two growing seasons were compared, correlations were generally low.

General combining ability estimates did predict the best parental combinations for obtaining the highest percentage of desireable progeny in segregating populations for most of the traits measured. However, interactions resulting from competition levels and variation due to growing seasons should be taken into consideration in obtaining estimates of genetic effects.

Influence of Competition on Combining Ability Estimates and Subsequent Prediction of Progeny Performance in Wheat (*Triticum aestivum* L. em Thell.)

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Typed by Kathleen Miller for Leonardo R. Corral

In dedication to my wife and children
who learned the hardships and joys of
working in wheat fields.

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INFLUENCE OF COMPETITION ON COMBINING ABILITY ESTIMATES AND SUBSEQUENT PREDICTION OF PROGENY PERFORMANCE IN WHEAT (*Triticum aestivum* L. em Thell)

INTRODUCTION

Since wheat will continue to be one of the most important sources of food, it is necessary that yield levels be increased and maintained by the application of sound agronomic practices. One approach to increasing yields is by changing the genetic constitution of the wheat plant. This is accomplished through the creation of new gene combinations as the result of hybridizing genetically different cultivars.

To preclude the loss of valuable genetic material, germplasm has been collected from primary and secondary centers of origin. A significant number of wheat genotypes including land race varieties and progenitors of wheat have been collected. In the germplasm repository at Beltsville, Maryland, there are currently 47,000 different accessions which are available to plant breeding programs.

With so many genotypes, the dilemma for the plant breeder is to decide which parental combinations will generate the highest proportion of desirable segregates. For simple inherited traits the decision is easy since the phenotype closely reflects the genotypic constitution of individuals. However, for complex traits such as grain yield, the decision is difficult.

Since it is impossible to test all genotypes of wheat, the breeder needs to identify those cultivars which when hybridized will result in the most promising progeny. With this objective, several biometrical models which provide estimates of genetic effects, including combining ability analysis, have been proposed.

A further complication is that most estimates of genetic effects have been obtained from space-planted populations while wheat is grown commercially under solid-seeded conditions. It is possible that some genotypes may respond differently to these two levels of competition, thus preventing the breeder from identifying the most productive progeny. Also, estimates of genetic effects are usually obtained from the F_1 generation grown in a single year. A study of genetic effects over generations and years could provide the breeder with valuable information about the reliability of these estimates.

The objectives of this investigation were: (1) to obtain estimates of general and specific combining ability over generations grown in two different growing seasons, as a means to identify the best parental combinations, (2) to assess the influence of plant competition resulting from different seeding densities on estimates of genetic effects in early segregating generations and (3) to evaluate the possibility of predicting grain yield using several prediction models.

LITERATURE REVIEW

Combining Ability

Combining ability can be defined as the relative capacity of an individual to transmit a desirable characteristic to its progeny. In this sense, combining ability is a measure of the value of a genotype based on the performance of its offspring. Even though Vilmorin in France in the 1850's applied with success progeny tests in the improvement of sugar beets, it became apparent in the 1920's and 1930's with the development of hybrid corn the need to test the performance of a large number of inbred lines in different combinations.

Jenkins and Brunson (1932) proposed a method to determine the value of inbred lines of corn on the basis of their relative performance when crossed to an open-pollinated variety. They suggested that with this procedure about fifty percent of the lines could be eliminated without danger of losing any superior material. This allowed the classification of lines as good or poor combiners.

Sprague and Tatum (1942) introduced the concepts of General Combining Ability (GCA) and Specific Combining Ability (SCA). They defined GCA as the average performance of a line in hybrid combinations, whereas SCA was defined as the deviation of individual crosses from the average performance of a line in hybrid combinations. General Combining Ability is primarily a function of additive gene action, however, if epistasis is present GCA may include additive forms of epistasis. Specific Combining Ability is primarily a function of dominance gene action but it may also include different types of epistatic components (Moll and Stuber, 1974).

Although estimates of GCA and SCA can be obtained from experiments with different mating designs, the diallel cross analysis has been used more extensively than any other design in maize and other plant species (Hallauer and Miranda, 1981).

Using these concepts, Rinkle and Hayes (1964) tested 15 inbred lines of corn in a diallel cross and concluded that those with the largest GCA estimates tended to produce the highest yielding single crosses.

These methods were soon applied to self-pollinated species. Combining ability estimates have been obtained in research on soybeans by Leffel and Hanson (1961), on wheat by Kronstad and Foote (1964) and on barley by Smith and Lambert (1968).

In a diallel cross study with ten different winter wheat parents, Kronstad and Foote (1964) reported that most of the variance generated in the resulting progeny was attributable to GCA effects for yield, components of yield and plant height. Because these effects can be fixed in the homozygous condition, the authors indicated the usefulness of this method for selecting parents for breeding programs. THese authors also found a significant SCA for grain yield and plant height.

Significant GCA estimates for yield and some components of yield in wheat have been reported by Brown et al. (1966), Gyawali et al. (1968), Kaltsikes and Lee (1971), Bitzer and Fu (1972) and Widner and Lebsock (1973). Reports on SCA estimates vary from statistically non-significant (Brown et al., 1966; Bitzer and Fu,

1972) to statistically significant estimates (Gyawali et al., 1968; Kaltsikes and Lee, 1971; Widner and Lebsock, 1973; Bhatt, 1971). However, SCA estimates have usually been of a lesser magnitude than the estimates for GCA for the traits investigated.

Combining Ability Estimates over Generations

In a self-pollinated species such as wheat, the amount of F_1 seed obtained by hand pollination is a shortcoming in a diallel cross designed to find out the kinds of gene actions involved in determining the expression of a quantitative trait (Jordaan and Laubscher, 1968). To overcome this problem, F_1 seed could be advanced one or more generations so as to have adequate amounts of seed for testing. This also could provide an estimation of the repeatability of General and Specific Combining Ability Effects over generations. Jinks (1956) and, more recently, Stuber (1970) examined the situations that included evaluation of inbred progenies when they are generated by bulk selfing of each F_1 cross. Because of inbreeding, the contribution to the population mean due to dominance gene action is expected to be reduced by one-half with each successive generation.

Jordaan and Laubscher (1968) estimated GCA and SCA for yield in F_1 through F_5 generations of wheat and found significant mean squares for both GCA and SCA in all generations. Even though SCA decreased with advancing generations, it still made a significant contribution to the total variation in the F_5 generation.

Paroda and Joshi (1970) reported from the ratios of GCA over SCA mean squares a preponderance of non-additive gene action for the expression of grain yield in F_1, F_2 and F_3 generations of wheat.

Tandom, et al. (1970) found highly significant SCA mean squares for yield in wheat in the F_1 and F_2 generations but they were not significant for number of spikes, number of kernels and kernel weight.

In an experiment which included F_1, F_2 and F_3 generations of durum wheat, Amaya et al. (1972) using least squares analysis found that dominance gene effects were relatively more important than additive effects in the inheritance of grain yield. However, the opposite was indicated for plant height and heading date. Busch et al. (1974) also using least squares analysis in an experiment with spring wheat, reported significant SCA mean squares even in F_4 and F_5 bulks.

Cregan and Busch (1978) found significant GCA mean squares for yield in F_1 through F_5 generations of spring wheat. A significant SCA mean square for yield was found only in the F_3 generation. They also performed a diallel analysis on the mean of F_5 lines from each cross and found a significant SCA mean square for yield. This, in accordance with these investigators, suggested the importance of additive x additive epistatic variance or higher order additive epistasis in the variance of near-homozygous lines.

Other researchers have also reported results from combining ability analyses on successive generations of wheat. Bhullar et al. (1979) found that SCA effects showed little consistency and lacked repeatability over generations in wheat. Mihaljev (1980) reported highly significant GCA mean squares and of larger magnitude that SCA mean squares, for yield in F_1 through F_6 generations of wheat, however, the ratio of GCA to SCA decreased with advancing generations.

From the results of an experiment that included crosses of winter x spring wheats, Brajcich (1981) reported significant GCA mean squares for yield and components of yield in F_1 and F_2 generations. Specific combining ability mean squares were significant for plant height, harvest index and 100 kernel weight in the F_1 generation but were not significant except for plant height in the F_2 generation. Significant interactions of GCA and SCA with years and locations were also reported.

It seems that some of the discrepancies encountered among the various research reports in relation to the relative importance of GCA or SCA for different traits could be accounted for in view of the different genetic material employed in the investigations. Peterson, et al. (1969) found in a diallel study that the estimates of GCA effects were lower than those for SCA for most measured traits. They attributed this to the fact that six of the seven lines used in the investigations were high-yielding experimental lines which resulted from selection that capitalized on the additive portion of genetic variance. Intercrossing these lines allowed for the expression of non-additive genetic variance and hence a larger estimate for SCA.

It appears that the additive x additive epistatic interaction could also be inflating the estimates of specific combining ability especially in advanced generations. Cregan and Busch (1978) attributed to this cause the presence of significant SCA mean squares in F_5 lines. Matzinger and Kempthorne (1956) showed that estimates of general combining ability variances include additive genetic variance and portions of the additive and higher order epistatic variances. Similarly, estimates of specific combining ability variances include dominance variance and portions of all the various types of epistatic variances. Baker (1978) indicated that epistatic effects unpredictably affect the GCA and SCA mean squares, variances and effects. Moll and Stuber (1974) concluded from a review of quantitative genetic studies in a wide range of crop species that epistatic effects can be safely ignored in predictions of selection response. However, Hallauer and Miranda (1981) suggested that the models used to detect epistatic variances are probably inadequate.

Plant Density and Progeny Performance

The process of selection in wheat improvement usually starts in the F_2 and continues in subsequent generations. These populations are often planted in the experimental field. Certain traits, such as plant height, some types of disease resistance and time of maturity, can usually be assessed satisfactorily in space planted F_2 and F_3 populations. However, in the case of a complex trait such as grain yield, the expression of a plant genotype may vary greatly due to the predominant type of gene action involved and to the genotype x environment interaction, both of which can be influenced by the level of competition imposed by different plant densities. The problem as indicated by Donald (1968) is that the performance of a plant growing in isolation may have little relationship to its potential for yield as a community.

Genetic differences among wheat cultivars in relation to ability to compete when grown in mixtures are apparent from the results obtained by different authors (Suneson and Wiebe, 1942; Jensen and Federer, 1965; Roy, 1976; Valencia, 1980).

Intragenotypic competition among 40 adapted spring wheat cultivars was studied by Fischer and Kertesz (1976). They found a highly significant interaction between genotypes and levels of competition from space planted to solid seeded conditions. They inferred that genotypes which can more fully occupy the increased space available in space planted conditions were favored, thus the performance of non-erect genotypes improved noticably relative to that of erect types.

The effect of competition has also been studied in F_1 plants and segregating generations of wheat. Knott (1965) tested two seeding rates and found that wide spacing favored the expression of heterosis. Abi-Antoun (1977) studied the effect of three different seeding rates in the expression of types of gene action. He determined that additive gene action was predominantly involved in the expression of differences of all characteristics studied under spaced planted conditions. Non-additive gene action became more important as the competition level increased. The characteristics more affected for this trend were yield, number of spikes, spikelets per spike and plant height. This result does not support the observation made by Cregan and Busch (1978) that non-additive genetic variance may not be well expressed in wheat under solid seeded conditions. Gyawali et al. (1968) on the other hand, indicated that the magnitude of heterosis were similar in both space and solid planted experiments. Similarly Zeven (1972) reported that there was not a density effect on the expression of heterosis for yield and its components. He attributed this result to the buffering capacity of wheat as a result of its polyploid constitution. These results contradict the observation by Briggle et al. (1967) who pointed out that the maximum yield in F_1 wheat plants was obtained when they were seeded at a high density.

The presence of a significant genotype x seeding rate interaction might be expected in experiments testing segregating populations under different seeding rates. This appears not to be the case as noted by Fonseca and Patterson (1968) who evaluated the effect of different seeding rates on the performance of seven parents and the resulting F_1 and F_2 plants from a diallel cross. Little or no interaction of genotype x seeding rate was found in hill plots. Knott and Sindagi (1969) reported that the yield of 15 F_1 wheat hybrids was closely correlated at two different seeding rates, results which indicate the absence of interaction between genotype and seeding rate. A non-significant interaction between the two variables under discussion was also reported by Bitzer et al. (1971).

The effectiveness of selecting in early generations planted at different seeding rates and later performance under solid seeded conditions has been experimented by various researchers.

Jordaan and Laubscher (1968) found that specific combining ability effects estimated on the basis of progeny bulks were not comparable to those obtained in space planted populations. They recommended the use of F_2 progeny bulks to determine the breeding value of parents.

Knott (1972) indicated from results of an experiment with eight wheat crosses that to be effective in selection, yield testing should be done in an early generation on a plot basis rather than on individual plants.

Nass (1978) reported that the mean yields of F_4 lines selected at high population densities were greater than those of lines selected at low populations densities, irrespective of plant head weight in the F_2 generation. He suggested that selection should be practiced at high population densities if the selected lines of wheat are subsequently to be evaluated at high population densities comparable to commercial seeding rates. The results obtained by Kelker and Briggs (1979) from an experiment with simulated segregating rows of wheat further confirmed the idea that the best prediction about plant performance in a monoculture can be made from a segregating population in which the plants are more closely spaced.

Since it is recognized that the yield of individual plants in early generations of wheat is not always an indication of later performance, wheat breeders have tried to identify a correlated response which could be a better indicator of yield than yield per se. One correlated response to yield as suggested by Donald (1962) could be harvest index, which is the ratio of plant grain weight to total above ground plant weight.

The value of harvest index as an indicator of yield has been investigated by different authors. Syme (1972) found the harvest index rather than grain yield of spaced plants was a better predictor of yielding ability in large plots. Fischer and Kertesz (1976) observed that harvest index was more closely correlated to yield than the primary components of yield: tiller number, kernels per spike and kernel weight. They also noted that this measurement offered promise as a predictor of yielding ability since it appeared to be little affected by environmental conditions. Kertesz et al. (1980) indicated that components of yield measured on space planted F_2 and F_3 generations were rather unreliable in selecting superior lines and that only harvest index and kernel weight per head can be regarded as good selection criteria in early generations. Brajcich (1981) on the other hand, found a rather low correlation between harvest index and grain yield.

Prediction of Progeny Performance

One of the contributions of quantitative genetics to plant breeding has been the development of models to predict population means and results from selection following controlled crosses (Hallauer and Miranda, 1981).

To be able to predict with some degree of accuracy possible progeny performance is very important because the number of crosses in all combinations increases geometrically with the number of parents. If reciprocal crosses are not included with a set of n parents, it is possible to obtain n (n-1)/2 different single crosses, n(n-1) (n-2)/2 three-way crosses and n (n-1) (n-2) (n-3)/8 four-way crosses. Since it would be almost impossible for a plant breeder to handle so many crosses the development and use of models to predict progeny performance are of immense value in a breeding program.

Prediction theories involving homozygous lines were first developed for self-pollinated crops, but they are useful in maize and other cross-pollinated crops where inbred lines are used (Hallauer and Miranda, 1981). Mather (1949) provided the general formula to predict population means in any generation under selfing without selection resulting from a single cross. Mather's formula takes into consideration additive and dominance gene actions but ignores any form of epistatic gene action.

Grafius et al. (1952) examined the data obtained in a large barley experiment (Harlan et al., 1940) and suggested the possibility of selecting the highest yielding crosses just on the basis of parental performance. Sikka et al. (1959) examined the potential of 12 wheat crosses based on parental means and early generation values. They concluded that the parental values could be used with advantage to predict progeny performance in subsequent generations. Fowler and Heyne (1955) on the other hand, observed that parental performance was of no value in predicting yield of the subsequent progeny of 45 crosses of hard red winter wheat. Petpisit (1980) found that the mid-parent value was very useful in predicting plant height, tiller number and harvest index in the F_1 generation of single crosses, however, the mid-parent value did not provide an accurate prediction of progeny yield.

Prediction methods for the performance of four-way crosses in maize using single-cross data were first reported by Jenkins (1934). He suggested four alternative methods for prediction: (a) The mean performance of six possible single crosses among any set of four inbred lines, (b) The average performance of the four non-parental single crosses, (c) average performance of the four inbred lines over a series of single crosses and (d) The average performance of a set of four inbred lines when tested by the topcross procedure. Four methods differ in relation to the type of gene action involved. Methods a, c and d would predict well if only additive gene action were involved. Method b, on the other hand, would give an accurate prediction if not only additive gene action were important but also non-additive gene action. The correlation between observed and predicted means was found to be significant for all four methods. However, Jenkins found the correlation of method b to be the greatest. The prediction of four-way cross performance using method b has become an important practice in hybrid corn production.

Similar procedures can be applied for predicting the performance of three-way crosses. Patanothai and Atkins (1974) found that the average yield of the two single crosses not used in making the three way cross, a procedure which is comparable to Jenkins's method b, provided a good estimate of yield in grain sorghum. An additive model, which uses the average performance of the three parents weighted for the parent that makes a fifty percent contribution, has also been used to predict the performance of three-way crosses. Both models are reported by Petpisit (1980) to have given satisfactory results in predicting the performance of F_1 and F_2 generations of three-way crosses of wheat for plant height, grain yield, tiller number and harvest index.

Other models to predict progeny performance have also been developed. Otsuka et al. (1972) provided equations for predicting performance of single, three-way and four-way crosses based on general and specific combining ability effects. The models for three-way and four-way crosses used a weighting coefficient for specific effects to account for different experimental conditions. If the data are balanced, the weighting coefficient are equal to one. The authors noted that the models for three-way and four-way crosses were comparable in efficiency to Jenkin's b method. They concluded that accuracy of prediction depends more on number of replications and environments than on small differences in prediction methods.

The literature review reveals the importance of obtaining accurate information about the types of gene action involved in the expression of agronomic traits. It is apparent that progeny performance is affected not only by the type of gene action and environmental conditions but also by the interaction of the two factors. An understanding of how estimates of gene action vary in different generations and under different plant densities could provide valuable criteria to be applied in breeding programs.

MATERIALS AND METHODS

Four genetically diverse winter wheat cultivars were selected for this study. They were: (1) Yamhill, a mid-tall cultivar developed from the cross Heines VII/Alba, (2) Stephens, a semi-dwarf cultivar resulting from the cross of Nord Desprez and Pullman Selection 101, (3) Daws, a semi-dwarf cultivar obtained from the cross CI 1484//CI 13645/PI 178383 and (4) Druchamp, a mid-tall cultivar developed in France from the cross Vilmorin 27/Fleche d'Or. These cultivars are well-adapted to the Pacific Northwest and present a good level of resistance to the major diseases. They are being used extensively in breeding programs in the region.

All possible single crosses, excluding reciprocals, were made during the spring of 1980. The other populations used in this study came from a previous investigation (Petpisit, 1980).

This study was carried out at the Hyslop Agronomy Farm of Oregon State University during the growing seasons 1980-81 and 1981-82.

Growing Season 1980-81

In 1980-81, the experimental material consisted of the following populations:

Four parents,

six F_1 single crosses,

six F_2 single crosses,

six F_3 single crosses,

twelve F_2 three-way crosses,

twelve F_3 three-way crosses,

three F_2 four-way crosses,

three F_3 four-way crosses.

The single, three-way and four-way crosses represented all possible combinations of two, three and four parents, respectively. Reciprocal crosses were not included.

No selection pressure was imposed from one generation to the next. In all cases the seed from 30 random plants was bulked and a random sample of 200 grams was extracted from it.

At the Hyslop Agronomy Farm the soil type is a Woodburn silt loam. A winter rainfall pattern provides a wet environment through most of the growing season. Total amount of precipitation during the 1980-81 season was 971 mm. Average minimum and maximum temperatures of the year were -1.2°C and 27°C in January and July, respectively.

The date of planting was October 20, 1980. An amount equivalent to 168 kg/ha of nitrogen in the form of urea was incorporated to the experimental area in split applications: 35 kg/ha at planting time and 133 kg/ha during early spring. The level of fertility of the soil for other nutrients was medium to high. An application of the herbicide Karmex at the rate of 1.68 kg/ha was carried out to control weeds, mainly the grass *Poa annua*. Nevertheless, weed infestation was rather severe and manual weeding was performed in the early spring.

A randomized complete block design arranged as a factorial with three replications was used in this experiment. The experimental unit was a plot with three rows 3.05 m long and 30.5 cm between rows. There were 92 treatments corresponding to 46 genotypes and two planting densities or competition levels.

The competition levels were: (1) a low competition level in which plants were space planted 15 cm apart and (2) a high competition level in which plants were solid seeded at the rate of 67 kg/ha.

Because the amount of F_1 seed was limited, it was space planted in four replications.

Barley seed was planted around the borders to provide for uniform competition.

Data were recorded on an individual plant basis at harvest time in August, 1981. For this, 15 plants were randomly selected from each plot. The data recorded included: (1) plant height in centimeters from ground level to the tip of the tallest tiller excluding awns if present, (2) number of spike-bearing tillers, (3) biological yield, which is the total plant weight excluding roots, in grams and (4) grain yield per plant in grams. Harvest index was obtained from the ratio of grain yield to biological yield.

The following statistical analyses were performed:

1. Analyses of variance to test the presence of significant differences among and within genotypes and between competition levels. The presence of possible interactions was also tested. Tukey's *w* Procedure as described by Steel and Torrie (1980) was

applied in conjunction with the analysis of variance to determine statistically significant mean differences.

2. Diallel analyses for the F_1, F_2, and F_3 single crosses to estimate general and specific combining ability. These analyses followed Model I, Method 4 as proposed by Griffing (1956). Model I, a fixed model was used because the parents represented a selected group of cultivars and they constituted the population about which inferences were to be made. Method 4 excludes parents and reciprocal crosses from the analysis. General and specific combining ability effects were obtained and their standard errors estimated. To test the relative importance of general combining ability in relation to specific combining ability the ratios of $[1/(n-1)]\Sigma\hat{g}_i^2$ to $[1/n(n-3)/2]\Sigma\Sigma\hat{s}_{ij}^2$ were estimated as indicated by Jordaan and Laubscher (1968), for the traits under study, where $\hat{g}_i$'s are the general combining ability effects and $\hat{s}_{ij}$'s are the specific combining ability effects.

3. Analyses to predict yield in populations of single crosses. Three models were used to predict yield. Model I predicted yield using the mid-parent value. Model II predicted yield in terms of the formula provided by Otsuka et al. (1972):

$$\hat{Y}_{ij} = m + \hat{g}_i + \hat{g}_j + \hat{s}_{ij}$$

Where: $\hat{Y}_{ij}$ is the population predicted yield, m is the mid-parent value, $\hat{g}_i$ and $\hat{g}_j$ are the general combining ability effects for the two parents and $\hat{s}_{ij}$ is the specific combining ability effect. Model III predicted yield in terms of the formula provided by Mather (1949):

$$\bar{F}_n = [1 - (\tfrac{1}{2})^{n-1}]\ \bar{P} + (\tfrac{1}{2})^{n-1}\ \bar{F}_1$$

Where: $\overline{F}_n$ is the predicted mean yield in the n generation, $\overline{P}$ is the mid-parent value and $\overline{F}_1$ is the mean of the F_1 generation. If other than the F_1 generation is to be used, n will change accordingly.

4. Analyses to predict yield in populations of three-way crosses. Three models were used to predict yield in populations of three-way crosses. Model I is an additive model that predicted yield using the following formula:

$$\hat{Y}_{(AXB)XC} = \tfrac{1}{4}(A + B) + \tfrac{1}{2}C$$

where $\hat{Y}_{(AXB)XC}$ is the predicted yield of the three-way cross generation and A, B and C are the yield means of the parents. Model II is similar to Jenkins' method b for yield prediction in four-way crosses. The formula in this case is the following:

$$\hat{Y}_{(AXB)XC} = \tfrac{1}{2}(A \times C) + \tfrac{1}{2}(B \times C) - \tfrac{1}{2}F(H_1 + H_2)$$

Where $\hat{Y}_{(AXB)XC}$ is the predicted yield, (AXC) and (BXC) are the yield means of the single crosses, F is the inbreeding coefficient of the generation in which the prediction is to be made and H_1 and H_2 are the heterosis values of the single crosses. Model III predicts yield in terms of the formula provided by Otsuka et al. (1972) and makes use of general and specific combining ability effects. The formula is the following:

$$\hat{Y}_{ij.k} = m + \tfrac{1}{2}(\hat{g}_i + \hat{g}_j) + \hat{g}_k + \tfrac{1}{2}(\hat{s}_{ik} + \hat{s}_{jk})$$

where the symbols have a similar meaning as in Model II for single crosses.

5. Analyses to predict yield in populations of four-way crosses. Three models were also used to predict yield in four-way crosses. Model I predicted yield using the mean performance of the six

possible single crosses. Model II was the same as Jenkins' method b and so predicted yield from the performance of the four non-parental single crosses. The quantity $\frac{1}{4}F(H_1+H_2+H_3+H_4)$ was subtracted in each case to account for the generation in which the prediction was made. Model III predicted yield using the formula given by Otsuka et al. (1972):

$$\hat{Y}_{ij.kl} = m + \tfrac{1}{4}(\hat{s}_{ik} + \hat{s}_{il} + \hat{s}_{jk} + \hat{s}_{jl})$$

where the symbols have the same meaning as in Model II for single crosses. Correlation coefficients between the observed and predicted values were calculated for all the models and compared among them.

6. Analysis to evaluate the usefulness of harvest index in predicting grain yield. For this analysis, the correlation coefficient between grain yield under high competitive conditions and harvest index from populations grown under low competitive conditions was calculated.

Growing Season 1981-82

The experimental material for this growing season consisted of the following populations:

Four parents,

six F_2 single crosses,

six F_3 single crosses,

six F_4 single crosses,

three F_3 three-way crosses and

three F_4 three-way crosses.

The three-way crosses included only the parents, Yamhill, Daws and Stephens.

As already indicated, no selection pressure was imposed in these populations. For each population the seed from 30 random plants from the previous growing season was bulked and a sample of 200 grams obtained.

The total amount of precipitation during the 1981-82 growing season was 1376 mm. Average minimum and maximum temperatures of the year were 0.44°C and 25.4°C in January and July, respectively.

The date of planting was October 24, 1981. Nitrogen fertilizer in the form of urea was applied to the experimental area in three split applications: 33 kg/ha at planting time, 70 kg/ha on February 9 and 45 kg/ha on March 29. Soil fertility for other nutrients was determined to be at an adequate level.

A week prior to planting date, the soil was fumigated with a mixture of methyl-bromide (66%) and chloropicrin (34%) at the rate of 420 kg/ha. The objective of this treatment was to eliminate weed seeds and soil-borne pathogens. In order to control major disease complexes, fungicide applications were made. A mixture of 1.7 l/ha of Bravo and 0.3 l/ha of Bayleton was applied on April 21. Thereafter, two applications of Tilt at the rate of 0.4 l/ha were made on May 7 and May 23. These treatments appeared to provide a good weed and disease control.

The experimental design was the same as in the previous year. There were 56 treatments corresponding to 28 genotypes and two planting densities or competition levels. The number of replications was three. The experimental unit was a plot with four rows, 3.05 m long. The distance between rows was 30.5 cm.

The two competition levels were (1) a low competition level in which plants were space planted 22.5 cm apart and (2) a high competition level in which plants were space planted 7.5 cm apart. Barley was planted around the borders to provide for uniform competition.

Data were collected in a similar form as in the previous year at harvest time in August 1982. The weight of 100 kernels in decigrams was also recorded. In addition to harvest index, the number of kernels per spike was calculated from the collected data.

The statistical analyses performed were similar to those carried out for the 1980-81 data, with the exception of the four-way cross evaluation.

EXPERIMENTAL RESULTS

Growing Season 1980-81

Evaluation of Populations

The observed mean squares for plant height, tiller number, biological yield, grain yield and harvest index are presented in Table 1. There were significant differences among treatments for all the traits studied. Differences among genotypes were found for plant height, tiller number and harvest index. Population differences for plant height, tiller number and harvest index were also noted. Parents also differ for plant height, tiller number and harvest index. Within segregating populations, differences were apparent for plant height except for four-way crosses. For the other traits, differences were detected among F_2 single crosses for tiller number and harvest index and among F_3 four-way crosses for harvest index. The effect of level of competition was significantly different for all the traits. Significant interactions involving genotypes, populations and parents with competition level were only detected for tiller number. No interactions were noted for the segregating populations with competition level for any trait. Coefficients of variation (C.V.) were low for plant height (4.27%) and harvest index (7.98%) and intermediate for tiller number (11.51%), biological yield (13.57%) and grain yield (13.96%).

Table 1. Observed mean squares for plant height, tiller number, biological yield, grain yield and harvest index for parents, single, three-way and four-way crosses for the year 1980-81.

Source	df	Mean Squares				
		Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
Replications	1	51.07	1.27	49.56	176.25	512.55
Treatments	91	101.92**	29.24**	2611.79**	245.93**	102.80**
Genotypes	45	154.49**	1.76**	102.15	12.92	26.20**
Populations	6	132.80**	3.79**	123.33	23.30	32.89*
Parents	3	421.43**	2.38*	33.56	11.47	54.97**
F_2 Single Crosses	5	221.34**	2.28*	78.73	19.51	38.94*
F_3 Single Crosses	5	226.35**	1.58	29.86	8.55	23.07
F_2 Three-way Crosses	11	96.90**	1.17	131.15	5.55	23.54
F_3 Three-way Crosses	11	106.68**	1.23	135.23	15.14	15.50
F_2 Four-way Crosses	2	135.74**	0.10	91.30	13.83	0.78
F_3 Four-way Crosses	2	70.87	1.67	50.08	5.85	37.79*
Competition Level	1	922.96**	2516.77**	229009.00**	21267.14**	7654.22**
Genotype x Competition	45	31.10	1.41*	90.39	11.82	11.60
Populations x Competition	6	33.22	2.33*	126.14	15.66	19.97
Parents x Competition	3	14.75	2.37*	50.67	10.91	1.92
F_2 Single Crosses x Comp.	5	3.55	1.83	81.06	15.75	14.98
F_3 Single Crosses x Comp.	5	39.18	2.09*	70.71	14.24	2.46
F_2 Three-way Crosses x Competition	11	28.85	1.15	67.99	5.90	11.72
F_3 Three-way Crosses x Competition	11	37.43	0.70	123.06	11.99	15.09
F_2 Four-way Crosses x Competition	2	79.99	0.47	127.58	15.51	3.48
F_3 Four-way Crosses x Competition	2	26.90	0.58	21.60	13.86	3.83
Error	91	26.77	0.82	76.53	12.04	11.82
C.V. (%)		4.27	11.51	13.57	13.96	7.98

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Evaluation of Parents

The performance of the four parents grown under high competitive and low competitive conditions is presented in Table 2 and 3, respectively. The tallest parent was Druchamp while the shortest was Stephens under both planting densities. Under low competitive conditions, Stephens produced more tillers, had larger biological and grain yields than the other parents although the differences for the other two traits were not significant. Druchamp had the lowest harvest index under both competition levels whereas Daws presented the largest harvest index under low competitive conditions. Significant differences were not detected among the parents for tiller number, biological yield, grain yield and harvest index under high competitive conditions. However, under this planting density, Druchamp had the highest mean for tiller number and biological yield, however its grain yield mean was smaller than that of the other parents.

Estimates of Combining Ability

The mean squares for plant height, tiller number, biological yield, grain yield and harvest index for the F_1 generation are indicated in Table 4. Differences among crosses were found for plant height, tiller number, biological yield and grain yield. No differences were detected for harvest index. The performance of the F_1 generation is shown in Table 5. The cross Stephens/Daws was the shortest of all parents and also had the largest mean value for tiller number. The cross Stephens/Druchamp resulted in the largest mean value for biological yield, but it was significantly

Table 2. Comparison of the performance for plant height, tiller number, biological yield, grain yield and harvest index of four parents grown under high competitive conditions in 1980-81.

Parents	Means				
	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill	118.03 b[1/]	4.07 a	30.83 a	15.90 a	52.31 a
Stephens	104.43 a	4.17 a	28.07 a	14.87 a	53.99 a
Daws	119.83 bc	4.23 a	29.67 a	15.67 a	53.56 a
Druchamp	132.37 c	4.66 a	32.07 a	14.47 a	45.84 a

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 3. Comparison of the performance for plant height, tiller number, biological yield, grain yield and harvest index of four parents grown under low competitive conditions in 1980-81.

Parents	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill	116.93 a[1/]	9.00 a	87.43 a	30.60 a	37.36 ab
Stephens	112.20 a	12.63 b	100.33 a	36.43 a	36.58 ab
Daws	120.60 ab	11.20 ab	87.50 a	33.67 a	39.37 b
Druchamp	133.96 b	10.40 ab	94.86 a	29.06 a	30.65 a

[1/] Means with a letter in common are not significant different, according to Tukey's test, at the 0.05 probability level.

Table 4. Mean square values for plant height, tiller number, biological yield, grain yield and harvest index for the F_1 single crosses grown in 1980-81.

		Mean squares				
Source	df	Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
Replications	3	243.36	36.26	5299.72	44.36	73.80
Crosses	5	1707.10**	37.70**	1728.94*	397.90**	35.89
Crosses x Replications	15	170.15	7.18	609.67	213.29	8.22
Error	336	28.78	7.61	776.52	107.96	47.26

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5. Mean values for plant height, tiller number, biological yield, grain yield and harvest index from the F_1 generation grown in 1980-81.

F_1 Single Crosses	Means				
	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill/Stephens	127.22 b[1/]	10.22 b	96.73 ab	41.00 b	42.93 a
Yamhill/Daws	131.25 c	9.42 a	90.68 a	39.22 b	43.70 a
Yamhill/Druchamp	132.33 c	10.20 b	98.13 ab	36.37 a	37.95 a
Stephens/Daws	118.53 a	11.65 c	93.41 ab	36.42 a	39.43 a
Stephens/Druchamp	131.58 c	10.45 b	106.20 b	38.40 a	37.17 a
Daws/Druchamp	131.65 c	9.58 a	94.50 ab	33.67 a	36.05 a

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

different only from the mean of Yamhill/Daws. For grain yield, mean values for Yamhill/Stephens and Yamhill/Daws were similar and significantly larger than the means of the other F_1 crosses.

The combining ability estimates for plant height, tiller number, biological yield, grain yield and harvest index for the F_1 generation are indicated in Table 6. General combining ability estimates were significant for all traits under study. Specific combining ability estimates were significant only for plant height and tiller number. The general combining ability effects for the four parents are presented in Table 7. Stephens had the lowest effect for plant height but the largest for tiller number. Although Druchamp had the largest effects for plant height and biological yield it had the lowest for grain yield and harvest index. The lowest effect for biological yield was that of Daws whereas the largest effect for grain yield was for Yamhill.

Specific combining ability effects for the four parents can be found in Table 8. The largest effects for plant height, biological yield, grain yield and harvest index resulted from the combinations of Yamhill/Daws and Stephens/Druchamp. For tiller number the combinations Yamhill/Druchamp and Stephens/Daws presented the largest effects.

Mean squares for different characteristics from individual plants of the F_2 generation are shown in Table 9. Crosses were significantly different for all the traits measured. The level of competition also resulted in differences for all traits. The

Table 6. Combining ability estimates for plant height, tiller number, biological yield, grain yield and harvest index of F_1 single crosses grown in 1980-81.

Source	df	Mean Squares				
		Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
GCA	3	35.03**	0.60*	44.67*	9.07**	15.36**
SCA	2	18.59**	0.68**	5.04	2.97	1.53
Error	336	0.48	0.13	12.94	1.80	0.79

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 7. Estimates of general combining ability effects from F_1 generation for plant height, tiller number, biological yield, grain yield and harvest index for the four parents.

Parents	General Combining Ability Effects				
	Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
Yamhill	2.26	-0.46	-2.15	2.03	2.98
Stephens	-4.48	0.78	3.26	1.64	0.46
Daws	-2.43	-0.07	-5.62	-1.62	0.28
Druchamp	4.64	-0.27	4.50	-2.05	-3.72
S.E. $(\hat{g}_i-\hat{g}_j)$	0.69	0.36	3.60	1.34	0.89

Table 8. Estimates of specific combining ability effects ($\hat{s}_{ij}$) for plant height, tiller number, biological yield, grain yield and harvest index from the F_1 generation for four parents grown in 1980-81.

Parent	Trait	Parent: Stephens	Daws	Druchamp
Yamhill	Plant Height	0.68	2.66	-3.33
	Tiller Number	-0.35	-0.32	0.67
	Biological Yield	-1.00	1.83	-0.84
	Grain Yield	-0.18	1.30	-1.12
	Harvest Index	-0.05	0.90	-0.85
Stephens	Plant Height		-3.33	2.66
	Tiller Number		0.66	-0.32
	Biological Yield		-0.84	1.83
	Grain Yield		-1.12	1.30
	Harvest Index		-0.85	0.90
Daws	Plant Height			0.68
	Tiller Number			-0.35
	Biological Yield			-1.00
	Grain Yield			-0.18
	Harvest Index			-0.05

Standard Error	Plant Height	Tiller Number	Plant Height	Grain Yield	Harvest Index
S.E. ($\hat{s}_{ij}$-$\hat{s}_{ik}$)	0.69	0.36	3.60	1.34	0.89

Table 9. Mean square values for plant height, tiller number, biological yield, grain yield and harvest index for F_2 populations grown in 1980-81.

Source	df	Mean squares				
		Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
Replications	1	49.14	1.23	918.40	334.46	1727.03
Treatments	11	1732.95**	552.43**	45336.50**	4667.46**	1823.13**
Crosses	5	3320.05**	34.27**	1180.96*	292.67**	584.19**
Competition	1	2195.34**	5768.00**	486717.00**	48697.10**	16009.30**
Crosses x Competition	5	53.38	27.47**	1215.90*	236.32**	224.83**
Replications x Treatments	11	669.02	11.01	1353.02	196.15	48.23
Error	336	156.68	4.26	459.68	62.48	43.69

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

interaction between crosses and the level of competition proved to be significant for all traits with the exception of plant height.

The performance of the F_2 generation grown under high and low competitive conditions is shown in Table 10 and 11, respectively. Only the mean values for plant height and harvest index were significantly different in the high competition level. Stephens/Daws presented the lowest mean value for plant height whereas Yamhill/Daws presented the largest mean value for the same trait. Yamhill/Daws, Stephens/Daws and Daws/Druchamp had a larger harvest index mean values than the other crosses. Although the differences among means for tiller number, biological yield and grain yield were not significant, Stephens/Druchamp produced the highest mean values for these traits. In the low competitive level, Stephens/Daws and Yamhill/Stephens had the lowest mean values for plant height whereas Yamhill/Druchamp had the highest mean value for this trait. For tiller number and grain yield, Stephens/Daws and Yamhill/Daws presented the highest mean values, respectively. Yamhill/Druchamp had the lowest mean value for grain yield and harvest index although the differences for this last trait were not significant.

Mean squares calculated from individual F_3 plants are shown in Table 12. Significant differences among treatments (populations and densities) were observed for traits. Differences among crosses were significant only for plant height, tiller number and harvest index. The level of competition produced significant differences for all the traits except plant height. A significant

Table 10. Comparison of the performance for five traits from six F_2 populations grown under high competitive conditions in 1980-81.

F_2 Single Crosses	Means: Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill/Stephens	116.43 ab[1/]	3.96 a	27.96 a	12.73 a	46.19 a
Yamhill/Daws	132.83 c	3.36 a	25.76 a	14.20 a	54.06 b
Yamhill/Druchamp	130.33 c	4.16 a	29.40 a	13.27 a	46.31 a
Stephens/Daws	114.06 a	4.20 a	25.80 a	13.50 a	53.41 b
Stephens/Druchamp	128.33 c	4.63 a	32.93 a	15.17 a	46.98 a
Daws/Druchamp	124.33 bc	3.56 a	24.50 a	13.00 a	54.19 b

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 11. Comparison of the performance for plant height, tiller number, biological yield, grain yield and harvest index of six F_2 populations grown under low competitive conditions in 1980-81.

F_2 single crosses	Means				
	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill/Stephens	111.90 a[1/]	11.67 a	106.03 a	38.52 bcd	37.29 a
Yamhill/Daws	125.87bc	11.83 a	108.33 a	42.83 d	40.24 a
Yamhill/Druchamp	128.40 c	11.40 a	105.10 a	31.93 a	30.84 a
Stephens/Daws	110.20 a	14.70 b	107.13 a	39.10 cd	36.47 a
Stephens/Druchamp	121.77 bc	11.33 a	94.33 a	36.10 abc	38.77 a
Daws/Druchamp	118.47 ab	11.00 a	87.67 a	32.90 ab	37.50 b

[1/]Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 12. Mean square values for plant height, tiller number, biological yield, grain yield and harvest index for F_3 populations grown in 1980-81.

Source	df	Mean Squares: Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
Replications	1	235.22	1.34	966.94	44.10	243.54
Treatments	11	1825.33**	497.66**	39890.70**	3352.25**	1747.00**
Crosses	5	3395.18**	23.77**	447.98	128.29	346.18**
Competition	1	164.03	5198.40**	431254.00**	35164.90**	17301.40**
Crosses x Competition	5	587.73**	31.39**	1060.76	213.67**	36.93
Replications x Treatments	11	624.71	18.16	1575.90	126.94	294.81
Error	336	179.97	6.76	548.04	61.45	44.41

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

interaction between crosses and competition level was noted for plant height, tiller number and grain yield.

Mean values of the six F_3 populations grown under high and low competitive conditions are presented in Tables 13 and 14, respectively. In the high competitive level, only the means for plant height and harvest index showed differences. Stephens/Daws and Yamhill/Stephens had the lowest mean value for plant height whereas the crosses involving Druchamp had the highest mean values for this trait. For harvest index, the mean of Stephens/Daws was the largest whereas that of Yamhill/Druchamp was the lowest. Although no differences were detected for tiller number, biological yield and grain yield, Yamhill/Druchamp had the largest mean values for these traits. In the low competitive level, differences among means were detected for all traits except for biological yield. For plant height the lowest mean value was that of Yamhill/Stephens although it was not different from the mean values of the Yamhill/Daws and Stephens/Daws crosses. Yamhill/Druchamp had the lowest mean values for tiller number, grain yield and harvest index. The largest mean values for tiller number and grain yield were those of the Yamhill/Stephens cross, whereas for harvest index it was that of Stephens/Daws.

Combining ability analyses for plant height from F_2 and F_3 generations are presented in Table 15. Differences for GCA were noted for both F_2 and F_3 generations. The SCA estimate was significant in the F_2 generation only. An interaction between SCA and level of competition was detected in the F_3 generation.

Table 13. Comparison of the performance for five traits from six F_3 populations grown under high competitive conditions in 1980-81.

F_3 Single Crosses	Means: Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill/Stephens	115.30 a[1/]	4.26 a	28.73 a	14.33 a	50.72 bc
Yamhill/Daws	122.80 ab	3.36 a	24.96 a	11.53 a	47.38 ab
Yamhill/Druchamp	127.93 b	4.80 a	33.40 a	14.40 a	44.19 a
Stephens/Daws	113.53 a	3.70 a	25.56 a	13.17 a	52.82 c
Stephens/Druchamp	129.06 b	4.43 a	28.60 a	13.73 a	49.44 bc
Daws/Druchamp	129.03 b	4.00 a	29.03 a	13.37 a	47.15 ab

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 14. Comparison of the performance for plant height, tiller number, biological yield, grain yield and harvest index of six F_3 populations grown under low competitive conditions in 1980-81.

F_3 Single Crosses	Means: Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	Harvest Index (%)
Yamhill/Stephens	109.90 a[1/]	13.80 c	102.60 a	36.63 b	35.83 ab
Yamhill/Daws	116.13 ab	11.13 ab	105.63 a	35.70 b	35.13 ab
Yamhill/Druchamp	129.43 cd	10.26 a	94.47 a	28.83 a	31.23 a
Stephens/Daws	118.50 abc	12.47 bc	99.76 a	35.63 b	36.31 b
Stephens/Druchamp	120.63 bc	11.23 ab	87.73 a	30.86 ab	35.88 ab
Daws/Druchamp	134.96 d	11.23 ab	95.43 a	31.47 ab	34.15 ab

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 15. Combining ability estimates for plant height of the F_2 and F_3 populations grown under two competition levels in 1980 - 81.

Source	df	Mean Squares for Plant Height F_2 single crosses	F_3 single crosses
GCA	3	61.18**	94.26**
SCA	2	46.61**	0.01
GCA X Competition	3	0.24	5.98
SCA X Competition	2	1.86	15.52**
Error	336	2.61	3.00

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Estimates for combining ability involving tiller number from the F_2 and F_3 populations are shown in Table 16. General and specific combining ability estimates were both significant in the F_2 generation whereas only GCA was significant for tiller number in the F_3 generation. The interaction of GCA with level of competition was significant in both generations. Interaction of SCA with level of competition was found only in the F_2 generation.

The F_2 and F_3 generation combining ability estimates for biological yield are presented in Table 17. General combining ability estimates were significant in the F_2 but not in the F_3 generation. Specific combining ability estimates were not significant in either the F_2 or the F_3 generation. There was an interaction between GCA and level of competition for both generations. No interaction was detected between SCA and competition levels in either generation for this trait.

The combining ability analyses for grain yield from F_2 and F_3 generations are presented in Table 18. General combining ability estimates were significant in both F_2 and F_3 generations for grain yield. Specific combining ability estimates were significant only in the F_2 generation. Interactions between GCA and competition level were observed in the F_2 and F_3 generations. No interaction was detected between SCA and competition for grain yield in either generation.

In Table 19, the combining ability analyses for harvest index are presented. Differences were detected for GCA, SCA and their

Table 16. Combining ability estimates for tiller number of the F_2 and F_3 populations grown under two competition levels in 1980-81.

Source	df	Mean squares for tiller number	
		F_2 single crosses	F_3 single crosses
GCA	3	0.54**	0.44*
SCA	2	0.62**	0.33
GCA X Competition	3	0.57**	0.72**
SCA X Competition	2	0.25*	0.23
Error	336	0.071	0.113

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 17. Combining ability estimates for biological yield of the F_2 and F_3 populations grown under two competition levels in 1980-81.

Source	df	Mean squares for biological yield	
		F_2 Single Crosses	F_3 Single Crosses
GCA	3	22.54*	10.73*
SCA	2	15.44	2.60
GCA X Competition	3	27.47*	28.51*
SCA X Competition	2	9.36	0.91
Error	336	7.66	9.13

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 18. Combining ability estimates for grain yield of the F_2 and F_3 populations grown under two competition levels in 1980-81.

Source	df	Mean squares for grain yield: F_2 Single Crosses	F_3 Single Crosses
GCA	3	4.89**	3.15*
SCA	2	4.87**	0.62
GCA X Competition	3	5.94**	5.43**
SCA X Competition	2	0.93	0.69
Error	336	1.04	1.02

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 19. Combining ability estimates for harvest index of the F_2 and the F_3 populations grown under two competition levels in 1980-81.

Source	df	Mean squares for harvest index	
		F_2 Single Crosses	F_3 Single Crosses
GCA	3	12.62**	8.82**
SCA	2	5.41**	0.45
GCA X Competition	3	3.94**	0.74
SCA X Competition	2	3.38**	0.43
Error	336	0.73	0.74

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

interactions with competition level in the F_2 generation. In the F_3 generation only GCA was significantly different for harvest index.

General combining ability effects estimated from the F_2 and F_3 generations for the high and low competition level are provided in Table 20.

For plant height, Druchamp presented larger effects than the other parents in both generations and under both competition levels. Stephens presented the lowest effects in both competition levels and generations. Yamhill had larger effects than Daws for plant height except under low competitive conditions in the F_3 generation.

Stephens consistently had positive effects across generations and competition levels for tiller number. The GCA effects of Yamhill for tiller number were negative in the F_2 generation and positive in the F_3 generation. Positive effects under high competitive conditions, but negative effects under low competitive conditions, were noted for Druchamp in the number of tillers. Effects of Daws were larger under low competitive conditions than under high competitive conditions. The GCA effects for tiller number were generally small.

The GCA effects for biological yield were all positive for Yamhill. Stephens had positive effects in the F_2 generation under both competition levels but negative effects in the F_3 generation. The smallest effects were those of Druchamp in both

Table 20. General combining ability effects estimated from plants of the F_2 and F_3 generations grown under high competitive conditions ($\hat{g}_1$) and low competitive conditions ($\hat{g}_2$) for plant height, tiller number, biological yield, grain yield and harvest index in 1980-81.

Trait and Parents	F_2		F_3	
	$\hat{g}_1$	$\hat{g}_2$	$\hat{g}_1$	$\hat{g}_2$
Plant Height				
Yamhill	3.24	3.94	-1.40	-4.66
Stephens	-7.14	-7.22	-5.47	-7.87
Daws	-0.99	-1.88	-1.74	2.41
Druchamp	4.89	5.16	8.60	10.12
S.E. ($\hat{g}_j-\hat{g}_i$)	1.62		1.73	
Tiller Number				
Yamhill	-0.22	-0.53	0.07	0.07
Stephens	0.42	0.87	0.07	1.22
Daws	-0.41	0.78	-0.62	-0.12
Druchamp	0.21	-1.12	0.48	-1.17
S.E. ($\hat{g}_j-\hat{g}_i$)	0.27		0.34	
Biological Yield				
Yamhill	0.23	7.58	0.97	4.92
Stephens	1.51	1.60	-1.12	-1.33
Daws	-3.31	-0.58	-2.79	3.98
Druchamp	1.57	-8.60	2.94	-7.57
S.E. ($\hat{g}_j-\hat{g}_i$)	2.77		3.02	
Grain Yield				
Yamhill	-0.37	1.31	-0.01	0.80
Stephens	0.23	1.53	0.49	1.79
Daws	-0.12	2.06	-1.10	1.62
Druchamp	0.25	-4.89	0.62	-4.20
S.E. ($\hat{g}_j-\hat{g}_i$)	1.02		1.01	
Harvest Index				
Yamhill	-2.00	-1.09	-1.78	-1.04
Stephens	-1.99	0.99	3.57	1.88
Daws	5.55	1.83	0.75	0.66
Druchamp	-1.55	-1.73	-2.54	-1.50
S.E. ($\hat{g}_j-\hat{g}_i$)	0.85		0.85	

generations under low competitive conditions, whereas Daws presented the smallest effects in the high competition level.

For grain yield Stephens had positive effects in both generations and under both competition levels. Yamhill and Daws had positive effects under the low competition level and negative effects under the high competition level in both generations. Druchamp had large negative effects under low competitive conditions and small positive effects under high competitive conditions in both generations for grain yield.

General combining ability effects for harvest index were all negative for Yamhill and Druchamp and of about the same magnitude. The effects of Daws were positive and larger than those of Stephens in the F_2 generation for both competition levels. The GCA effects of Stephens for harvest index were larger than the effects of Daws in the F_3 generation under both competitive conditions.

Specific combining ability effects estimated from F_2 and F_3 generation data are provided in Tables 21 and 22, respectively.

For plant height, Yamhill/Daws and Stephens/Druchamp presented the largest SCA effects in the F_2 generation for both competition levels. The crosses Yamhill/Stephens and Daws/Druchamp had the lowest effects for this trait in the F_2 generation. In the F_3 generation, SCA effects were inconsistent. Under high competitive conditions, Yamhill/Daws and Stephens/Druchamp presented the largest effects, while the same crosses had the smallest effects under low competitive conditions.

Table 21. Estimates of specific combining ability effects under high ($\hat{s}_1$) and low ($\hat{s}_2$) competitive conditions for plant height, tiller number, biological yield, grain yield and harvest index from F_2 populations grown in 1980-81.

Parent and Trait	Stephens $\hat{s}_1$	Stephens $\hat{s}_2$	Daws $\hat{s}_1$	Daws $\hat{s}_2$	Druchamp $\hat{s}_1$	Druchamp $\hat{s}_2$
Yamhill						
Plant Height	-4.04	-4.24	6.21	4.38	-2.17	-0.13
Tiller Number	-0.22	-0.65	0.02	-0.41	0.20	1.06
Biological Yield	-1.66	-4.58	1.96	-0.10	-0.29	4.68
Grain Yield	-0.78	-1.17	1.04	2.56	-0.26	-1.39
Harvest Index	0.00	0.55	0.33	2.65	-0.33	-3.20
Stephens						
Plant Height			-2.17	-0.13	6.21	4.38
Tiller Number			0.20	1.06	0.02	-0.41
Biological Yield			-0.29	4.68	1.96	-0.10
Grain Yield			-0.26	-1.39	1.04	2.56
Harvest Index			-0.33	-3.20	0.33	2.65
Daws						
Plant Height					-4.04	-4.24
Tiller Number					-0.22	-0.65
Biological Yield					-1.66	-4.58
Grain Yield					-0.78	-1.17
Harvest Index					0.00	0.55

Standard Error	Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
S.E. ($\hat{s}_{ij}-\hat{s}_{ik}$)	1.62	0.27	2.77	1.02	0.85

Table 22. Estimates of specific combining ability effects under high ($\hat{s}_1$) and low ($\hat{s}_2$) competitive conditions for plant height, tiller number, biological yield, grain yield and harvest index from F_3 populations grown in 1980-81.

Parent and Trait	Stephens $\hat{s}_1$	Stephens $\hat{s}_2$	Daws $\hat{s}_1$	Daws $\hat{s}_2$	Druchamp $\hat{s}_1$	Druchamp $\hat{s}_2$
Yamhill						
Plant Height	-0.78	0.84	2.99	-3.21	-2.21	2.37
Tiller Number	0.05	0.83	-0.21	-0.51	0.16	-0.32
Biological Yield	0.50	1.39	-1.60	-0.89	1.10	-0.50
Grain Yield	0.43	0.86	-0.79	0.10	0.36	-0.96
Harvest Index	0.32	0.24	-0.21	0.75	-0.11	-0.99
Stephens						
Plant Height			-2.21	2.37	2.99	-3.21
Tiller Number			0.16	-0.32	-0.21	-0.51
Biological Yield			1.10	-0.50	-1.60	-0.89
Grain Yield			0.36	-0.96	-0.79	0.10
Harvest Index			-0.11	-0.99	-0.21	0.75
Daws						
Plant Height					-0.78	0.84
Tiller Number					0.05	0.83
Biological Yield					0.50	1.39
Grain Yield					0.43	0.86
Harvest Index					0.32	0.24

Standard Error	Plant Height	Tiller Number	Biological Yield	Grain Yield	Harvest Index
S.E. ($\hat{s}_{ij}-\hat{s}_{ik}$)	1.73	0.34	3.02	1.01	0.85

Specific combining ability effects were small and consistent in each generation for both competition levels for tiller number. Stephens/Daws and Yamhill/Druchamp presented the largest effects in the F_2 generation. In the F_3 generation, Yamhill/Stephens and Daws/Druchamp had the largest SCA effects for tiller number.

Yamhill/Druchamp and Daws/Stephens in the F_2 generation had the largest SCA effects for biological yield. In the F_3 generation, the SCA effects were the largest for Yamhill/Stephens and Daws/Druchamp.

For grain yield, Yamhill/Daws and Stephens/Druchamp presented the largest SCA effects under both competition levels in the F_2 generation. In the F_3 generation, Yamhill/Stephens and Daws/Druchamp had the largest SCA effects under both competition levels.

The SCA effects for harvest index were the largest for Yamhill/Daws and Stephens/Druchamp in both competition levels for the F_2 generation. In general, SCA effects were small in the F_3 generation with the largest effects being those of Yamhill/Daws and Stephens/Druchamp under the low competition level.

The ratios of GCA effects to SCA effects estimates from the F_1, F_2, and F_3 generations are provided in Table 23. Ratios larger than one were observed for plant height in the F_3 generation under both competition levels. For tiller number, ratios larger than one were observed for the F_2 and F_3 generations under high competitive conditions. All the ratios were larger than one for biological yield except for the ratios of the

Table 23. Comparison of the ratios of general combining ability effects to specific combining ability effects for five traits and two competition levels from F_1, F_2 and F_3 single crosses grown in 1980-81.

Trait	Generation	Low Competition	High Competition	Both Levels
Plant Height	F_1	0.942	--	--
	F_2	0.875	0.483	0.656
	F_3	3.85	2.510	242.94
Tiller Number	F_1	0.444	--	--
	F_2	0.564	1.641	0.431
	F_3	0.912	2.884	0.674
Biological Yield	F_1	1.475	--	--
	F_2	1.044	0.786	0.730
	F_3	11.109	1.544	2.060
Grain Yield	F_1	1.527	--	--
	F_2	1.090	0.051	0.499
	F_3	4.809	0.648	2.523
Harvest Index	F_1	4.996	--	--
	F_2	0.162	62.990	1.172
	F_3	1.521	48.187	10.262

F_2 generation under the high level of competition. Ratios were larger than one for grain yield with the exception of those for the high level of competition. For harvest index, only the ratio from the F_2 generation under low competitive conditions was smaller than one. In general, it can be observed that ratios tended to increase with advancing generations.

Grain Yield Prediction

Three models were used to predict the grain yield of six single crosses for the F_1, F_2 and F_3 generations. The observed and predicted values are presented in Table 24. Model I which predicts grain yield using the mid-parent value had a correlation coefficient with observed yield of 0.492. Model II which estimates potential grain yield in terms of GCA and SCA effects had a correlation coefficient of 0.806. Model III which relies on the mean of the parents, the F_1 generation mean and inbreeding coefficients had a correlation of 0.812.

The observed and predicted values and the respective correlation coefficients for the F_2 and F_3 generations of three-way crosses using three models are shown in Table 25. Preditions from Model I, an additive model which uses a weighted contribution from each parent depending on the order of the cross, had a correlation coefficient with actual yield of 0.11. Model II, an additive and non-additive model that relies for prediction on the mean performance of the two non-parental single crosses, resulted in a correlation coefficient between predicted and actual yield of 0.20. Model III, that predicts in terms of GCA and SCA effects, resulted

Table 24. Comparison and correlation involving three models for predicting yield of six single crosses from the F_1, F_2 and F_3 generations grown in 1980-81.

Single Crosses	Yield in grams			
	Observed Yield (g)	Model I	Model II	Model III
F_1 Yamhill/Stephens	41.00	33.52	37.01	--
F_2 Yamhill/Stephens	38.57	33.52	36.36	37.26
F_3 Yamhill/Stephens	36.63	33.52	36.97	35.39
F_1 Yamhill/Daws	39.22	32.14	33.85	--
F_2 Yamhill/Daws	42.83	32.14	38.07	35.68
F_3 Yamhill/Daws	35.70	32.14	34.66	33.91
F_1 Yamhill/Druchamp	36.37	29.83	28.69	--
F_2 Yamhill/Druchamp	31.93	29.83	24.86	33.10
F_3 Yamhill/Druchamp	28.83	29.83	25.47	31.47
F_1 Stephens/Daws	36.42	35.05	34.40	--
F_2 Stephens/Daws	39.10	35.05	37.25	35.74
F_3 Stephens/Daws	35.63	35.05	37.50	35.39
F_1 Stephens/Druchamp	38.40	32.75	33.64	--
F_2 Stephens/Druchamp	36.10	32.75	31.95	35.58
F_3 Stephens/Druchamp	30.86	32.75	30.44	34.16
F_1 Daws/Druchamp	33.67	31.37	27.52	--
F_2 Daws/Druchamp	32.90	31.37	27.37	32.52
F_3 Daws/Druchamp	31.47	31.37	29.65	31.40
Correlation coefficient with observed yield		0.492*	0.806**	0.812**
n		18	18	12

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 25. Comparison of three models for predicting grain yield of F_2 and F_3 generations resulting from three-way crosses grown in 1980-81.

Three-way Crosses	Yield in grams: Observed Yield (g)	Model I	Model II	Model III
F_2 Yamhill/Stephens//Daws	39.70	33.59	35.71*	37.66
F_3 Yamhill/Stephens//Daws	35.00	33.59	34.65	36.08
F_2 Yamhill/Stephens//Druchamp	33.47	31.78	34.34	28.40
F_3 Yamhill/Stephens//Druchamp	41.73	31.28	33.39**	27.95
F_2 Yamhill/Daws//Stephens	35.73	34.28	36.50	36.22
F_3 Yamhill/Daws//Stephens	36.23	34.38	35.40	37.23
F_2 Yamhill/Daws//Druchamp	37.00	30.60	32.81	26.12
F_3 Yamhill/Daws//Druchamp	32.26	30.60	31.71	27.56
F_2 Yamhill/Druchamp//Stephens	39.13	33.13	36.42	33.57
F_3 Yamhill/Druchamp//Stephens	34.83	33.13	34.78	33.60
F_2 Yamhill/Druchamp//Daws	33.97	31.75	34.11	32.72
F_3 Yamhill/Druchamp//Daws	39.90	31.75	32.93**	32.05
F_2 Stephens/Daws//Yamhill	38.83	32.83	36.47	36.63
F_3 Stephens/Daws//Yamhill	42.96	32.83	34.65**	35.82
F_2 Stephens/Daws//Druchamp	37.73	32.06	34.05	29.66
F_3 Stephens/Daws//Druchamp	37.63	32.06	33.06**	30.05
F_2 Stephens/Druchamp//Yamhill	37.80	31.67	35.19	30.02
F_3 Stephens/Druchamp//Yamhill	33.53	31.67	33.43	31.22
F_2 Stephens/Druchamp//Daws	37.33	33.21	34.13	32.31
F_3 Stephens/Druchamp//Daws	33.83	33.21	33.67	33.58
F_2 Daws/Druchamp//Yamhill	36.83	30.98	34.40	31.46
F_3 Daws/Druchamp//Yamhill	36.00	30.98	32.69	30.01
F_2 Daws/Druchamp//Stephens	33.23	33.90	35.66	34.60
F_3 Daws/Druchamp//Stephens	40.70	33.90	34.78**	33.92
Correlation coefficient with observed yield		0.11	0.20	0.16
n		24	24	24

*,** Significantly different from the observed value at the 0.05 and 0.01 probability levels, respectively.

t = 4.25 for paired-observation test between observed value and Model II in a correlation coefficient, between predicted and actual yield, of 0.16. None of the correlation coefficients was significant. The calculated t-value from a paired observation test between observed and predicted grain yield under Model II was 4.25. Significant deviations estimated by this test could indicate the relative importance of epistasis. The differences in grain yield, when the parents participated as the third parent in the three way crosses, between observed and predicted grain yield under Model II are presented in Table 26. The order in which the third parent contributed to grain yield in the three-way crosses, from highest to lowest were Druchamp, Yamhill, Daws and Stephens. For comparison, the sum of GCA effects for grain yield obtained from F_2 and F_3 generations are also presented in Table 26. The parental order for the sum of GCA effects was reversed in relation to the previous case.

Prediction of grain yield for four-way crosses from F_2 and F_3 populations also involved three models. The observed and predicted values and the respective correlation coefficients are presented in Table 27. The correlation coefficients between actual and predicted grain yield were 0.377, -0.152 and 0.523 under Models I, II, and III, respectively. None of the correlation coefficients were significant. The t-test for paired observations between observed and predicted values under Model II was not significant.

The degree of association between harvest index calculated from plants grown under low competitive conditions and grain yield

Table 26. Comparison between deviations of observed grain yield from predicted value under Model II for the third parent in three-way crosses and sum of GCA effects from F_2 and F_3 generations of single crosses grown in 1980-1981.

Parents	Observed-Predicted (Model II) (g)	Σg_i from F_2 & F_3
Druchamp	20.43	-8.22
Yamhill	19.12	1.73
Daws	14.53	2.43
Stephens	6.35	4.04

Table 27. Comparison of three models for predicting grain yield of four-way crosses for F_2 and F_3 populations grown in 1980-1981.

Four-way crosses	Yield in grams: Observed Yield (g)	Model I	Model II	Model III
F_2 Yamhill/Stephens//Daws/Druchamp	31.97	32.62	35.02	38.19
F_3 Yamhill/Stephens//Daws/Druchamp	38.30	34.91	33.73	37.17
F_2 Yamhill/Daws//Stephens/Druchamp	29.17	32.62	34.66	35.59
F_3 Yamhill/Daws//Stephens/Druchamp	32.66	34.91	33.55	36.82
F_2 Yamhill/Druchamp//Stehens/Daws	36.73	32.62	35.26	38.76
F_3 Yamhill/Druchamp//Stehens/Daws	33.76	34.91	33.85	38.55
Correlation coefficient with observed yield		0.377	-0.153	0.523
n		6	6	6

t = -0.405 for paired-observation test between observed yield and Model II.

from the high level of competition was also estimated. The correlation coefficient was -0.09, which is not significant.

Growing Season 1981-82

Evaluation of Populations

Observed mean squares for plant height, tiller number, biological yield, grain yield, 100 kernel weight, harvest index and kernels per spike are presented in Table 28. Treatments were different for all traits except for grain yield. Genotypes were also significantly different for all traits except for grain yield. Differences among populations were found for plant height, 100 kernel weight and kernels per spike. The level of competition produced significant differences for all the traits measured. No interaction between genotypes and level of competition was observed. There was no interaction between populations and competition level for any trait. Within populations significant differences were detected for various characteristics. Parents, single crosses and three-way crosses showed significant differences for plant height, 100 kernel weight, harvest index and kernels per spike. For tiller number, only parents, the F_4 generation of single crosses and the F_3 generation of three-way crosses, presented significant differences. For biological yield, differences were detected for parents and the F_4 generation of three-way crosses. For grain yield, only the F_4 generation of single crosses proved to be different. Interactions between populations and level of competition were not significant except

Table 28. Observed mean squares for plant height, tiller number, biological yield, grain yield, 100 kernel weight, harvest index and kernels per spike for parents, single and three-way crosses for the year 1981-82.

Source	df	Plant Height	Tiller Number	Biological Yield	Grain Yield	100 Kernel Weight	Harvest Index	Kernels Per Spike
Replications	2	117.29	13.23	4085.96	354.98	15.37	46.72	104.97
Treatments	55	295.64**	146.16**	6468.14**	1099.41**	17.87**	30.38**	62.92**
Genotypes	27	518.22**	10.78**	469.94**	67.67	33.04**	55.70**	108.35**
Among Populations	5	456.26**	3.80	185.11	37.71	57.53**	44.58**	40.85*
Parents	3	1177.22**	16.03*	675.98*	103.09	79.82**	191.20**	366.75**
F_2 Single Crosses	5	508.25**	2.11	483.32	69.30	24.58**	38.41**	97.88**
F_3 Single Crosses	5	321.94**	8.27	522.95	7.90	16.71**	49.39**	94.74**
F_4 Single Crosses	5	442.09**	21.42**	357.31	118.26*	11.78**	31.01**	47.05*
F_3 Three-Way Crosses	2	299.35**	21.41*	120.67	36.57	27.93**	6.86	142.31**
F_4 Three-Way Crosses	2	574.42**	11.13	1337.83**	124.41	21.91**	49.77**	68.85*
Competition Level	1	1410.15**	7550.66**	335569.00**	57081.00**	23.76**	87.55**	126.50**
Genotype x Competition	27	31.79	7.29	277.37	57.74	2.49	2.94	15.13
Among Populations x Competition	5	69.12	9.02	345.01	69.64	1.32	4.14	22.01
Parents x Competition	3	11.22	6.66	359.97	74.92	2.95	0.69	22.98
F_2 Single Crosses x Competition	5	6.89	2.82	112.38	14.33	2.64	1.85	13.16
F_3 Single Crosses x Competition	5	28.77	1.61	151.15	8.72	2.93	1.29	17.18
F_4 Single Crosses x Competition	5	27.54	19.45**	857.10**	136.95**	2.63	3.89	11.28
F_3 Three-Way Crosses x Competition	2	34.21	1.07	242.69	28.73	2.14	8.36	3.98
F_4 Three-Way Crosses x Competition	2	47.39	5.14	349.97	64.19	3.21	2.30	6.74
Error	110	53.53	4.52	234.07	41.07	2.61	3.95	16.80
C.V. (%)		6.10	11.24	12.62	13.15	3.23	4.82	7.88

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

for those of the F_4 generation of single crosses for tiller number, biological yield and grain yield. Coefficients of variation were low for plant height (6.10%), 100 kernel weight (3.23%), harvest index (4.82%) and kernels per spike (7.88%) and intermediate for tiller number (11.24%), biological yield (12.62%) and grain yield (13.15%).

Evaluation of Parents

The performance of parents grown under a high and a low competition level is presented in Tables 29 and 30, respectively. Under the high competition level, differences among mean values were detected for plant height, 100 kernel weight, harvest index and kernels per spike. Druchamp presented the largest and the lowest mean values for plant height and 100 kernel weight, respectively. Stephens had the largest mean values for 100 kernel weight and harvest index whereas Yamhill presented the largest mean value for kernels per spike. Under the low competition level, significant differences were determined for all the characteristics under study except for tiller number. The mean values for Stephens were the lowest for plant height but the largest for grain yield, 100 kernel weight and harvest index. Although Druchamp had the largest mean values for plant height and biological yield, its mean value for grain yield, 100 kernel weight, harvest index and kernels per spike were the lowest. Yamhill had the largest mean value for kernels per spike. Daws had the second largest mean value for 100 kernel weight. This, however, was not statistically different from the mean value of Stephens for 100 kernel weight.

Table 29. Comparison of the performance for seven traits of four parents grown under high competitive conditions in 1981-82.

Parents	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill	116.20 a[1/]	9.64 a	66.28 a	30.07 a	51.55 b	43.33 b	65.31 b
Stephens	104.29 a	12.64 a	65.06 a	31.91 a	56.33 c	50.21 c	46.22 a
Daws	113.53 a	12.33 a	68.06 a	31.55 a	54.11 bc	46.96 bc	47.70 a
Druchamp	137.31 b	13.31 a	78.35 a	28.26 a	47.66 a	36.93 a	46.20 a

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 30. Comparison of the performance for seven traits of four parents grown under low competitive conditions in 1981-82.

Parents	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill	110.40 a[1/]	25.04 a	178.71 ab	76.13 ab	49.48 a	42.99 b	62.10 b
Stephens	103.49 a	27.11 a	166.13 ab	78.82 b	56.60 b	47.39 b	51.12 a
Daws	106.91 a	23.06 a	145.24 a	64.95 ab	54.17 b	45.21 b	52.50 ab
Druchamp	134.75 b	28.06 a	185.09 b	63.53 a	48.93 a	34.59 a	46.51 a

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Evaluation of F_2 Generation Single Crosses

The mean squares for the traits under study from individual plants of the F_2 generation grown under two competition levels are presented in Table 31. Significant differences for treatments were found for all traits measured. Differences among crosses were detected for all traits except for tiller number. The level of competition was significantly different for all the traits except for kernels per spike. Interactions between crosses and competition level were not detected for any of the traits under consideration.

Since interactions were not significant, the performance of individual F_2 generation single crosses were averaged over the two competition levels and are presented in Table 32. Stephens/Daws produced the shortest population, but exhibited the largest mean values for 100 kernel weight and harvest index. The cross Yamhill/Stephens had the largest mean value for grain yield whereas the cross Yamhill/Druchamp had the lowest mean value for this trait. The largest mean value for biological yield was found with Daws/Druchamp. This was true for kernels per spike as well. Stephens/Daws closely followed by Yamhill/Daws and Yamhill/Stephens had the highest harvest index values.

Evaluation of F_3 Generation Single Crosses

Mean squares for the traits under study from individual plants of the F_3 generation are indicated in Table 33. Significant differences were detected among treatments and crosses for all the traits. Differences between competition levels were also detected

Table 31. Mean square values for seven traits from F_2 populations grown in 1981-82.

Source	df	Plant Height	Tiller Number	Biological Yield	Grain Yield	100-Kernel Weight	Harvest Index	Kernels Per Spike
Replications	2	956.15	385.42	37342.39	5466.39	38.15	42.32	891.58
Treatments	11	3817.30**	1851.43**	90681.00**	13254.00**	192.78**	337.80**	758.01**
Crosses	5	7623.69**	31.61	7249.88**	1039.44**	368.77**	576.27**	1468.30**
Competition	1	3355.03**	19995.90**	952812.00**	139523.00**	78.58*	695.42**	9.55
Crosses x Competition	5	103.36	42.35	1685.8	215.02	39.62	27.80	197.50
Replications x Treatments	22	724.38	58.01	5037.59	840.72	30.17	54.98	294.32
Error	504	222.50	38.01	2076.02	315.73	18.52	41.07	98.85

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 32. Comparison of the performance for seven traits from F_2 populations grown in 1981-82.

F_2 Single Crosses	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill/Stephens	118.63 b[1/]	18.97 a	126.91 b	52.78 b	51.37 b	42.44 b	53.86 b
Yamhill/Daws	122.55 b	18.47 a	124.57 ab	51.68 ab	50.05 b	42.63 b	56.60 b
Yamhill/Druchamp	128.93 d	18.27 a	125.62 ab	45.26 a	48.10 a	37.52 a	51.44 a
Stephens/Daws	104.55 a	18.05 a	107.35 a	45.57 ab	52.55 b	43.75 b	48.90 a
Stephens/Druchamp	127.64 cd	19.27 a	125.72 ab	47.50 ab	51.36 b	38.68 a	47.64 a
Daws/Druchamp	127.34 cd	19.55 a	134.55 b	51.88 ab	47.41 a	39.39 a	57.54 b

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 33. Mean square values for seven traits from F_3 populations grown in 1981-82.

Source	df	Plant Height	Tiller Number	Biological Yield	Grain Yield	100-Kernel Weight	Harvest Index	Kernels Per Spike
Replications	2	588.76	26.66	5097.97	626.40	147.87	230.99	277.37
Treatments	11	2584.33**	2565.33**	123133.00**	18893.00**	144.15**	356.29**	778.53**
Crosses	5	4829.14**	124.05**	7844.30**	118.47	250.76**	740.86**	1421.17**
Competition	1	2124.15**	27477.60**	1303900.00**	206585.00**	112.06**	118.44*	169.23
Crosses x Competition	5	431.55	24.16	2267.24	130.79	43.95	19.28	257.73
Replications x Treatments	22	327.78	90.73	3919.63	581.02	69.55	42.44	260.41
Error	504	251.01	37.46	2088.45	291.42	21.86	30.99	239.07

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

for all traits except for kernels per spike. No interaction was observed between crosses and competition level for any traits.

The performance of the individual F_3 single crosses is provided in Table 34. Yamhill/Druchamp produced the largest mean values for plant height and biological yield and the second largest mean value for tiller number. This cross also had the lowest mean value for harvest index. Stephens/Daws had the largest mean values for tiller number and grain yield, although there were not significant differences among crosses for the last trait. Yamhill/Stephens was superior to the other crosses for 100 kernel weight, harvest index and kernels per spike.

Evaluation of F_4 Generation Single Crosses

Mean squares for the traits under study calculated from individual plants of the F_4 generation are presented in Table 35. Differences among treatments, crosses and levels of competition were statistically significant for all the traits with the exception of 100 kernel weight for competition level. Interactions between crosses and competition level were significant with the exception of plant height and harvest index.

Mean values for the performance of F_4 generation single crosses grown under high and low competitive conditions are provided in Tables 36 and 37, respectively. Significant differences among mean values from the high competition levels were observed for plant height, 100 kernel weight, harvest index and kernels per spike. Under the low competition level significant differences among mean values were observed for all traits under

Table 34. Comparison of the performance for seven traits from F_3 populations grown in 1981-82.

F_3 Single Crosses	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill/Stephens	107.46 a	17.75 a	109.65 a	48.65 a	50.32 c	44.99 e	57.36 c
Yamhill/Daws	110.73 ab	17.71 a	113.56 ab	49.51 a	48.05 b	44.10 de	57.14 c
Yamhill/Druchamp	127.90 d	19.37 ab	136.67 c	49.60 a	47.78 ab	37.40 a	54.86 bc
Stephens/Daws	114.37 bc	20.86 b	122.38 abc	50.00 a	47.46 ab	42.13 cd	49.36 ab
Stephens/Druchamp	120.82 c	19.21 ab	120.81 abc	47.10 a	50.11 c	39.61 ab	47.89 a
Daws/Druchamp	117.08 bc	19.10 ab	123.02 abc	47.75 a	45.94 a	40.29 bc	54.10 abc

[1/]Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 35. Mean square values for seven traits from F_4 populations grown in 1981-82.

Source	df	Plant Height	Tiller Number	Biological Yield	Grain Yield	100 Kernel Weight	Harvest Index	Kernels Per Spike
Replications	2	407.40	64.28	11006.00	902.80	24.74	293.56	190.75
Treatments	11	3616.47**	2885.48**	130880.00**	20258.30**	100.85**	250.34**	469.92**
Crosses	5	6631.33**	321.38**	5359.71*	1773.97**	176.70**	465.14**	705.89**
Competition	1	4558.82**	28674.50**	1348600.00**	203700.00**	28.93	136.10*	793.97**
Crosses x Competition	5	413.14	291.76	12856.60**	2054.21**	39.40*	58.38	169.26*
Replications x Treatments	22	862.74	37.08	2582.36	348.37	26.57	60.27	169.52
Error	504	188.18	39.73	1948.02	290.95	14.99	35.70	71.64

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 36. Comparison of the performance for seven traits from F_4 populations grown under high competitive conditions in 1981-82.

F_4 Single Crosses	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill/Stephens	124.91 bc[1/]	11.57 a	71.44 a	28.71 a	47.62 ab	41.12 ab	52.46 bc
Yamhill/Daws	121.93 ab	12.00 a	79.53 a	32.22 a	49.91 bc	42.38 bc	55.40 c
Yamhill/Druchamp	135.04 d	11.82 a	75.77 a	27.71 a	49.42 ab	37.63 a	47.70 ab
Stephens/Daws	115.95 a	12.37 a	67.28 a	29.31 a	51.77 c	44.76 c	45.95 a
Stephens/Druchamp	132.75 cd	13.22 a	83.48 a	31.28 a	50.28 c	38.34 a	47.24 a
Daws/Druchamp	144.53 a	11.53 a	67.17 a	24.93 a	47.40 a	38.25 a	46.26 a

[1/] Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

Table 37. Comparison of the performance for seven traits from F_4 populations grown under low competitive conditions in 1981-82.

F_4 Single Crosses	Plant Height (cm)	Tiller Number	Biological Yield (g)	Grain Yield (g)	100 Kernel Weight (dg)	Harvest Index (%)	Kernels Per Spike
Yamhill/Stephens	117.64 ab	31.08 d	201.88 c	80.02 b	49.93 a	40.06 a	52.50 ab
Yamhill/Daws	121.60 abc	22.00 a	147.64 a	59.28 a	49.31 a	40.33 bc	54.44 b
Yamhill/Druchamp	124.73 bc	23.13 ab	169.00 ab	60.86 a	49.68 a	36.64 a	52.50 ab
Stephens/Daws	114.37 a	29.93 d	188.20 bc	77.84 b	52.62 b	41.73 c	50.68 ab
Stephens/Druchamp	127.75 cd	27.77 cd	163.84 ab	64.24 a	48.93 a	40.10 abc	48.10 a
Daws/Druchamp	134.15 d	26.04 bc	173.82 ab	64.97 a	48.71 a	37.60 ab	51.34 ab

1/ Means with a letter in common are not significantly different, according to Tukey's test, at the 0.05 probability level.

study. The crosses Daws/Druchamp and Stephens/Daws produced the tallest and shortest progeny, respectively, under both competition levels. For tiller number, the crosses Yamhill/Stephens and Stephens/Daws presented intermediate mean values under high competitive conditions while the same crosses had the largest mean values for tiller number under the low competition level. For biological yield and grain yield, the progeny of the cross Yamhill/Daws had large mean values under high competitive conditions. However, under low competition conditions, the lowest mean values for biological yield and grain yield were those of Yamhill/Daws. Stephens/Daws presented the largest mean values for 100 kernel weight and harvest index under both competition levels. Low values for these two traits were noted for the cross Daws/Druchamp in both competition levels. For kernels per spike, large mean values were noted for the crosses Yamhill/Stephens and Yamhill/Daws under both competition levels. The crosses Stephens/Daws and Daws/Druchamp had the lowest mean values for kernels per spike under high competitive conditions. Under low competitive conditions, these crosses presented intermediate values for kernels per spike.

Combining Ability Analysis

Combining ability analyses for plant height from the F_2, F_3 and F_4 generations are presented in Table 38. General combining ability and SCA were statistically significant in all three generations. No interactions were noted between GCA and the

Table 38. Combining ability analysis for plant height of F_2 , F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for plant height		
		F_2	F_3	F_4
GCA	3	115.93**	62.86**	102.49**
SCA	2	37.74**	39.84**	30.38**
GCA X Competition	3	1.81	2.36	4.57
SCA X Competition	2	0.29	8.46 *	4.78
Error	504	2.47	2.79	2.09

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

level of competition. A significant interaction between SCA and competition level was observed for the F_3 generation.

Estimates of combining ability for tiller number are presented in Table 39. Significant differences for GCA and SCA were detected in the F_4 and F_3 generations, respectively. Interactions between GCA and competition level were determined to be significant in the F_4 generation.

Combining ability estimates are given in Table 40 for biological yield. Significant differences for GCA were observed in all three generations. Specific combining ability differences were significant only in the F_2 and F_3 generations. Large interactions for GCA and SCA with competition level were observed for the F_4 generation.

Combining ability estimates for grain yield are provided in Table 41. A significant SCA estimate was noted in the F_2 generation. Significant GCA and SCA were found in the F_4 generation. The interactions GCA x competition level proved also to be significant in the F_4 generation.

In Table 42, the combining ability estimates for 100 kernel weight are presented. General combining ability and SCA were significant in all three generations. A significant interaction between GCA and competition level was noted in the F_3 generation. Significant SCA x competition level interactions were detected in the F_2 and F_4 generations.

For harvest index, the combining ability analyses are presented in Table 43. General combining ability was significant

Table 39. Combining ability analysis for tiller number of F_2, F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for tiller number		
		F_2	F_3	F_4
GCA	3	0.17	1.04	5.37**
SCA	2	0.62	1.88**	0.87
GCA X Competition	3	0.57	0.27	3.54**
SCA X Competition	2	0.32	0.27	2.80**
Error	504	0.42	0.42	0.44

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 40. Combining ability analysis for biological yield of F_2, F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for biological yield		
		F_2	F_3	F_4
GCA	3	65.54*	72.52*	65.28*
SCA	2	103.04*	109.08**	50.97
GCA X Competition	3	29.56	27.84	61.80*
SCA X Competition	2	2.56	21.26	264.54**
Error	504	23.07	23.21	21.64

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 41. Combining ability analysis for grain yield of F_2 , F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for grain yield		
		F_2	F_3	F_4
GCA	3	3.08	1.13	18.30**
SCA	2	24.29**	1.59	14.76**
GCA X Competition	3	3.90	1.58	28.07**
SCA X Competition	2	0.08	1.36	21.99**
Error	504	3.51	3.24	3.23

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 42. Combining ability analysis for 100 kernel weight of F_2, F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for 100 kernel weight		
		F_2	F_3	F_4
GCA	3	6.23**	3.91**	1.25**
SCA	2	0.92*	1.10*	3.03**
GCA X Competition	3	0.11	0.66*	0.09
SCA X Competition	2	0.91*	0.25	0.98**
Error	504	0.21	0.24	0.17

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 43. Combining ability analysis for harvest index of F_2 , F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for harvest index		
		F_2	F_3	F_4
GCA	3	10.65**	10.79**	8.17**
SCA	2	0.05	4.42**	0.65
GCA X Competition	3	0.50	0.24	0.81
SCA X Competition	2	0.02	0.15	0.45
Error	504	0.46	0.34	0.40

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

in all three generations. A significant SCA estimate was detected for the F_3 generation only. No interactions were found in any generation.

Combining ability estimates for kernels per spike are given in Table 44. General and specific combining ability were significant in the F_2 and F_3 generations for this trait. Only GCA was observed to be significant in the F_4 generation. The interactions GCA x competition level in the F_2 and SCA x competition level in the F_4 generations were significantly different.

General combining ability effects for all traits from the F_2, F_3 and F_4 generations are presented in Table 45.

For plant height, GCA effects were large and positive for Druchamp in contrast with the negative values noted for Stephens in all generations and under both competition levels. Yamhill had positive effects in the F_2 generation but negative effects in the F_3 and F_4 generations for this trait. The GCA effects for Daws were negative in the F_2 and F_3 generations and under the high competition level in the F_4 generation.

For tiller number, the GCA effects of Yamhill were consistently low in all three generations under both competition levels. Stephens had positive effects for this trait except when estimated from the F_2 generation under low competitive conditions. Druchamp exhibited somewhat low but positive effects except in the F_4 generation in the low competition level. The GCA effects of Daws for tiller number were negative under high and

Table 44. Combining ability analysis for kernels per spike of F_2, F_3 and F_4 populations grown under two competition levels in 1981-82.

Source	df	Mean squares for kernels per spike		
		F_2	F_3	F_4
GCA	3	16.69**	21.09**	11.57**
SCA	2	15.74**	7.84*	2.29
GCA X Competition	3	3.53*	2.73	1.19
SCA X Competition	2	0.23	3.06	2.89*
Error	504	1.10	2.66	0.80

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 45. Comparison between GCA effects estimated from F_2, F_3 and F_4 populations grown under high competitive conditions ($\hat{g}_{i1}$) and low competitive conditions ($\hat{g}_{i2}$) in 1981-82.

Trait and Parents	F_2 $\hat{g}_{i1}$	F_2 $\hat{g}_{i2}$	F_3 $\hat{g}_{i1}$	F_3 $\hat{g}_{i2}$	F_4 $\hat{g}_{i1}$	F_4 $\hat{g}_{i2}$
Plant Height						
Yamhill	3.55	1.73	-2.73	-0.72	-2.84	-3.08
Stephens	-6.78	-7.22	-3.17	-3.36	-6.97	-5.18
Daws	-5.02	-5.36	-1.99	-5.00	-2.58	0.01
Druchamp	8.25	10.85	7.54	9.08	12.39	8.25
S.E. ($\hat{g}_j-\hat{g}_1$)	1.57		1.67		1.45	
Tiller Number						
Yamhill	0.11	-0.69	-0.55	-1.62	-0.43	-1.88
Stephens	0.47	-0.47	0.25	0.57	0.46	4.41
Daws	-0.77	0.55	0.25	0.42	-0.18	-1.01
Druchamp	0.19	0.61	0.05	0.63	0.15	-1.52
S.E. ($\hat{g}_j-\hat{g}_1$)	0.65		0.65		0.66	
Biological Yield						
Yamhill	2.49	2.25	2.09	-5.25	2.20	-1.83
Stephens	-1.07	-11.32	-5.00	-5.21	-0.07	15.87
Daws	-4.10	-1.78	-0.68	-3.41	-4.18	-6.27
Druchamp	2.68	10.85	3.59	13.86	2.05	-7.77
S.E. ($\hat{g}_j-\hat{g}_1$)	4.80		4.82		4.65	
Grain Yield						
Yamhill	1.80	0.59	1.81	-0.30	0.78	-1.72
Stephens	0.94	-2.43	-1.35	0.75	1.11	9.24
Daws	-0.31	2.11	0.37	0.64	-0.31	-0.76
Druchamp	-2.43	-0.27	-0.82	-1.08	-1.58	-6.77
S.E. ($\hat{g}_j-\hat{g}_1$)	1.87		1.80		1.80	
100 Kernel Weight						
Yamhill	-0.80	-0.10	1.14	0.18	-0.63	-0.33
Stephens	2.44	2.42	0.99	2.07	0.74	0.94
Daws	-0.05	-0.36	-1.19	-2.20	0.44	0.52
Druchamp	-1.59	-1.97	-0.94	-0.06	-0.55	-1.13
S.E. ($\hat{g}_j-\hat{g}_1$)	0.49		0.49		0.41	

Table 45. (continued)

Trait and Parents	F_2		F_3		F_4	
	$\hat{g}_{i1}$	$\hat{g}_{i2}$	$\hat{g}_{i1}$	$\hat{g}_{i2}$	$\hat{g}_{i1}$	$\hat{g}_{i2}$
Harvest Index						
Yamhill	0.80	-0.41	1.29	0.94	-0.06	-0.60
Stephens	1.45	1.22	0.92	1.55	1.50	1.84
Daws	1.69	1.89	0.85	1.42	2.08	0.72
Druchamp	-3.96	-2.70	-3.05	-3.91	-3.52	-1.95
S.E. $(\hat{g}_j-\hat{g}_1)$	0.68		0.58		0.63	
Kernels Per Spike						
Yamhill	2.58	1.32	6.08	2.94	4.03	2.33
Stephens	-2.99	-4.60	-3.38	-2.37	-0.92	-1.75
Daws	3.07	1.99	-1.06	1.30	0.05	0.85
Druchamp	-2.66	1.29	-1.64	-1.86	-3.16	-1.43
S.E. $(\hat{g}_j-\hat{g}_1)$	1.05		1.63		0.89	

positive under low competitive conditions in the F_2 generation while in the F_3 and F_4 generations they were positive and negative, respectively.

The GCA effects for biological yield presented large inconsistencies among generations and within competition levels. Stephens had negative effects for this trait in all cases except under low competitive conditions in the F_4 generation where it had a large, positive effect. The GCA effects of Druchamp were large and positive in the F_2 and F_3 generation under both competition levels. In the F_4 generation the effects of Druchamp were positive under high competitive conditions and negative under low competitive conditions. Daws had negative effects for biological yield in all three generations and under both competition levels. Most of the GCA effects of Yamhill were positive except under low competitive conditions in the F_3 and F_4 generations.

For grain yield, the GCA effects of Yamhill were positive in the F_2 generation under both competition levels and in the F_3 and F_4 generations under the high competition level. Stephens had positive effects except under low competitive conditions in the F_2 generation and under high competitive conditions in the F_3 generation. The effects of Daws were small in the high competition level for the F_2, F_3 and F_4 generations. Somewhat larger effects were observed for Daws under low competitive conditions of growth except in the F_4 generation where it was negative. Druchamp exhibited negative effects which were often the largest for grain yield under both competition levels in all three generations.

For the trait 100 kernel weight, GCA effects were consistent across generations and competition levels. Stephens had the largest positive effects in all cases, except in the F_3 generation under the high competition level where it was second to Yamhill. Druchamp had negative effects in all three generations and under both competition levels. The effects of Yamhill were negative in the F_2 and F_4 generations, but positive in the F_3 generation. Daws had small negative effects in the F_2 generation, large negative effects in the F_3 generation and small positive effects in the F_4 generation for this trait.

General combining ability effects for harvest index were large and positive for Daws and Stephens and large and negative for Druchamp. Yamhill had positive GCA effects in the F_3 generation and small and negative effects in the F_4 generation for this trait. The effects of Yamhill in the F_2 generation were positive in the high competition level and negative in the low competition level.

General combining ability effects for kernels per spike were positive and large for Yamhill. Stephens and Druchamp had negative GCA effects for this trait but in general the effects of Stephens were smaller than those of Druchamp in all three generations. Daws had large positive effects in the F_2 generation and small positive effects in the F_4 generation. In the F_3 generation, the GCA effects of Daws were negative under high competitive conditions but positive under low competitive conditions.

A comparison between GCA effects for plant height and grain yield from the F_2 and F_3 generations in two growing seasons and two competition levels are presented in Table 46. For plant height, good agreement was observed between the GCA effects of the two growing seasons. Druchamp had the largest positive effects in the F_2 and F_3 generations. Stephens consistently presented the lowest negative effects across generations in both growing seasons. Daws also had negative effects for plant height for all comparisons except for the F_3 generation grown in 1980-81 under low competition. The GCA effects of Yamhill for plant height were positive in both F_2 generations but negative in the F_3 generations. The magnitude of the GCA effects was similar in both growing seasons and under both competition levels, although somewhat higher estimates were observed under low competitive conditions.

For grain yield, GCA effects also showed some consistency between generations and growing seasons. However, the GCA effects for grain yield were of a lesser magnitude and were more variable than the GCA effects for plant height across generations and growing seasons. Stephens had positive GCA effects in both generations and under both competition levels in the 1980-81 growing season. However, in the 1981-82 growing season, the effects of Stephens were negative in the F_2 and F_3 generations under the low and the high competition levels, respectively. In general,

Table 46. Comparison between general combining ability effects estimated in two growing seasons from F_2 and F_3 populations for plant height and grain yield under high competitive conditions ($\hat{g}_{i1}$) and low competitive conditions ($\hat{g}_{i2}$).

Traits and Parents	F_2: 1980-81		F_2:1981-82		F_3:1980-81		F_3:1981-82	
	$\hat{g}_{i1}$	$\hat{g}_{i2}$	$\hat{g}_{i1}$	$\hat{g}_{i2}$	$\hat{g}_{i1}$	$\hat{g}_{i2}$	$\hat{g}_{i1}$	$\hat{g}_{i2}$
<u>Plant Height</u>								
Yamhill	3.24	3.94	3.55	1.73	-1.40	-4.66	-2.37	-0.72
Stephens	-7.14	-7.22	-6.78	-7.22	-5.47	-7.87	-3.17	-3.36
Daws	-0.99	-1.88	-5.02	-5.36	-1.74	2.41	-1.99	-5.00
Druchamp	4.89	5.16	8.25	10.85	8.61	10.12	7.53	9.08
$\Sigma \hat{g}_i^2$	86.36	97.81	151.83	201.51	108.86	191.87	76.47	119.25
<u>Grain Yield</u>								
Yamhill	-0.37	1.31	1.80	0.59	-0.01	0.80	1.81	-0.30
Stephens	0.23	1.53	0.94	-2.43	0.49	1.79	-1.35	0.75
Daws	-0.12	2.06	-0.31	2.11	-1.10	1.62	0.37	0.64
Druchamp	0.25	-4.89	-2.43	-0.27	0.62	-4.20	-0.82	-1.08
$\Sigma \hat{g}_i^2$	0.27	32.21	10.12	10.77	1.83	24.10	5.91	2.22

Stephens, Yamhill and Daws had positive GCA effects while Druchamp generally exhibited low or negative GCA effects for grain yield.

Correlation coefficients among GCA effects of different traits estimated from F_2 and F_3 generations in both growing seasons are presented in Table 47. High correlation coefficients were observed between F_2 and F_3 generations in the same growing season for most traits. The correlation coefficients for the GCA effects of tiller number and grain yield were significant between the F_2 and F_3 generations grown in the 1980-81 season but they were not significant between the F_2 and F_3 generations grown the in 1981-82 season. The correlation coefficient between GCA effects for harvest index was significant in the 1981-82 growing season but it was not in the 1980-81 growing season. Correlation coefficients between GCA effects for traits in generations growing in different seasons were generally low for tiller number, biological yield and grain yield. A negative significant correlation coefficient, however, was observed for biological yield between the F_2 and F_3 generations grown in 1980-81 and 1981-82 seasons, respectively. All correlation coefficients were found to be significant for plant height. Correlation coefficients for harvest index were all positive and rather high. However, they were significant only between the F_2 and F_3 generations grown in the 1980-81 season and between the F_3 and F_3 generations grown in the 1981-82 and 1980-81 seasons, respectively.

Table 47. Degree of association among GCA effects between F_2 and F_3 generations in both growing seasons calculated from low and high competition level values.

CORRELATION COEFFICIENTS[1/]

	F_3 80-81	F_2 81-82	F_3 81-82
F_2: 1980-81			
Plant Height	0.70*	0.90**	0.69*
Tiller Number	0.76*	0.09	0.31
Biological Yield	0.83**	-0.37	-0.77*
Grain Yield	0.96**	0.07	0.38
Harvest Index	0.29	0.51	0.37
F_3: 1980-81			
Plant Height		0.79**	0.82**
Tiller Number		-0.28	-0.10
Biological Yield		-0.22	-0.62
Grain Yield		-0.01	0.35
Harvest Index		0.72*	0.57
F_2: 1981-82			
Plant Height			0.89**
Tiller Number			0.45
Biological Yield			0.77*
Grain Yield			0.27
Harvest Index			0.92**

[1/] n = 8 in all cases.,

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Specific combining ability effects calculated from the F_2, F_3 and F_4 generations grown in the 1981-82 growing season are provided in Tables 48, 49, and 50, respectively.

In general, good agreement was observed between the SCA effects from the two competition levels, especially in the F_2 and F_3 generations. However, little agreement was observed among SCA effects from the generations under study. For instance, Yamhill/Daws had the largest positive SCA effect for plant height in the F_2 generation, but the same cross had the second lowest SCA effects in the F_3 and F_4 generations for the same trait. For tiller number, the SCA effects of Yamhill/Stephens were the largest in the F_2 and F_4 generations, while Yamhill/Druchamp were the largest in the F_3 generation. For biological yield and grain yield, the SCA effects of Yamhill/Stephens were the largest in the F_2 and F_4 generations but not in the F_3 generation. The combination Yamhill/Druchamp exhibited the largest SCA effects for biological yield and grain yield in the F_3 generation. The SCA effects for 100 kernel weight were rather small with the combination of Yamhill/Daws having the largest effects in the F_2 and F_3 generations. In the F_4 generation, it was Yamhill/Druchamp that had the largest SCA effects for 100 kernel weight. For harvest index and kernels per spike, Yamhill/Stephens had the largest SCA effects in the F_2 and F_3 generations. In the F_4 generation, specific combining ability effects for harvest index and kernels per spike were the highest for Yamhill/Daws and Yamhill/Stephens. A clear tendency for SCA effects to decrease

Table 48. Estimates of specific combining ability effects ($\hat{s}_{ij}$) for seven traits from F_2 populations grown under high ($\hat{s}_1$) and low ($\hat{s}_2$) competitive conditions in 1981-82.

		Parent					
		Stephens		Daws		Druchamp	
Parent	Trait	$\hat{s}_1$	$\hat{s}_2$	$\hat{s}_1$	$\hat{s}_2$	$\hat{s}_1$	$\hat{s}_2$
Yamhill	Plant Height	0.96	1.79	3.61	3.37	-4.57	-5.16
	Tiller Number	0.94	0.06	0.00	0.21	-0.94	-0.27
	Biological Yield	7.02	6.21	-0.24	2.30	-6.78	-8.50
	Grain Yield	3.26	3.18	0.23	0.73	-3.48	-3.91
	100 Kernel Weight	-1.23	-0.27	0.27	0.86	0.96	-0.59
	Harvest Index	0.27	0.09	-0.12	-0.05	-0.16	-0.04
	Kernels per Spike	2.83	3.25	-0.15	-0.94	-2.68	-2.31
Stephens	Plant Height			-4.57	-5.16	3.61	3.37
	Tiller Number			-0.94	-0.27	0.00	0.21
	Biological Yield			-6.78	-8.50	-0.24	2.30
	Grain Yield			-3.48	-3.91	0.23	0.73
	100 Kernel Weight			0.96	-0.59	0.27	0.86
	Harvest Index			-0.16	-0.04	-0.12	-0.05
	Kernels per Spike			-2.68	-2.31	-0.15	0.94
Daws	Plant Height					0.96	1.79
	Tiller Number					0.94	0.06
	Biological Yield					7.02	6.21
	Grain Yield					3.26	3.18
	100 Kernel Weight					-1.23	-0.27
	Harvest Index					0.27	0.09
	Kernels per Spike					2.83	3.25

Standard Error	Plant Height	Tiller Number	Biological Yield	Grain Yield	100 kernel Weight	Harvest Index	Kernels Per Spike
S.E. ($\hat{s}_{ij}-\hat{s}_{ik}$)	1.57	0.65	4.80	1.87	0.49	0.68	1.05

Table 49. Estimates of specific combining ability effects ($\hat{s}_{ij}$) for seven traits from F_3 populations grown under high ($\hat{s}_1$) and low ($\hat{s}_2$) competitive conditions in 1981-82.

Parent	Trait	Stephens $\hat{s}_1$	Stephens $\hat{s}_2$	Daws $\hat{s}_1$	Daws $\hat{s}_2$	Druchamp $\hat{s}_1$	Druchamp $\hat{s}_2$
Yamhill	Plant Height	-2.22	-6.03	-0.35	-0.90	2.56	6.92
	Tiller Number	-0.33	-0.82	-0.37	-0.72	0.70	1.54
	Biological Yield	-1.21	-8.15	-4.29	-3.38	5.51	11.52
	Grain Yield	0.31	-1.46	-1.21	0.34	0.91	1.13
	100 Kernel Weight	0.03	-0.32	0.40	1.21	-0.43	-0.88
	Harvest Index	1.21	1.24	0.18	0.70	-1.39	-1.93
	Kernels per Spike	3.52	1.03	-2.15	0.28	-1.37	-1.31
Stephens	Plant Height			2.56	6.92	-0.35	-0.90
	Tiller Number			0.70	1.54	-0.37	-0.72
	Biological Yield			5.51	12.52	-4.29	-3.38
	Grain Yield			0.91	1.13	-1.21	0.34
	100 Kernel Weight			-0.43	-0.88	0.40	1.21
	Harvest Index			-1.39	-1.93	0.18	0.70
	Kernels per Spike			-1.37	-1.31	-2.15	0.28
Daws	Plant Height					-2.22	-6.03
	Tiller Number					-0.33	-0.82
	Biological Yield					-1.21	-8.15
	Grain Yield					0.31	-1.46
	100 Kernel Weight					0.03	-0.32
	Harvest Index					1.21	1.24
	Kernels per Spike					3.52	1.03

Standard Error	Plant Height	Tiller Number	Biological Yield	Grain Yield	100 Kernel Weight	Harvest Index	Kernels Per Spike
S.E. ($\hat{s}_{ij}$-$\hat{s}_{ik}$)	1.67	0.65	4.82	1.80	0.49	0.58	1.63

Table 50. Estimates of specific combining ability effects ($\hat{s}_{ij}$) for seven traits from F_4 populations grown under high ($\hat{s}_1$) and low ($\hat{s}_2$) competitive conditions in 1981-82.

		Parent					
		Stephens		Daws		Druchamp	
Parent	Trait	$\hat{s}_1$	$\hat{s}_2$	$\hat{s}_1$	$\hat{s}_2$	$\hat{s}_1$	$\hat{s}_2$
Yamhill	Plant Height	5.53	2.52	-1.84	1.30	-3.69	-3.82
	Tiller Number	-0.53	1.90	0.52	-1.77	0.01	-0.13
	Biological Yield	-4.81	13.79	7.39	-18.33	-2.58	4.54
	Grain Yield	-2.21	4.63	2.73	-6.11	-0.52	1.48
	100 Kernel Weight	-1.89	-0.55	0.70	-0.75	1.20	1.29
	Harvest Index	-0.73	-0.58	-0.05	0.81	0.78	-0.23
	Kernels per Spike	0.19	0.33	2.15	-0.32	-2.34	-0.01
Stephens	Plant Height			-3.69	-3.82	-1.84	1.30
	Tiller Number			0.01	-0.13	0.52	-1.77
	Biological Yield			-2.58	4.54	7.39	-18.33
	Grain Yield			-0.52	1.48	2.73	-6.11
	100 Kernel Weight			1.20	1.29	0.70	-0.75
	Harvest Index			0.78	-0.23	-0.05	0.81
	Kernels per Spike			-2.34	-0.01	2.15	-0.32
Daws	Plant Height					5.53	2.52
	Tiller Number					-0.53	1.90
	Biological Yield					-4.81	13.79
	Grain Yield					-2.21	4.63
	100 Kernel Weight					-1.89	-0.55
	Harvest Index					-0.73	-0.58
	Kernels per Spike					0.19	0.32

Standard Error	Plant Height	Tiller Number	Biological Yield	Grain Yield	100 Kernel Weight	Harvest Index	Kernels Per Spike
S.E. ($\hat{s}_{ij}-\hat{s}_{ik}$)	1.45	0.66	4.65	1.80	0.41	0.63	0.89

with advancing generations was not observed in any characteristic under analysis.

The ratios of GCA effects to SCA effects from the F_2, F_3 and F_4 generations for seven traits are presented in Table 51. General combining ability appeared to be more important for plant height, 100 kernel weight and harvest index. Specific combining ability on the other hand seemed to prevail for biological yield and grain yield. A clear difference between high and low competitive conditions in relation to the prevalence of one or the other type of combining ability was not observed with the exception, perhaps, of tiller number. Although substantial variations were noted among generations, larger ratios were observed in the F_2 generation. Under low competitive conditions, ratios decreased with advancing generations for biological yield and 100 kernel weight and increased for grain yield and kernels per spike. For plant height, tiller number and harvest index, a clear tendency for the ratios to change consistently in any direction was not observed. Under high competitive conditions, only the ratios for tiller number tended to increase with advancing generations. The ratios for the other traits did not show any clear tendency. When the ratios were calculated averaged across competition levels, only the ratios for tiller number, biological yield, grain yield and kernels per spike appeared to increase with advancing generations. The ratios for 100 kernel weight tended to decrease over successive generations. A clear tendency for the ratios for plant height and harvest index to consistently change over

Table 51. Comparison of the ratio of general combining ability effects over specific combining ability effects for seven traits and two competition levels from F_2, F_3 and F_4 populations grown in 1981-82.

Trait	Generation	Low Competition	High Competition	Both Levels
Plant Height	F_2	1.63	1.45	1.53
	F_3	0.47	2.20	0.79
	F_4	1.53	1.52	1.68
Tiller Number	F_2	3.79	0.16	0.13
	F_3	0.33	0.20	0.28
	F_4	1.29	0.29	3.11
Biological Yield	F_2	0.74	0.11	0.32
	F_3	0.41	0.28	0.33
	F_4	0.22	0.10	0.64
Grain Yield	F_2	0.14	0.15	0.06
	F_3	0.21	0.82	0.34
	F_4	0.74	0.12	0.62
100 Kernel Weight	F_2	2.83	1.21	3.40
	F_3	1.30	4.42	1.81
	F_4	0.34	0.09	0.21
Harvest Index	F_2	341.80	62.13	109.02
	F_3	1.19	1.22	1.21
	F_4	2.57	5.53	6.32
Kernels Per Spike	F_2	0.57	0.70	0.87
	F_3	2.27	0.92	1.35
	F_4	18.31	0.89	2.53

successive generations was not noted.

Grain Yield Prediction

Grain yield for single crosses was predicted using three models. The observed and predicted values are given in Table 52. Under Model I, the correlation coefficient between actual and predicted grain yield was 0.203. Model II makes use of GCA and SCA effects to predict grain yield. For Model II, Part A, the combining ability effects estimated from populations grown under high competitive conditions were used to predict grain yield under similar competitive conditions. The correlation coefficient between actual and predicted grain yield of 0.775 calculated for Model II, Part A was found to be significant. For Model II, Part B, the combining ability effects estimated from populations grown under low competitive conditions were used to predict grain yield under high competitive conditions of growth. The correlation coefficient between actual and predicted grain yield of 0.125 for Model II, Part B was not significant. Model III predicts grain yield in terms of mid-parent value, heterosis and inbreeding coefficient. The correlation coefficient of 0.141 was not significant for this comparison.

For three-way crosses, yield prediction involved three models. The observed and predicted values and their correlation coefficients are provided in Table 53. For Model I, the correlation coefficient of -0.10 between observed and predicted grain yield was found. For Model II the correlation coefficient between the two variables was 0.439. Under Model III, Part A, which takes into

Table 52. Comparison of three models for predicting grain yield of F_2, F_3 and F_4 generations resulting from single crosses grown under a high competition level in 1981-82.

	Yield in grams				
Single Crosses	Observed Yield	Model I	Model II Part A	Model II Part B	Model III
F_2 Yamhill/Stephens	39.04	30.985	36.985	32.325	--
F_3 Yamhill/Stephens	30.00	30.985	31.755	29.975	35.013
F_4 Yamhill/Stephens	28.71	30.985	30.665	43.135	32.999
F_2 Yamhill/Daws	34.75	30.805	32.525	34.285	--
F_3 Yamhill/Daws	30.02	30.805	31.775	31.485	32.778
F_4 Yamhill/Daws	32.22	30.805	34.005	22.215	31.791
F_2 Yamhill/Druchamp	28.93	29.160	25.050	25.570	--
F_3 Yamhill/Druchamp	31.13	29.160	31.060	28.910	29.045
F_4 Yamhill/Druchamp	27.71	29.160	27.840	22.150	29.103
F_2 Stephens/Daws	30.20	31.730	28.880	27.500	--
F_3 Stephens/Daws	29.15	31.730	31.660	34.250	30.965
F_4 Stephens/Daws	29.31	31.730	32.010	41.690	31.348
F_2 Stephens/Druchamp	31.77	30.085	28.825	28.115	--
F_3 Stephens/Druchamp	25.86	30.058	26.705	30.095	30.928
F_4 Stephens/Druchamp	31.28	30.085	32.345	26.445	30.506
F_2 Daws/Druchamp	33.55	29.905	30.425	34.925	--
F_3 Daws/Druchamp	29.08	29.095	29.765	28.005	31.728
F_4 Daws/Druchamp	24.93	29.905	25.805	27.005	30.816
Correlation Coefficient with observed yield		0.203	0.775**	0.125	0.141

*Significant at the 0.01 probability level.

Table 53. Comparison of three models for predicting grain yield of F_3 and F_4 generations resulting from three-way crosses grown under a high competition level in 1981-82.

Three-Way Crosses	Yield in grams				
	Observed Yield	Model I	Model II	Model III Part A	Model III Part B
F_3 Yamhill/Stephens//Daws	27.02	31.268	31.569	31.718	32.868
F_4 Yamhill/Stephens//Daws	27.24	31.268	31.418	33.008	31.953
F_3 Yamhill/Daws//Stephens	35.42	31.358	32.173	31.728	32.283
F_4 Yamhill/Daws//Stephens	31.48	31.358	31.765	31.338	42.413
F_3 Stephens/Daws//Yamhill	29.88	30.895	32.395	31.765	30.730
F_4 Stephens/Daws//Yamhill	34.04	30.895	31.645	32.335	32.675
Correlation coefficient with observed yield		-0.10	0.439	-0.283	0.109

t = -0.72 for paired-observation test between observed and predicted value under Model II.

consideration GCA and SCA effects from populations grown under high competitive conditions, a correlation coefficient of -0.283 between actual and observed grain yield was found. For Model III, Part B, which uses for prediction combining ability effects from populations grown under low competitive conditions, the correlation coefficient between the two variables was 0.109. None of the correlation coefficients was significant. The calculated t-value for a paired observation test between actual and predicted grain yield under Model II was -0.724, which was not significant.

The degree of association between harvest index calculated from plants grown under low competitive conditions and grain yield from the high level of competition was also calculated. The correlation coefficient between the two characteristics was 0.181, which proved to be non-significant.

DISCUSSION

In the genetic improvement of a self-pollinated species like wheat, the plant breeder faces two major problems. The first is to select those parents which, when hybridized will result in the highest percentage of agronomically superior progeny, while the second problem is the identification in segregating populations of genetically superior individuals. Both of these situations are influenced by the breeder's ability to estimate the nature of inheritance and the manner in which parents can transmit favorable alleles for desired traits to their progeny.

These tasks are not difficult when the objective of the breeder is directed to the improvement of traits controlled by one or a few genes. Plant height, date of maturity, resistance to some diseases, seed color, etc., fall in this category. Since the phenotype of individuals for these traits is highly correlated with their genotypic constitution, the selection of parents can safely be performed based on their phenotypic expression. Furthermore, the intensity of selection in early segregating generations can be very high without losing any superior genotypes.

When the objective of the breeder is to improve a quantitatively inherited trait, such as grain yield, complications arise due to the fact that the phenotype may not be a true reflection of the genotype of an individual. The cumulative action of minor genes and the effects of environmental conditions contribute to the expression of a quantitative trait. However, the genetic component may be masked by the last factor. Under these circumstances, plant breeding becomes a game of probability in which large numbers of hybridizations are performed and extensive segregating populations grown with the hope of obtaining the desired progeny. Thus, if the breeder had a method of identifying those parents with the greatest genetic potential, the plant improvement program would be much more effective.

Different biometric models have been employed for the purpose of determining the genetic potential of parents. Models based on combining ability analysis look promising since they allow for the partition of the genetic component of variation in additive and non-additive genetic effects, based on the individual effects contributed by the parents. These effects are estimated by General Combining Ability (GCA) and Specific Combining Ability (SCA), respectively.

Because the objective of a breeder of self-pollinated species is usually to obtain high yielding homozygous lines, the additive portion of the total genetic effects is of primary interest. However, if a commercial hybrid is the end product, then the breeder must capitalize on both additive and non-additive genetic effects.

The presence of genotype x environment interactions further complicates the task of the plant breeder since it masks the nature of inheritance by influencing the expression of the desired traits. Usually genotype x environment interaction refers to that obtained from different locations, but it could also be expressed in the same location as the result of different growing seasons. How valid genetic estimates for specific traits are from one year to the next is a question of importance to plant breeders.

Genotype x environment interactions can also result from the competition level in which segregating generations are grown. This has important implications for the plant breeder since selection in early generations is often carried out under space planted conditions. It could be that selected genotypes under space planted conditions do not perform well under more competitive conditions similar to those of commercial production.

Estimates of genetic effects have usually been obtained from early generations such as the F_1 or F_2. Estimates of genetic effects over early segregations can provide additional information about the reliability of these estimates and the predominant types of gene action involved. The presence of significant SCA estimates over generations could indicate the relative importance of non-additive genetic effects, especially of the component due to epistasis. These genetic interactions have usually been disregarded in most biometrical models and thought to be of no consequence in the expression of quantitatively inherited traits. However, additive types of epistasis can be fixed in a homozygous condition. Should a trait be influenced largely by dominance genetic action, one-half of the effects will be lost each generation of selfing. This would further reduce the ability of the plant breeder to improve such a trait.

The number of crosses and segregating populations that can be handled impose an additional constraint on the plant breeder. In the United States germplasm collection alone, there are 47,000 different genotypes all available to be used as potential parents. Hybridization between the majority of these genotypes would not result in the release of significant amounts of usable genetic variability for traits such as grain yield. This becomes even more of a factor as yield levels continue to increase with possible yield plateaus being realized. The prediction of progeny performance with a given degree of precision would be an advantageous procedure for the breeder to use in sorting out which parental combination would be the most productive.

It was the purpose of this investigation to study how estimates of GCA and SCA may vary when calculated over generations grown at different plant densities and during two growing seasons. The relative importance of genetic effects in the expression of various agronomic traits, as well as the possibility of predicting grain yield under different models, were also analyzed. It was hoped that this information would help the wheat breeder to become more efficient in the development of superior cultivars.

Effects of Competition

When plants grow in a community, competition for the limiting factors is usually the case. Since plants compete for nutrients, available moisture and light, the amount of space per plant greatly influences their development. In this experiment, under high competitive conditions of growth, taller plants with fewer tillers and consequently less biological yield and grain yield per plant were observed. The mean values of 100 kernel weight and kernels per spike were also smaller under the high competition level. Similar results have been reported by Puckridge and Donald (1967), Pelton (1969), Syme (1972), Abi-Antoun (1977) and others. The mean values for harvest index, however, were larger under the higher competition level, probably due to the presence of fewer but more uniformly developed tillers.

Combining Ability and Competition Effects

The results of the combining ability analysis for the traits measured for the F_1 generation grown under space planted conditions in 1980-81 are in general agreement with what has been reported by different authors (Kronstad and Foote, 1964; Brown et al., 1966; Bitzer and Fu, 1972; Widner and Lebsock, 1973). The significant GCA estimates indicated that additive genetic effects were present for most traits and the possibility of improvement through selection including grain yield was possible. It is interesting to note that although the parents did not differ for biological and grain yield, still GCA estimates for the F_1 were significant for these traits. This could indicate that transgressive segregates could be expected from these populations.

When the 1980-81 data for the F_2 and F_3 generations were analyzed on an individual plant basis, interactions between crosses and level of competition were detected. This suggests that different crosses were not responding in the same way to competition. When the interactions between crosses and competition level were partitioned, the GCA x competition level interactions proved to be generally more important than the interactions for SCA and competition level. This was true in both F_1 and F_2 generations. Although additive genetic effects were generated in the hybridization process, their estimates varied within crosses as the competition level changed. Donald (1968) anticipated that the performance of a plant growing under space planted conditions might have little relationship to its potential for yield when grown in a community. Kelker and Briggs (1979) indicated that in the expression of agronomic traits of wheat cultivars grown under different plant densities, variability appears to be specific to each genotype. These observations support the results of this experiment. Falconer (1980) has suggested that the physiological mechanisms required for optimum performance in two different environments could require different genotypes. Abi-Antoun (1977) reported that additive genetic effects were predominantly involved in the expression of all characters studied under space planted conditions. However, non-additive genetic effects gained more influence as competition increased. It appears therefore, that either the same group of genes show a different type of gene action under dissimilar levels of competition or different genes are activated during plant development in response to competition levels. If the latter is the case, then selection of individuals within those crosses which are involved in interactions will not be effective if the resulting progenies are to be grown in a different competition level, and estimates of the nature of gene action controlling specific traits cannot be uniformly applied to all crosses. Selection could increase the frequency of alleles which do not contribute to the expression of the trait when the plant is exposed to a different environmental condition. Selection experiments designed to study the effect of plant competition seem to corroborate this concept (Jordaan and Laubscher, 1968; Knott, 1972; Nass, 1978).

No significant interactions between crosses and level of competition for any of the traits under study were observed in the 1981-82 growing season involving the F_2 and F_3 populations. The factor which had more influence on the observed differences between growing seasons could have been the presence of a heavy disease incidence caused by Septoria spp. in 1980-81.

The Septoria disease could have reduced the amount of seed of some susceptible genotypes, altering the population composition in 1981-82 in relation to the previous year. Changes in population composition because of natural selection can take place in a very short time as illustrated by the work of Harlan and Martini (1938). The theoretical curves that they provided on the effects of natural selection show that even small differences in fertility of genotypes can produce drastic changes in population composition. These changes are more pronounced during the first growing seasons proceeding asymptotically afterwards. A reduced fertility eventually causes the complete elimination of that genotype from the population. Therefore, the different performance of the populations in the two growing seasons could be accounted for by natural selection if certain genotypes were more tolerant of the Septoria disease. The performance of the F_4 population, however, differed from that of the F_2 and F_3 populations. This was unexpected since they were subjected to the same environmental factors and treated similarly in all aspects. However, the possibility exists that by chance alone the small random sample of seed taken to propagate the F_4 generation deviated somewhat from the true population parameters.

The observations in this experiment that SCA was significant for a number of characteristics whereas the respective interactions between SCA and competition level were often not significant are in agreement with the findings of Gyawali et al. (1968). They reported that the magnitude of heterosis was similar in both spaced and solid planted conditions. Zeven (1972) also reported that there was not a density effect on the expression of heterosis for yield and its components in wheat. He attributed this result to a possible buffering capacity in wheat because of its polyploid constitution. If dominance genetic effects which influence heterosis are relatively constant, then it could be assumed that the same set of genes determine the expression of the trait under the two different environmental conditions. The buffering capacity that is mentioned by Zeven (1972) could have little to do with the polyploid constitution of wheat but with the fact that heterozygous individuals are less affected by changes in environmental conditions (Allard, 1960; Falconer, 1980).

Changes in Combining Ability Estimates over Generations

In populations in which selective forces are not acting, the amount of variation due to additive genetic effects should remain fairly constant over generations. Since GCA effects provide an estimation of the contribution to additive genetic effects by each parent, an analysis of these values over successive generations could give important clues to plant breeders. Small changes in the estimates of genetic effects in the absence of artificial selection could be attributed to random variation. However, large changes could indicate the presence of natural selection forces in a given environment or growing season.

Good agreement was observed between the GCA effects of the F_2 and F_3 generations within growing seasons. However, when GCA effects were compared between the two growing seasons, some degree of inconsistency was noted for most of the traits measured. Only the correlation coefficients of the effects for plant height were significant in all cases. This could be due to the fact that plant height is influenced by few genes and therefore interactions with growing season is probably negligible. For a quantitatively inherited trait such as grain yield, the different genes which affect its expression probably interact more significantly and in varying degrees with growing season. It could also be that the Septoria disease of 1980-81 put a stronger selection pressure on genes related to grain yield than on genes for plant height. It has also been observed that taller plants tend to be less affected by the disease. These factors could account for the low association between the GCA effects of some traits between growing season. These results could imply the importance of obtaining estimates of genetic effects not only from different locations but also from different growing seasons, especially if there were marked dissimilarities between years or locations for disease problems or other major limiting factors.

A reduction in the magnitude of SCA estimates going from the F_2 to the F_3 generation was observed for all the traits under study in 1980-81. This response agrees with the theoretical expectations. Because of inbreeding, the contribution to the population mean due to dominance genetic effects is expected to be reduced by one-half with each successive generation. The weighted ratios of the squares of GCA and SCA effects for the low and high competition levels indicate a similar tendency. Since GCA should remain unchanged over successive generations in the absence of selection, the ratio of GCA and SCA effects should increase over generations. Although there were some exceptions, in general, the ratios did increase with advancing generations. Nevertheless, some differences were noted between the ratios from the two competition levels. For plant height, biological yield and grain yield, the ratios were larger under the low competition level. For tiller number and harvest index, the ratios were larger under the high competition level. This supports the idea that additive genetic effects and dominance genetic effects are expressed in different ways under different competition levels. This could also indicate that selection for agronomically important traits in the populations of this experiment should be performed under high competitive conditions of growth. Comparable results were obtained by Abi-Antoun (1977) who observed that compensating effects for yield among yield components varied in relation to planting densities and location.

In the 1981-82 growing season a clear tendency of an increase in the relative importance of GCA to SCA in successive generations was not observed. However, when both levels of competition were considered, the GCA over SCA ratios tended to increase for all traits except for 100 kernel weight and harvest index. The ratios for tiller number, biological yield and number of kernels per spike were clearly larger under the low competition level than under the high competition level. For the other traits, consistent differences from one competition level to the other were not observed. The noted difference in ratios because of competition levels might be attributable to different genes being expressed under those conditions and to the resulting interactions as already mentioned.

When the two growing seasons were considered, it was noted that only the ratios for biological yield were consistently smaller under the high competition level than under the low competition level. The magnitude of the ratios, however, did not seem to be related to competition level. This disagrees with the suggestion made by Cregan and Busch (1978) that dominance genetic effects may not be well expressed in wheat under high competitive conditions of growth. The presence of dominance genetic effects for traits such as biological yield could be important in the modification of plant type in a hybrid wheat breeding program which takes advantage of dominance genetic effects.

With an increase in the level of homozygosity, a comparable reduction in dominance genetic effects is expected. The inbreeding coefficient of an F_3 unselected wheat population is 0.75 whereas it is 0.875 in an F_4 population. Although SCA estimates for all the traits decreased from the F_2 to the F_3 population in the 1980-81 growing season, it was not the case for the populations in the 1981-82 season. Significant SCA estimates were larger than in the F_2 generation when compared to either the F_3 or F_4 populations. This was the case for all the traits under study. Significant SCA estimates in up to the F_6 generation of wheat have been reported by Jordaan and Laubscher (1968), Cregan and Busch (1978) and Milhaljev (1980).

A significant SCA in an advanced generation under continuous selfing cannot be indicative of the presence of dominance effects since they must have been reduced to negligible levels because of inbreeding. This should also be the case for dominance and dominance by additive types of epistatic effects. The total variance to be found in a population with an inbreeding coefficient of one is only variance among lines due to additive effects. Genes which contributed to additive x additive epistasis and higher order additive interactions, can be fixed. Thus, they influence the variance among lines. There is also the possibility of dominance types of epistasis being manifested from the interaction of certain genes at homologous gene loci in the different genomes of wheat.

Stutham and Stucker (1975) and Cregan and Busch (1978) attributed the significant SCA estimates of near-homozygous lines to these additive interactions, in oats and wheat, respectively. However, in unselected advanced populations, the additive types of epistatic effects should appear in the GCA estimates along with additive genetic effects. It could be that the significant SCA estimates found in the F_4 generation in this experiment are either the result of random sampling error or the action of natural selection in a previous generation. Natural selection could have favored some specific combinations of genes in genotypes resistant to the Septoria diseases. If this was the case, the observed deviations from the reference population could not have been anticipated.

Prediction of Yield

The models used for the prediction of grain yield in single crosses were different in terms of the types of genetic effects on which an accurate prediction was expected. Model I which uses only the mid-parent value for prediction is an additive model and was not as efficient as Model II and Model III in predicting yield in the 1980-81 growing season. Both Model II and Model III predict yield in terms of additive and non-additive genetic effects. The difference between the two models is related to the precision with which combining ability effects or heterosis values can be taken into account. The significant and near equal correlation coefficients obtained for the two models indicate the usefulness of either model in the prediction of single cross grain yield performance. However, this is only valid for these particular populations of single crosses in which additive and dominance genetic effects appear to be important in the variation observed for grain yield. If epistatic genetic effects were present then none of the models would probably be useful since, as indicated by Baker (1978), epistasis affect performance in an unpredictable manner.

For the three-way crosses grown in 1980-81, the models used to predict yield failed to do so. The number of possible three-way crosses resulting from a group of parents is considerably larger than the number of single crosses from the same group of parents, except when the number of parents is three. In this case, three three-way crosses and three single crosses are possible without including reciprocals. However, if only two loci are considered, the number of different epistatic interactions in the F_1 generation of three single crosses will still be three, whereas in the F_1 generation of three three-way crosses it will be 12. Therefore, if epistasis is important, it is expected that larger epistatic effects will exist in three-way crosses than in single crosses. If interallelic interactions were not present or important, then the population mean of three-way crosses should be equal to the population mean of single crosses in the absence of natural or artificial selection. This is because gene frequencies and intrallelic interactions are expected to be the same in both populations. Sprague et al. (1962) devised a simple method which provides a test for the presence of interallelic interactions or epistasis. A t-test for paired observations is performed for the observed and predicted grain yield of three-way crosses under the additive and dominance model, that is Model II in this study. They indicated that a significant difference between observed and predicted values can be interpreted as due to epistasis. This test was performed for the data of this experiment, and significant differences were detected. Although epistatic effects cannot be quantified with the model employed in this investigation, nevertheless they may be present and producing considerable deviations from the expected models. This could justify the increasing use of three-way crosses in different breeding programs. It is significant that an inverse relationship was observed between the sum of GCA effects and the deviations of the observed from the predicted values for grain yield in three-way crosses. In this experiment, the parent with the lowest GCA effects for grain yield presented the largest deviations from predicted values when used as the third parent in three-way crosses. It could be, as suggested by Peterson et al. (1969), that non-additive and, in this case, especially the portion due to epistatic genetic effects, are better expressed when additive genetic effects have been exhausted in the process of artificial selection.

Similar arguments as the preceding ones could be employed in the discussion of yield prediction for four-way crosses. Predicted values under the different models employed were not significantly correlated with actual values. Epistatic interactions in a population of four-way crosses are expected to be even greater than in three-way crosses since more genetic recombinations are possible in four-way crosses than in three-way crosses. Although the test proposed by Sprague was not significant for the four-way crosses, due to the small number of observations, it is still possible that epistasis can account for the lack of correlation of observed and predicted values.

In the 1981-82 growing season only Model II, Part A predicted grain yield accurately for single crosses grown under high competitive conditions. That is when combining ability effects calculated from the high competition level of growth were used in the prediction formula. The presence of interactions as already discussed could have determined that combining ability effects from the low competition level were not important in the prediction of grain yield from the high competition level. The observed superiority of Model II in relation to Model III in the 1981-82 growing season was not the case in the previous year. This raises questions about the reliability of this method for predicting yield in different growing seasons. However, it is apparent that in this experiment, grain yield in high competitive conditions of growth could not have been predicted accurately with data from low competitive conditions.

The trait harvest index estimated from plants grown under low competitive conditions, presented a low non-significant correlation coefficient with grain yield from plants grown under high competitive conditions in both growing seasons. This observation seems to indicate that for the populations of this experiment, harvest index could not be used as an indicator of plant yield in high competitive conditions. This finding is opposed to the reports of Syme (1972) and Fischer and Kertesz (1976) who advocated the value of harvest index as a predictor of grain yield. Since harvest index is obtained from the ratio of grain weight to biological yield, a high value of harvest index indicates a high proportion of grain weight in relation to straw weight. The argument that Syme (1972) presented was that the proportion of the products of photosynthesis which accumulate in the grain and straw is relatively constant and not affected to a significant degree by population density. However, in this experiment, it was observed that harvest index under the low competition level was of a lesser magnitude than harvest index under the high competition level. This was probably due to the presence of more secondary tillers with relatively smaller spikes in plants grown under the low competition level. Populations, furthermore, interacted significantly with the level of competition for harvest index. This is not surprising since populations also interacted significantly with level of competition for the variables which intervene directly in the calculation of harvest index. Plant height and tiller number may also have some influence on harvest index, although rather indirectly. Populations showed significant interactions with competition level for these traits, too. These observations do not support the constancy of a photosynthetic distribution factor as proposed by Syme (1972). Harvest index was found to be of no value as a yield predictor in this experiment.

From the results of this experiment, it would appear that GCA effects can help the breeder identify the best parental combinations. From estimates of GCA effects for grain yield over years, generations and competitive levels, it appears that the most promising combinations would be Stephens and Yamhill followed by Stephens and Daws. It was found that on a per plant basis in the advanced populations, the mean values for these crosses were higher with a higher percentage of plants yielding more than the overall mean value. Based on GCA effects for tiller number and 100 kernel weight, it would be predicted that the best combinations would also be Stephens and Yamhill and Stephens and Daws. However, the GCA effects for kernels per spike indicated that the combination Daws x Yamhill should be the best. This again agrees with the actual observations for the advanced generations. The fact that the same parent tended to produce the most promising progeny for grain yield and its components is not surprising due to the close association of these variables. It appears, therefore, that GCA effects can help to predict the parental combinations which will result in the most promising segregates.

SUMMARY AND CONCLUSIONS

The objectives of this investigation were: 1) to obtain estimates of GCA and SCA over generations grown in two different growing seasons as a means to identify the best parental combinations, 2) to assess the effect of plant competition resulting from two different seeding densities on estimates of genetic effects in early segregating generations and 3) to evaluate the possibility of predicting grain yield using several models.

Four winter wheat parents, F_1, F_2 and F_3 generations of single crosses and F_2 and F_3 generations of three-way and four-way crosses were planted at Hyslop Agronomy Farm in 1980-81. Four parents, F_2, F_3 and F_4 generations of single crosses and F_3 and F_4 generations of three-way crosses were planted at the same location in 1981-82. A low and a high seeding density were used in both growing seasons to provide different competition levels within populations. Segregating populations were advanced from one generation to the next by taking a random sample of 200 grams from the bulked seed of 30 randomly selected plants from the previous generation.

Data were collected on an individual plant basis. For this 15 plants were selected at random from each plot. The traits measured were plant height, tiller number, biological yield, grain yield and harvest index in 1980-81. In 1981-82 data were collected for the same traits plus weight of 100 kernels and number of kernels per spike.

Statistical analyses to determine possible differences among populations, generations and competition levels were performed. The presence of interactions between populations and competition level was also evaluated. Combining ability analyses over generations for each trait were carried out. Estimates of GCA and SCA and their interactions with the level of competition were obtained. The nature of gene action, the correlations among generations in the same growing season and between growing seasons for these genetic effects and the influence of the level of competition were evaluated. The possibility of predicting grain yield using different models was studied.

Based on the results of this investigation and the experimental populations used, the following conclusions were drawn:

1. The performance of the different populations was affected by the level of competition. Plants grown under low competitive conditions had larger mean values for all traits except harvest index.
2. Significant interactions between crosses and competition level indicated that not all genotypes were affected in a similar manner. However, interactions were more important in the 1980-81 growing season than in the 1981-82 growing season.
3. Significant GCA estimates for most traits, including grain yield, showed that additive genetic effects can be generated from this population of parents.
4. Specific combining ability estimates were also important,

although of a lesser magnitude than those of GCA. Expression of heterosis from some crosses was observed.

5. The presence of significant GCA x competition level interactions in 1980-81 for tiller number, biological yield and grain yield indicate that additive genetic effects are altered in their expression under different competition levels.
6. The absence of interactions between SCA and competition level in most cases, suggests that non-additive genetic effects are influenced less by different environments.
7. Natural selection could have produced the noted differences in estimates of GCA and SCA between growing seasons. Interactions between combining ability estimates and competition level were also probably affected by this factor.
8. A clear tendency of a reduction in the magnitude of SCA effects over generations was observed for some traits. For other traits, the significant SCA effects in F_3 and F_4 generations possibly indicate the importance of epistasis in influencing their expression. Intergenomic interaction among the chromosomes of wheat could account for the presence of different types of epistasis in advanced generations.
9. For single crosses, grain yield prediction was possible with the additive and dominance model and by means of combining ability effects. Prediction of yield failed in three-way and four-way crosses probably due to the presence of larger epistatic effects.
10. Prediction of grain yield by means of genetic effects estimated from a different competition level was not possible in this

experiment. Harvest index did not prove to be a good indicator of grain yield.

11. Data from this experiment suggested that higher yielding lines could be generated in three-way crosses when the third parent exhibited small GCA effects. This result can be attributed to a maximum expression of epistatic genetic effects under these circumstances.
12. Additive genetic effects estimated from one competition level could indicate the possibility of generating superior progeny if selection was performed under the same competition level. This applies to the populations of this experiment and to all the traits studied. Thus, breeders may wish to consider methods of selection which involve high seeding densities.
13. For non-additive genetic effects it appears that results obtained in one competition level could be extrapolated to the other competition level. If this were a generalized tendency it could prove to be valuable in the developing of hybrid wheat.
14. Due to changes in the environment over growing seasons, it is suggested that estimates of genetic effects be carried out over a representative sample of the prevalent conditions in the area. Genetic estimates obtained during an unusual growing season such as one with a severe disease infection should be looked at with caution when used as tools in selection.
15. From the observations in this experiment it can be concluded that GCA effects can help the plant breeder in identifying the best parental combinations for the traits studied. Based on

GCA effects the best parental combinations would be Stephens x Yamhill and Stephens x Daws for grain yield and the yield components. This prediction is supported by the actual data observed from the advanced generations of this study.

REFERENCES

Abi-Antoun, M. 1977. Compensating effects and gene action estimates for the components of grain yield in winter wheat (*Triticum aestivum* L. em Thell). Ph.D. Thesis. Oregon State University, Corvallis.

Allard, R. W. 1960. Principles of Plant Breeding. John Wiley and Sons, Inc. New York, NY.

Amaya, A. A., R. H. Busch, and K. L. Lebsock. 1972. Estimates of genetic effects of heading date, plant height and grain yield in durum wheat. Crop Sci. 12:478-481.

Baker, R. J. 1978. Issues in diallel analysis. Crop Sci. 18:533-536.

Bhatt, G. M. 1971. Heterotic performance and combining ability in a diallel cross among spring wheats (*Triticum aestivum* L.). Aust. J. Agric. Res. 22:359-368.

Bhullar, G. S., K. S. Gill, and A. Bhatia. 1979. Combining ability over successive generations in diallel crosses of bread wheat. Cereal Res. Com. 7:207-213.

Bitzer, M. J., F. L. Patterson, and W. E. NyQuist. 1971. Hybrid vigor and gene action in a six-parent diallel cross of soft winter wheat. Can. J. Genet. Cytol. 13:131-137.

Bitzer, M. J. and S. H. Fu. 1972. Heterosis and combining ability in southern soft red winter wheats. Crop Sci. 12:35-37.

Brajcich, P. 1981. Nature of inheritance, genotype-environment interactions and association of selected agronomic characters in crosses of winter x spring wheats (*Triticum aestivum* L. em Thell). Ph.D. Thesis. Oregon State University, Corvallis.

Briggle, L. W., E. L. Cox and R. M. Hayes. 1967. Performance of a spring wheat hybrid, F_2, F_3 and parent varieties at five population levels. Crop Sci. 7:465-470.

Brown, C. M., R. O. Weibel, and R. D. Seif. 1966. Heterosis and combining ability in common winter wheat. Crop Sci. 6:382-383.

Busch, R. H., J. C. Janke, and R. C. Frehberg. 1974. Evaluation of crosses among high and low yielding parents of spring wheat (*Triticum aestivum* L.) and bulk prediction of line performance. Crop Sci. 14:47-50.

Cregan, P. B. and R. H. Busch. 1978. Heterosis, inbreeding and line performance in crosses of adapted spring wheats. Crop Sci. 18:247-251.

Donald, C. M. 1962. In search of yield. J. Aust. Inst. Agric. Sci. 28:171-178.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Falconer, D. S. 1980. Introduction to Quantitative Genetics. 2nd ed. Longman, Inc. New York, NY.

Fischer, R. A. and Z. Kertesz. 1976. Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. Crop Sci. 16:55-59.

Fonseca, S. and F. L. Patterson. 1968. Hybrid vigor in a seven-parent diallel cross in common winter wheat. Crop Sci. 8:85-88.

Fowler, W. L. and E. G. Heyne. 1955. Evaluation of bulk hybrid tests for predicting performance of pure line selections in hard red winter wheat. Agron. J. 47:430-434.

Gyawali, K. K., C. O. Qualset and W. T. Yamazaki. 1968. Estimates of heterosis and combining ability in winter wheat. Crop Sci. 8:322-324.

Grafius, J. E., W. L. Nelson, and V. A. Dirks. 1952. Heritability of yield in barley as measured by early generation bulked progenies. Agron. J. 44:253-257.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9:463-493.

Hallauer, A. R. and J. B. Miranda, Fo. 1981. Quantitative Genetics in Maize Breeding. Iowa State University Press. Ames, Iowa.

Harlan, H. V. and M. L. Martini. 1938. The effect of natural selection in a mixture of barley varieties. Jour. Agric. Res. 57:189-199.

Harlan, H. V., M. L. Martini, and H. Stevens. 1940. A study of methods in barley breeding. USDA Tech. Bull. No. 720.

Jenkins, M. T. 1934. Methods of estimating the performance of double crosses in corn. Jour. Amer. Soc. Agron. 26:199-204.

Jenkins, M. T. and A. M. Brunson. 1932. Methods of testing inbred lines of maize in crossbred combinations. Jour. Amer. Soc. Agron. 24:523-530.

Jensen, N. F. and W. T. Federer. 1956. Competing ability in wheat. Crop Sci. 5:449-452.

Jinks, J. L. 1956. The F_2 and backcross generations from a set of diallel crosses. Heredity 10:1-30.

Jordaan, J. P. and F. X. Laubscher. 1968. The repeatability of breeding values for eleven wheat varieties estimated over generations. Proc. 3rd Int. Wheat Genetics Symposium. Canberra, Australia. pp. 416-420.

Kaltsikes, P. J. and J. Lee. 1971. Quantitative inhertiance in durum wheat. Can. J. Genet. Cytol. 13:210-218.

Kelker, H. A. and K. G. Briggs. 1979. The effects of intergenotypic competition and interplant spacings in simulated segregating rows of wheat. Proc. 5th Int. Wheat Genetics Symposium. New Delhi, India. pp. 778-786.

Kertesz, Z., J. Matuz and Z. Barabas. 1980. Selecting superior winter wheat crosses and lines in early generations. Proc. 3rd Int. Wheat Conference. Madrid, Spain. pp. 89-95.

Knott, D. R. 1965. Heterosis in seven wheat hybrids. Can. J. Plant Sci. 45:499-501.

Knott, D. R. 1972. Effects of selection for F_2 plant yield on subsequent generations in wheat. Can. J. Plant Sci. 52:721-726.

Knott, D. R. and S. S. Sindagi. 1969. Heterosis in diallel crosses among six varieties of hard red spring wheat. Can. J. Genet. Cytol. 11:810-822.

Kronstad, W. E. and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat. Crop Sci. 4:616-618.

Leffel, R. C. and W. D. Hanson. 1961. Early generation testing of diallel crosses of soybean. Crop Sci. 1:169-175.

Mather, K. 1949. Biometrical Genetics. Methuen, London.

Matzinger, D. F. and O. Kempthorne. 1956. The modified diallel table with partial inbreeding and interactions with environment. Genetics 41:822-833.

Mihaljev, I. 1980. Combining ability for grain yield in F_1 - F_6 generations of diallel wheat crosses. Proc. 3rd Int. Wheat Conference. Madrid, Spain. pp. 102-109.

Moll, R. H. and C. W. Stuber. 1974. Quantitative genetics: Empirical results relevant to plant breeding. Adv. Agron. 26:277-313.

Nass, H. G. 1978. Comparison of selection efficiency for grain yield in two population densities of four spring wheat crosses. Crop Sci. 18:10-12.

Otsuka, Y., S. A. Eberhart and W. A. Russell. 1972. Comparisons of prediction formulas for maize hybrids. Crop Sci. 12:325-331.

Paroda, R. S. and A. B. Joshi. 1970. Genetic architecture of yield and components of yield in wheat. Indian J. Genet. 30:298-314.

Patanothai, A. and R. E. Atkins. 1974. Genetic effects of mean yield responses to environments in three-way and single cross of grain sorghum. Crop Sci. 14:485-488.

Pelton, W. L. 1969. Influence of low seeding rates on wheat yield in southwestern Saskatchewan. Can. J. Plant Sci. 49:607-614.

Peterson, C. J., W. E. Kronstad and O. A. Vogel. 1969. Maximizing heterosis in winter wheat. Agronomy Abstracts. p. 15.

Petpisit, V. 1980. Progeny tests for predicting grain yield and selected agronomic traits in single, three-way and double crosses in wheat (*Triticum aestivum* L. em Thell). Ph.D. Thesis. Oregon State University, Corvallis.

Puckridge, D. W. and C. M. Donald. 1967. Competition among wheat plants sown at a wide range of densities. Aust. J. Agric. Res. 18:193-211.

Rinke, E. H. and H. K. Hayes. 1964. General and specific combining ability in diallel crosses of 15 inbred lines of corn. Bot. Bull. Acad. Sinica 5:36-41.

Roy, N. N. 1976. Inter-genotypic plant competition in wheat under single seed descent breeding. Euphytica 25:219-223.

Sikka, S. M., K. B. L. Jain, and K. S. Parmer. 1959. Evaluation of potentialities of wheat crosses based on mean parental and early generation values. Indian J. Genet. 19:150-169.

Smith, E. L. and J. W. Lambert. 1968. Evaluation of early generation testing in spring barley. Crop Sci. 8:490-493.

Sprague, G. F. and L. A. Tatum. 1942. General vs. specific combining ability in single crosses of corn. Jour. Amer. Soc. Agron. 34:923-932.

Sprague, G. F., W. A. Russell, L. H. Penny, T. W. Horner and W. D. Hanson. 1962. Effect of epistasis on grain yield in maize. Crop Sci. 2:205-208.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and Procedures of Statistics. 2nd edition. McGraw-Hill Book Company, Inc. New York, NY.

Stuber, C. W. 1970. Estimation of genetic variances using inbred relatives. Crop Sci. 10:129-135.

Stutham, D. D. and R. E. Stucker. 1975. Combining ability analysis of near-homozygous lines derived from a 12-parent diallel cross in oats. Crop Sci. 15:800-803.

Suneson, C. A. and G. A. Wiebe. 1942. Survival of barley and wheat varieties in mixtures. Jour. Amer. Soc. Agron. 34:1052-1056.

Syme, J. R. 1972. Single-plant characters as a measure of field plot performance of wheat cultivars. Aust. J. Agric. Res. 23:753-760.

Tandom, J. P., A. B. Joshi and K. B. L. Jain. 1970. Comparison of graphic and combining ability analyses of diallel crosses in wheat. Indian J. Genet. 30:91-103.

Valencia, J. A. 1980. Competitive effect for grain yield of four cultivars in pure and mixed populations in wheat (*Triticum aestivum* Vill.; Host). Ph.D. Thesis. Oregon State University, Corvallis.

Widner, J. N. and K. L. Lebsock. 1973. Combining ability in durum wheat: I. Agronomic characteristics. Crop Sci. 13:164-167.

Zeven, A. C. 1972. Plant density effect on expression of heterosis for yield and its components in wheat and F_1 versus F_3 yields. Euphytica 21:468-488.