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Title: ESTIMATES OF HETEROSIS FOR FIVE AGRONOMIC TRAITS IN SELECTED WINTER X SPRING AND WINTER X WINTER WHEAT CROSSES (*Triticum aestivum* L. em Thell).

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Concern regarding the lack of genetic variability and the apparent yield plateau reached in wheat breeding have prompted this investigation. The systematic crossing of spring and winter wheat types which have evolved to form somewhat different gene pools, may provide a source of additional usable genetic variability for future yield increases.

Five winter and five spring wheat cultivars with different degrees of genetic similarities in their pedigrees were crossed to obtain F1's and F2's. The parents plus winter x spring F1's were planted in two growing seasons at Hyslop Agronomy Farm near Corvallis, Oregon. During the second season the winter x spring F2 and winter x winter F1 crosses were also included. Agronomic traits were measured on an individual plant basis. These traits were plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield. Analyses of variance were conducted for each trait. Estimates of the amount of usable genetic variation were determined by heterosis values, inbreeding depression and parent-progeny standard regressions. Possible interactions between years and the above five characters were determined for the winter x spring F1's.

Evidence of non-additive gene action was found in the expression of heterosis and subsequent inbreeding depression which depended on the specific trait measured and the parents involved in the cross. The greatest heterosis values were noted for grain yield per plant. Crosses with the winter parent, Weique Red Mace, resulted in the highest estimates for grain yield. This was due to the late maturity of these hybrids and to the diverse genetic background of this winter parent compared to the five spring parents.

Parent-progeny regressions indicated that a large amount of additive genetic variance was present for plant height, 100 kernel weight and grain yield an intermediate amount for kernels per spike and tillers per plant.

Winter x spring F1 crosses resulted in higher heterosis estimates and a wider range of values between crosses than winter x winter F1 crosses. Parent-progeny regression estimates were similar in value for the two types of F1 populations. Thus, these results indicate that the systematic crossing between winter and spring wheats will produce greater total genetic variability for further wheat improvement. This is true for the development of hybrid wheat (non-additive) and may also be promising for conventional breeding programs when only the additive portion of the total genetic variance can be used.

The data support the general conclusion that the amount of heterosis is a function of genetic diversity between the two parents. Those breeders working on hybrid wheat may wish to look at winter x spring crosses as a means of maximizing heterosis. However, since a significant interaction between years x F1's was noted for the traits measured, more than one year of evaluation will be necessary if winter x spring crosses are employed.

Estimates of Heterosis for Five Agronomic Traits in Selected Winter X Spring and Winter X Winter Wheat Crosses (Triticum aestivum L. em Thell)

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Typed by Kathie Klahn for Pedro Brajcich

IN DEDICATION TO:

Juana Maria, my wife

Rady, my son

Rodolfo and Petronila, my parents

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES -- continued

LIST OF TABLES -- continued

LIST OF APPENDIX TABLES

ESTIMATES OF HETEROSIS FOR FIVE AGRONOMIC TRAITS IN SELECTED WINTER X SPRING AND WINTER X WINTER WHEAT CROSSES (*Triticum aestivum*, L. em Thell)

INTRODUCTION

World food shortages and rapidly expanding human population have created an urgent need for increased food production. Breeding and research for improved crop yields has been very successful in recent years. Unfortunately, in several major food crops including wheat, possible plateaus for yield are being reached. One approach to increasing grain yield in wheat is through hybridization of winter and spring cultivars, thus broadening the usable genetic variation for further cultivar improvement. A second possibility would be the development of hybrid wheat thus taking advantage of the total genetic variability available to the wheat breeder.

Spring and winter type wheats have evolved separately over time due to their different ecological requirements, and the reluctance of breeders to make crosses between them. It is significant, however, that the limited amount of winter x spring crossing carried out in the past gave rise to some well-known varieties. These include cultivars such as Hybrid 128, Ridit, Rex, Thatcher, Mentana and Federation 41. More recently the cultivars which launched the "Green Revolution" resulted from combining daylength insensitivity from a spring wheat (Gabo) with the semidwarf stature obtained from a winter wheat (Norin 10).

Large scale field crossing of winter x spring wheats became possible when the International Maize and Wheat Improvement Center (CIMMYT) discovered, in 1972, that both types would flower simultaneously in the field at the Toluca Experimental Station in Mexico. This has allowed CIMMYT and Oregon State University to capitalize on the increased genetic diversity from such crosses to improve both spring and winter wheat using the conventional breeding methods of self-pollinated species.

A second way of increasing yield in normally self-pollinated species such as wheat is to develop male sterile and restorer lines, thus obtaining hybrids for commerical production. One of the major questions which must be answered before this approach is feasible would be how much hybrid vigor is available in wheat. Since spring and winter wheat types have diverged genetically over time, the question is if greater hybrid vigor would be expected between winter x spring against winter x winter or spring x spring parents.

It was the objective of this investigation to: 1) determine the nature of gene action influencing plant height, yield components and yield in winter x spring and winter x winter F1's; 2) investigate the influence of different years on the expression of heterosis in the winter x spring F1 wheat crosses; and 3) compare the extent of heterosis in winter x spring with winter x winter F1's.

LITERATURE REVIEW

Heterosis, Heterobeltiosis and Inbreeding Depression.

For plant breeders of self-pollinated crop success in selection is restricted to that portion of the total genetic variance which is additive in controlling the expression of the agronomic characters. If the total amount of genetic variability could be utilized, which would include the non-additive genetic portion as well, greater yields may be achieved.

Heterosis, the superiority of the F1 over the average of its parents, is an estimation of gene action in the F1 generation. In the utilization of heterosis in commerical crops only that value in excess of the better parent is of significance. Fonseca and Patterson (1968a) proposed the term heterobeltiosis to describe the improvement of the heterozygote in relation to the better parent.

Inbreeding depression in the F2 generation may also give some indication of the type of gene action involved in the expression of a particular agronomic character. Inbreeding depression has just the opposite effect of heterosis and results from the increase in frequency of homozygous genotypes and decrease of heterozygous genotypes.

In 1963, Briggle presented a comprehensive review of literature concerning heterosis in wheat and reported several investigations where significant heterosis levels were reported for different characters in wheat.

Observations of heterosis in wheat date back to 1919 when Freeman (cited by Briggle, 1963) studied flowering date, height and leaf width in crosses between a durum wheat and three common wheats. He noticed heterosis only for plant height in two crosses.

Spring Wheats

Seven wheat crosses were tested to determine the presence of heterosis by Knott (1965). The parents represented a wide range of different genetic types. Heading date in the F1's tended to be close to the early parent. Four of the crosses yielded more than the mid-parent value. The greatest increase was 22.5 percent. He concluded that high-yielding F1's can be expected only from crosses involving high-yielding parents. Later, Wells and Lay (1970) studied grain yield and seed weight in the F1 and F2 generations of 22 wheats crossed with two tester lines. No evidence was found in this study that crosses between high yielding pure lines resulted in higher yielding hybrids.

Two complete diallel crosses, with five and eight parents, respectively were used by Walton (1971) to study the expression of heterosis in wheats of Canadian, Mexican and American origin. He noted that the increase in yield over the high parent in the two years were very different. The first year he obtained a range from 17 to 20 percent. For the second year the range was from 17 below to four percent above the higher yielding parent. The author concluded that the decline in the performance of the hybrids in relation to the parents indicates an F1 by year interaction. He suggested that genetic diversity alone will not guarantee the expression of heterosis if environmental conditions are not suitable.

Heterosis for yield and yield components was studied by Singh and Singh (1971) in F1, F2 and F3 generations in ten wheat crosses. They noticed that eight F1's exceeded their better parent for yield with values ranging from 1.8 to 42.3 percent. They also observed that there was a sharp inbreeding depression for yield in F2's and F3's compared to F1's. The F2 and F3 yields were respectively 35.0 and 45.4 percent lower than the F1. They observed positive heterosis values over the best parent for kernel wieght and spikes per plant with values of 1.4 and 6.1 percent, respectively. Negative values for spikelets per spike and kernels per spike were observed. It was concluded that, in general, kernel weight and spikes per plant were responsible for the increase in yield of the F1's. Crosses involving high yielding parents from different ecogeographic regions produced higher heterosis values. They suggested that well adapted high yielding parents with greater genetic diversity should be chosen to find the best combination for the expression of heterosis. Negative heterosis values over the best parent in the F2 for yield, kernel weight, spikes per plant, spikelets per spike and kernels per spike were also observed.

Heterosis for earliness, plant height, four yield components and yield were examined by Bhatt (1971) in a diallel cross of eight wheat cultivars. The highest values were expressed for kernel weight and kernels per spike. The author also examined the geographic origin of the parents. They formed two groups, Australian and Mexican. Small gain in plant height and grain yield was exhibited by crosses between groups over the crosses within groups and no gain was observed for the other traits. He pointed out that either the level of diversity of one group was similar to that of the other or that geographical diversity may not have been a true index of genetic diversity.

Four wheat cultivars differing for kernel weight were intercrossed by Sun et al (1972). They calculated heterosis for kernel weight as the percent increase of F1 above mid-parent performance and found a range from -4.3 to 31.2 percent. The authors observed that heterosis was greater in crosses between more distantly related parents.

A diallel of eight parents was used by Bhatt (1973) to study yield potential in the F2 generation. The investigation was conducted under low and high moisture levels. He obtained values for yield over the mid-parent for low moisture conditions ranging from 79 to 122 percent and for high moisture from 72 to 138 percent. Heterosis values over the best parent for low moisture ranged from 73 to 119 percent and for high moisture from 69 to 136 percent. The author noted a persistance of some heterosis in the F2 for certain crosses, indicating a negligible genotype x environment interaction.

The following conclusions were reached by Fedin (1976) using ten wheats crossed in a diallel manner: dominant gene action was the source of heterosis for plant height, number of kernels and kernel weight per ear and protein; dominance and epistasis caused heterosis for number of tillers; and dominance or dominant - epistatic effects were responsible for heterosis in kernel weight. The author added that dominant gene action is more stable under environmental changes than epistasis.

Eight adapted high-yielding wheats were crossed by Cregan and Busch (1978) in a diallel manner. The F1 yields exhibited heterosis over the mid-parents from five to 58 percent and over the better parent from -17 to 41 percent. On the average, the F2 showed no significant heterosis over the mid-parents. Significant heterosis over the mid-parents, however, was noted in three crosses. The results indicated that, for this study, the potential for yield improvement via conventional breeding was about equal to that of the F1 hybrids.

Winter Wheats

Heterosis in yield and yield components was studied by Brown et al (1966), with seven winter wheat parents. Five of the 16 F1's were significantly higher in grain yield than the best parent in the cross. Twelve of the 16 F1's were significantly higher than the mid-parents. The heterosis values of grain yield over the mid-parent ranged from 107 to 138 percent and the values over the best parent were from 96 to 131 percent. They also observed small heterosis effects for spikes per plant and kernel weight. Most of the high heterosis values were obtained from hard x soft wheat crosses.

A seven-parent diallel cross in wheat was examined by Fonseca and Patterson (1968a) for heterobeltiosis for two years. The first year 19 of the 21 crosses exceeded the better parent in grain yield. Four of them were significantly different. Negative values were found for heading date, plant height, spikes per hill, kernels per spike and kernel weight. In the second year all the crosses exceeded the better parent for grain yield, 19 of them significantly. Positive values were reported for spikes per hill, kernel weight and kernels per spike, but the values were lower than the value for grain yield. The results in the F2 indicated that some crosses still retain some heterosis for grain yield, spikes per hill, kernel weight and kernels per spike.

From a seven-parent diallel cross using soft red, soft white and hard red wheat varieties, Gyawali, et al (1968) estimated heterosis.

They found that ten of the 21 crosses were significantly different than the better parent for grain yield and eleven when compared to the mid-parent. Greater heterosis was found for grain yield than kernel weight and spikes per plant. Soft red x soft red and soft red x hard red crosses gave similar heterosis values, indicating that interclass diversity is not necessary for heterosis expression in the parents used in this study. Crosses between early and late maturing parents produced greater heterosis for grain yield than hybrids with both early or late parents.

Liver and Heyne (1968) grew a nine-parent diallel cross for four years. The F1's exceeded the parents for grain yield by 20, 37, 37 and 35 percent in the four years. Heading date tended to be earlier than the mid-parents. High heterosis values were evident for plant height. Heterosis values for spikes per plot, kernel weight and grain yield were consistent over years. The F2's were grown for two years and were found to be six percent better for grain yield than the mid-parent but inferior to the better parent.

A diallel cross of six soft red wheats consisting of parents, F1's and F2's was examined by Bitzer et al (1972) over two years. Years x genotype interaction was significant for heading date, spikes per plant, kernel weight and grain yield. This indicated that the genotypes responded somewhat differently each year. Thirteen out of the 15 F1's yielded more than the better parent, but none was significantly higher. The heterosis values noted in the F1 were mostly lost in the F2.

Winter X Spring Wheat Crosses

Wheat cultivars are classified as winter, spring or facultative type.

This classification refers to their habit of growth, which is considered to be an inherited character. The spring growth habit is governed by at least three dominant genes (Vrn1, Vrn2, Vrn3) any one of which is able to inhibit the expression of the winter habit (Pugsley, 1970). Winter wheat carries recessive alleles of the three loci and Vrn1 is epistatic to Vrn2 (Pugsley, 1972 and Gotoh, 1979).

Until recently most studies using spring x winter crosses endeavored to increase variability in spring wheat. Pinthus (1967) concluded that the higher grain yield of winter wheat is due to its long period of kernel development which acts as a strong sink. The author suggested that winter wheat should be able to contribute to an increase in yield in crosses with spring wheat. Rupert (1971) recommended the use of winter x spring crosses. He felt that, given the existence of two elite but isolated germ plasm pools, much could be gained by systematically combining these pools.

Significant levels of heterosis were demonstrated by Grant and McKenzie (1970) in F1 yield trials from crosses between spring and winter wheats. Yields up to 40 percent higher than those of the spring parent were attributed to heterosis resulting from hybridization of genetically diverse spring and winter types. The authors observed the possibility in a conventional breeding program of selecting good spring types, retaining at the same time the genes for greater yield from winter parents. Pinthus (1973) concluded that the exploitation of the high yielding potential of the winter x spring crosses was dependent upon their relative earliness and on their protection from stem rust and leaf rust.

Heterosis in winter x spring crosses was studied by Mani and Rao

(1975). Heterosis over the mid-parent ranged from -19 to 193 percent for grain yield. Twenty-four F1's out of 55 exhibited significant heterosis, but when compared to the better parent none of the crosses gave significant heterobeltiosis. For tillers per plant, only 27 F1 crosses exhibited positive heterosis when compared to the better parent. Significant heterosis values over the better parent were reported for kernels per spike, tillers per plant, and kernel weight. The authors concluded that heterosis was a function of the late maturity of the hybrids compared to spring parents and, to some extent, tillers per plant.

A diallel of six winter and two spring wheats were used by Mihaljev (1976) to study the expression of heterosis. Five of the 28 F1's exceeded the better parent in grain yield. The range was from three to 21 percent. Twelve F1's exceeded the mid-parent, ranging from three to 25 percent. Heterosis in kernel weight also was observed in 12 F1's when compared to the better parent, ranging from one to 21 percent.

Heritability

Heritability may be defined as that proportion of the total variability which is due to genetic causes (Allard 1960) or it can also be referred to as the degree to which the characteristics of a plant are repeated in its offspring (Briggs and Knowles, 1967). Heritability can be regarded in two ways (Lush, 1945); broad-sense which measures the total genetic variance including both additive and non-additive gene action and as such is not an index of transmissibility and narrow-sense which measures the additive genetic variance and may be considered as an index of transmissibility, especially in self-pollinated crops where only additive gene action can be fixed in succeeding generations.

Techniques for estimating the degree of heritability fall into three main categories: 1) parent-offspring regression, 2) variance components from an analysis of variance and 3) approximation of environmental variance from non-segregating populations (Warner, 1952). Heritability estimates are termed high if greater than 0.50, low if less than 0.20 and medium if equal to or between 0.50 and 0.20 (Stansfield, 1969).

Spring Wheats

Heritability values for heading date, plant height and kernel weight were determined by Bhatt (1972) in two crosses. High broad-sense heritability estimates were obtained for the three characters. Medium to high narrow-sense heritability estimates were reported for heading date and plant height. High narrow-sense heritability was observed for kernel weight.

Broad-sense heritability was calculated by Sun et al (1972) in six wheat crosses for kernel weight. The estimate was high, ranging from 51 to 85 percent in five crosses.

Narrow-sense heritability was estimated in two wheat crosses by Knott and Kumar (1975). The estimates were made from the regression and correlation of F5 means on F3 means. The two methods gave similar values. Low values were found for grain yield and medium to high for plant height. The authors suggested that effective selection can be made in early generations for plant height and in later generations for grain yield.

Winter Wheats

Narrow-sense heritabilities using parent-F1 regression techniques were obtained by Kronstad and Foote (1964). The estimates were high for plant height and medium for spikes per plant, kernel weight and grain yield. The authors further indicated that a similar pattern was noted in the ratio of general to specific combining ability with the exception of kernel weight.

A cross of hard red wheats was used by Johnson, et al (1966) to estimate heritability. Narrow-sense estimates were low for grain yield and tillers per plant, medium for plant height and high for kernel weight. Broad-sense estimates were low for grain yield, medium for tillers per plant and high for kernel weight and plant height. The authors indicated that selection in F2 could be effective for plant height and kernel weight, but uneffective for tillers per plant or grain yield.

Heritability estimates in the narrow-sense were obtained by Fonseca and Patterson (1968b) from the regression of F1 on F2 means on mid-parent. The estimate was high for plant height, medium for kernels per spike and low to medium for kernel weight and grain yield. These estimates were in agreement with the ratio of general and specific combining ability.

Narrow-sense heritability was estimated by Ketata et al (1976) using the variances of the F2 and backcrosses. The estimates were high for plant height and kernel weight, medium for tillers per plant and low for kernels per spike and grain yield. The authors indicated that heritability estimates tended to be high for those characters exhibiting wide differences between the two parents.

The parents, F1's, F2's and backcrosses derived from the two hard red wheat cultivars were used by Sidwell _et al_ (1976) to estimate heritability, using the variance component estimates. Broad-sense estimates were high for kernel weight and medium for tillers per plant, kernels per spike and grain yield. Narrow-sense estimates were medium for tillers per plant and kernel weight, low for kernels per spike and grain yield. They concluded that kernel weight would be the character most responsive to direct selection pressure, adding that heritability estimates alone do not present the entire picture suggesting that the correlation between each of the characters must be considered.

MATERIALS AND METHODS

Five winter and five spring wheat cultivars were chosen for this study. The winter wheat cultivars were Kavkaz, Roussalka, Yamhill, Hyslop and Weique Red Mace (W.R. Mace). The spring wheat cultivars were Inia 66, Siete Cerros 66 (7Cerros 66), Torim 73, Jupateco 73 and Huacamayo "S". These ten cultivars differ genetically not only in growth habit but in plant height, grain yield, yield components and other traits. Pedigree and description of each cultivar is listed in the Appendix Table 1. Two studies were conducted at Hyslop Agronomy Farm, Corvallis, Oregon during two crops seasons (1976-77 and 1977-78). They are identified as Study I and Study II.

Crosses between the winter and spring wheats were made in the summer of 1976 at the Toluca Experimental Station in Mexico. During the spring of 1977, the parents and winter x spring F1's were grown in the greenhouse at Corvallis, Oregon where additional winter x spring crosses and all possible combinations of crosses within the winter parents were made. At the same time the winter x spring F2's were obtained for each cross.

Study I

The winter and spring wheat parents and the F1 generation resulting from crosses between the two groups were planted on October 23, 1976. A complete randomized block design with four replications was used to determine possible significant differences for the traits and generations measured.

Each replication consisted of one row for each parent and F1. Each row consisted of ten plants spaced 20 cm apart with 30 cm spacing between rows. Where missing plants occurred, barley was planted in the spring to provide uniform competition. Weeds were controlled by hand cultivation. Before planting, 300 kg/ha of fertilizer (16-20-0) was applied. Later, at the tillering stage, an additional 400 kg/ha of Urea was broadcast.

Study II

This experiment was similar to Study I but included also the winter x spring F2 populations and the winter x winter F1's. Each replication had parents and F1's (winter x spring and winter x winter) represented by one row with ten plants. The winter x spring F2's had six rows with ten plants per row. This experiment was planted on October 12, 1977. On May 18, 1978, 0.5 kg/ha of Bayleton was applied to avoid a stripe rust epidemic. A summary of climatic data for both crop seasons is presented in Appendix Table 2.

Data were collected on an individual plant basis in both studies.

1. Plant height was obtained at maturity by measuring from the base of the crown to the tip of the spike of the main tiller, excluding awns if present.
2. Number of tillers per plant was recorded as the number of culms bearing fertile spikes.
3. 100 kernel weight was recorded in grams, by weighing 100 kernels randomly selected from each individual plant.
4. The number of kernels per spike (x) was determined indirectly from the following data: (a) grain yield per plant, (b) 100 kernel weight and (c) number of tillers per plant

$$x = \frac{100\ (a/b)}{c}$$

5. Grain yield per plant was determined by the weight of the grain in grams.

An analysis of variance was done on the above characteristics. Each study was analyzed separately and then the two years' data combined and analyzed. The F test was utilized to determine significant differences (Snedecor and Cochran, 1967). Plot means were used for the analysis. The group effects (genotypes) in the analysis of variance were divided into component effects to detect differences between and within groups. The mean values for each group (Study I: winter parents, spring parents and winter x spring F1's; Study II: winter parents, spring parents, winter x spring F1's, winter x winter F1's and winter x spring F2's) were compared using Duncan's multiple range test.

Heterosis was calculated for each trait as the percentage increase of the F1 above the mean of the parental lines. The formula used was that described by Matzinger _et al_ (1962):

$$\text{Heterosis} = \frac{F1-MP}{MP} \times 100$$

where MP is the mid parent value and F1 is the mean of the first generation.

Possible hybrid performance superior to the winter parent was calculated for each study using the formula:

$$\text{Heterosis} = \frac{F1-WP}{WP} \times 100$$

where WP is the mean value of the winter parent and F1 is the mean of the first generation.

Hybrid performance superior to the highest parent was calculated for winter x winter crosses in the second study using the formula proposed by Fonseca and Patterson (1968a):

$$\text{Heterobeltiosis} = \frac{F1-HP}{HP} \times 100$$

where HP is the mean value of the highest parent and F1 is the mean of the first generation.

Inbreeding depression was measured as the average percent decrease of the F2 (winter x spring) from the F1 (winter x spring) for each trait in each cross. The formula used was that described by Matzinger et al (1962):

$$\text{Inbreeding depression} = \frac{F1-F2}{F1} \times 100$$

Using these formulas, a positive heterosis value is an increase in performance while a negative heterosis value is a decrease in performance. The opposite is true for inbreeding depression; a positive value is equivalent to a decrease in performance while a negative value is an increase in performance.

Parent-progeny regression estimates were obtained for the five characters by the regression in standard units (Frey and Horner, 1957) of the performance of the F1 on the mid-parent and the F2 mean values on the corresponding F1 mean value.

EXPERIMENTAL RESULTS

The results are presented separately for each study conducted at Hyslop Agronomy Farm, Corvallis, Oregon during two crop seasons (1976-77 and 1977-78).

Study I, 1976-77

Analysis of Variance

The experimental materials used were winter and spring wheat cultivars selected for their grain yield potential and differing genetic backgrounds. The analysis of variance was computed to detect possible differences among genotypes and between and within the three experimental groups for five agronomic characters. The three groups consisted of five winter parents, five spring parents and all 25 F1 combinations of each winter parent crossed with the five spring cultivars (Table 1). Highly significant differences were noted among the 35 populations (genotypes) for the five characters measured. A similar difference was found between the three groups (winter parents, spring parents and winter x spring F1's) for all the characters with the exception of tillers per plant and for all the characters within the groups. The sources of variation were further partitioned within each of the three groups. Significant differences (P = 0.01) were detected within winter parents and F1's for the characters measured. Within spring parents, the same was true with the exception of tillers per plant which was significantly different at a lower probability level (P = 0.05).

The coefficient of variation (C.V.) was low for plant height, 100 kernel weight and kernels per spike: 2.68, 4.33 and 9.60 percent, respectively. The C.V. values for tillers per plant and grain yield per

Table 1. Observed mean square values for five agronomic characters in wheat obtained from five winter parents, five spring parents and the 25 winter x spring F1's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

Source of Variation	df	Plant Height	Tillers Per Plant	100 Kernel Weight	Kernels Per Spike	Yield Per Plant
Replications	3	50.73**	0.94	0.11*	123.24**	123.26
Genotypes	34	422.59**	14.89**	1.21**	310.46**	436.45**
Between Groups	2	2,341.70**	4.61	8.45**	213.21**	1,707.99**
Within Groups	32	302.65**	15.53**	0.76**	316.53**	356.98**
W/Winter Parents	4	350.63**	35.66**	0.53**	202.79**	398.98**
W/Spring Parents	4	270.08**	13.93*	0.79**	231.70**	491.70**
W/ Winter X Spring F1's	24	300.08**	12.44**	0.79**	349.63**	327.52**
Error	102	6.93	6.25	0.04	27.02	66.79
Total	139					
C.V. %		2.68	14.78	4.33	9.60	18.54

* Significant at the 5 percent probability level.

** Significant at the 1 percent probability level.

plant were relatively high, 14.78 and 18.54 percent, respectively.

Mean values for the winter parents (Table 2) indicated that Kavkaz was the taller parent and was significantly different from the other four winter parents. Hyslop had a significantly higher value for tillers per plant and had more kernels per spike and grain yield, although it was not significantly different from the other parents for the latter traits. Roussalka was superior for 100 kernel weight; however, it was not significantly different from Kavkaz.

The mean values for spring parents (Table 3) indicated that Huacamayo "S" was the superior cultivar for the five characters studied. Significant differences were noted for plant height and grain yield per plant. Huacamayo "S", however, was not significantly different for tillers per plant from Torim 73 and Siete Cerros 66. This was also true for 100 kernel weight when compared to Inia 66 and for kernels per spike when compared to Siete Cerros 66.

Mean values of the winter x spring F1 crosses for the five characters studied are found in Table 4. Plant height ranged from 87.00 cm for Roussalka-Torim 73 to 123.75 cm for the cross Kavkaz-Huacamayo "S". For tiller number, the range was 14.42 to 20.86 for the cross Roussalka-Inia 66 and Hyslop-Huacamayo "S", respectively, with the highest value not significantly different for 13 out of the 25 winter x spring Fl's. The cross Kavkaz-Huacamayo "S" gave the highest value for 100 kernel weight and was significantly different from all other Fl's (6.56 gm). The Hyslop-Torim 73 F1 had the lowest kernel weight (4.61 gm). For number of kernels per spike, the F1 Weique Red Mace-Jupateco 73 population was the highest and Kavkaz-Siete Cerros 66 was the lowest (69.07

Table 2. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for the winter wheat parents grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

Winter Parents	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Kavkaz	108.91 a*	15.96 bc	5.01 ab	58.29 a	46.70 ab
Roussalka	85.93 d	13.15 c	5.05 a	44.08 b	29.37 c
Yamhill	99.14 b	17.29 b	4.27 c	58.47 a	43.23 b
Hyslop	92.71 c	21.41 a	4.34 c	61.40 a	57.20 a
Weique Red Mace	87.75 d	17.52 b	4.77 b	50.44 b	42.22 b
Average	94.89	17.07	4.69	54.54	43.74

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

Table 3. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for the spring wheat parents grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

Spring Parents	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Inia 66	92.90 c*	14.73 b	4.80 a	43.94 c	30.99 b
7 Cerros 66	97.73 b	16.85 ab	3.92 c	57.24 ab	37.50 b
Torim 73	80.52 d	17.57 ab	4.30 b	44.73 c	33.19 b
Jupateco 73	93.22 c	14.44 b	4.05 bc	50.09 bc	29.41 b
Huacamayo "S"	102.63 a	18.80 a	4.91 a	61.19 a	56.61 a
Average	93.40	16.48	4.40	51.44	37.54

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

Table 4. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for the winter x spring Fl's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

Winter X Spring Fl's	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Kavkaz-Inia 66	111.41 ef*	15.01 cd	5.90 b	42.25 gh	37.35 h
Kavkaz-7Cerros 66	116.00 cd	17.66 a-d	5.83 b	41.74 h	42.74 e-h
Kavkaz-Torim 73	106.70 g-j	16.30 b-d	5.63 b-d	45.81 f-h	42.09 f-h
Kavkaz-Jupateco 73	112.78 de	18.45 a-d	5.91 b	42.09 gh	45.75 d-h
Kavkaz-Huacamayo "S"	123.75 a	16.09 b-d	6.56 a	51.27 ef	54.37 b-f
Roussalka-Inia 66	97.64 lm	14.42 d	5.29 d-g	50.37 e-g	38.30 gh
Roussalka-7Cerros 66	99.64 kl	16.17 b-d	5.19 e-h	55.30 de	46.32 d-h
Roussalka-Torim 73	87.00 o	15.85 b-d	4.97 g-i	52.06 e	41.17 f-h
Roussalka-Jupateco 73	95.45 mn	15.69 b-d	5.12 e-i	51.60 e	41.04 f-h
Roussalka-Huacamayo "S"	103.08 jk	14.79 d	5.34 d-f	58.92 b-e	46.57 d-h
Yamhill-Inia 66	108.11 f-i	16.82 a-d	5.09 e-i	63.78 a-d	55.03 b-f
Yamhill-7Cerros 66	118.12 bc	17.78 a-d	4.82 ij	68.90 a	59.25 a-d
Yamhill-Torim 73	108.45 e-h	16.44 b-d	5.00 f-i	66.57 ab	54.81 b-f
Yamhill-Jupateco 73	117.14 b-d	15.89 b-d	5.00 f-i	65.94 ab	52.18 b-f
Yamhill-Huacamayo "S"	120.76 ab	16.52 a-d	5.19 e-h	62.66 a-d	53.62 b-f
Hyslop-Inia 66	105.06 h-j	19.73 ab	5.09 e-i	51.05 ef	51.06 b-g
Hyslop-7Cerros 66	104.74 h-j	19.54 ab	4.93 h-j	46.19 f-h	44.26 e-h
Hyslop-Torim 73	93.43 n	19.60 ab	4.61 j	55.16 de	49.81 c-h
Hyslop-Jupateco 73	99.60 kl	19.50 ab	4.64 j	46.10 f-h	41.63 f-h
Hyslop-Huacamayo"S"	103.78 jk	20.86 a	5.02 f-i	56.86 c-e	59.40 a-d
W.R. Mace-Inia 66	110.69 e-g	17.51 a-d	5.79 bc	65.60 a-c	66.30 ab
W.R. Mace-7Cerros 66	108.24 e-i	19.31 a-c	5.44 c-e	66.46 ab	70.54 a
W.R. Mace-Torim 73	105.75 h-j	17.22 a-d	5.29 d-g	67.11 ab	60.75 a-c
W.R. Mace-Jupateco 73	108.19 f-i	15.54 b-d	5.31 d-g	69.07 a	56.24 b-e
W.R. Mace-Huacamayo "S"	107.43 f-j	17.85 a-d	5.30 d-g	66.80 ab	62.98 a-c
Average	106.92	17.22	5.25	56.39	50.94

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

and 41.74, respectively). Nine out of the 25 F1 populations were not significantly different from the Weique Red Mace-Jupateco 73 cross. For grain yield, the highest F1 population was Weique Red Mace-Siete Cerros 66 and the lowest was Kavkaz-Inia 66 (70.54 and 37.35 gm, respectively). Five F1 populations were not significantly different from the highest cross for this trait.

The mean values and the results of the analysis of variance confirm the existence of genetic diversity among winter and spring parents and between the F1 crosses for all traits measured.

Performance of F1 Compared to Mid-Parent and Winter Parent

Results of the F1's compared to their respective mid- and winter parent for plant height are summarized in Table 5. All hybrid populations were taller than their respective mid-parent value. The percentage of the F1's over the mid-parent ranged from 4.54 to 25.69 with an average of 13.55. A range of -2.03 to 26.14 percent with an average of 13.02 percent was observed when F1's were compared to their respective winter parent. The highest values resulted from crosses involving the winter parents, Weique Red Mace and Yamhill. Lower values, when compared to the mid-parent, were found in crosses with Roussalka while crosses with Kavkaz had the lowest value.

Values for tillers per plant (Table 5) compared to the mid-parent ranged from -8.45 to 21.38 percent with an average of 2.87 percent. The Kavkaz-Jupateco 73 F1 had the highest value. When F1's were compared with the winter parent a range of -11.30 to 22.97 percent was detected with an average of 2.14 percent. The highest value noted was with the Roussalka-Siete Cerros 66 F1. Crosses involving the spring parents,

Table 5. Heterosis as a percentage of the mid-parent (MP) and winter parent (WP) for plant height and tillers per plant of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

	Plant Height		Tillers Per Plant	
Cross	MP	WP	MP	WP
Kavkaz-Inia 66	10.41	2.30	-2.18	-5.95
Kavkaz-7Cerros 66	12.27	6.51	7.65	10.65
Kavkaz-Torim 73	12.65	-2.03	-2.77	2.13
Kavkaz-Jupateco 73	11.59	3.55	21.38	15.60
Kavkaz-Huacamayo "S"	17.00	13.63	-7.42	0.81
Average	12.78	4.79	3.33	4.65
Roussalka-Inia 66	9.20	13.63	3.44	9.66
Roussalka-7Cerros 66	8.50	15.95	7.80	22.97
Roussalka-Torim 73	4.54	1.25	3.19	20.53
Roussalka-Jupateco 73	6.56	11.08	13.74	19.32
Roussalka-Huacamayo "S"	9.33	19.96	-7.42	12.47
Average	7.63	12.37	4.15	16.99
Yamhill-Inia 66	12.59	9.05	5.06	-2.72
Yamhill-7Cerros 66	20.00	19.14	4.16	2.83
Yamhill-Torim 73	20.73	9.39	-5.68	-4.92
Yamhill-Jupateco 73	21.79	18.16	0.16	-8.10
Yamhill-Huacamayo "S"	19.70	21.81	-8.45	-4.45
Average	18.96	15.51	-0.95	-3.47
Hyslop-Inia 66	13.21	13.32	9.19	-7.85
Hyslop-7Cerros 66	10.00	12.98	2.14	-8.73
Hyslop-Torim 73	7.87	0.78	0.56	-8.45
Hyslop-Jupateco 73	7.14	7.43	8.79	-8.92
Hyslop-Huacamayo "S"	6.26	11.94	3.76	-2.57
Average	8.90	9.29	4.89	-7.30
W.R. Mace-Inia 66	22.55	26.14	8.59	-0.06
W.R. Mace-7Cerros 66	16.71	23.35	12.37	10.22
W.R. Mace Torim 73	25.69	20.51	-1.85	-1.71
W.R. Mace Jupateco 73	19.57	23.29	-2.75	-11.30
W.R. Mace Huacamayo "S"	12.86	22.43	-1.71	1.88
Average	19.48	23.14	2.93	-0.19
Overall Average	13.55	13.02	2.87	2.14

Torim 73 and Huacamayo "S", gave the lowest values when compared to their respective mid-parent. On the average, F1's with Hyslop as the winter parent had the highest values when compared to the mid-parent for tiller number. All F1 crosses were superior in tillers per plant to the mid-parent when Roussalka was the winter parent. The same was true for crosses with Kavkaz except with the Kavkaz-Inia 66 cross.

Of all the yield components, 100 kernel weight had the greatest heterosis values when compared to the mid- and winter parent values (Table 6). All the F1's exceeded their respective mid-parent value. The values over the mid-parent ranged from 6.31 to 32.26 percent with an average of 16.12 percent. A range of -1.58 to 30.94 percent with an average of 12.99 percent was found when the F1's were compared to the respective winter parents. In both instances, the cross Kavkaz-Huacamayo "S" resulted in the highest value. On the average, the winter parents Kavkaz and Weique Red Mace produced offspring with higher values. The other parents, in descending order, were Yamhill, Hyslop and Roussalka.

Number of kernels per spike for the F1's ranged from -27.74 to 41.03 percent with an average of 8.32 percent over the mid-parent (Table 6). In crosses with Weique Red Mace, Yamhill and Roussalka the F1 gave high and positive values. The values compared to the winter parent ranged from -28.39 to 36.93 percent with an average of 5.29 percent. The highest values came from crosses where Weique Red Mace was a parent and from the Roussalka-Huacamayo "S" F1.

Grain yield per plant produced the highest heterosis when compared with the other traits measured (Table 7). With the excpetion of two crosses (Hyslop-Jupateco 73 and Kavkaz-Inia 66), all the F1's were higher

Table 6. Heterosis as a percentage of the mid-parent (MP) and winter parent (WP) for 100 kernel weight and kernels per spike of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

	100 Kernel Weight		Kernels Per Spike	
Cross	MP	WP	MP	WP
Kavkaz-Inia 66	20.29	17.76	17.34	-27.52
Kavkaz-7Cerros 66	30.57	16.37	-27.74	-28.33
Kavkaz-Torim 73	20.05	12.38	-11.07	-21.41
Kavkaz-Jupateco 73	30.46	17.06	-22.33	-27.79
Kavkaz-Huacamayo "S"	32.26	30.94	-14.18	-12.04
Average	24.91	19.08	-11.60	-23.43
Roussalka-Inia 66	7.41	4.75	14.45	14.27
Roussalka-7Cerros 66	15.72	2.77	9.16	25.45
Roussalka-Torim 73	6.31	-1.58	17.24	18.10
Roussalka-Jupateco 73	12.53	1.39	9.59	17.06
Roussalka-Huacamayo "S"	7.23	5.74	11.94	33.67
Average	9.82	2.61	12.48	21.71
Yamhill-Inia 66	12.24	19.20	24.51	9.08
Yamhill-7Cerros 66	17.70	12.88	9.24	17.84
Yamhill-Torim 73	16.69	17.10	29.01	13.85
Yamhill-Jupateco 73	20.19	17.10	21.48	12.78
Yamhill-Huacamayo "S"	13.07	21.55	4.73	7.17
Average	15.98	17.57	17.79	12.14
Hyslop-Inia 66	11.38	17.28	-3.08	-16.86
Hyslop-7Cerros 66	19.37	13.59	-22.13	-24.77
Hyslop-Torim 73	6.71	6.22	3.95	-10.16
Hyslop-Jupateco 73	10.61	6.91	-17.30	-24.92
Hyslop-Huacamayo "S"	8.54	15.67	-7.24	-7.39
Average	11.32	11.93	-9.16	-16.82
W.R. Mace-Inia 66	21.00	21.38	39.01	30.06
W.R. Mace-7Cerros 66	25.20	14.05	23.44	31.76
W.R. Mace-Torim 73	16.65	10.90	41.03	33.05
W.R. Mace-Jupateco 73	20.41	11.32	37.41	36.93
W.R. Mace-Huacamayo "S"	9.50	11.11	19.68	32.43
Average	18.55	13.75	32.11	32.85
Overall Average	16.12	12.99	8.32	5.29

Table 7. Heterosis as a percentage of the mid-parent (MP) and winter parent (WP) for grain yield per plant of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77.

Cross	Grain Yield Per Plant	
	MP	WP
Kavkaz-Inia 66	-3.85	-20.02
Kavkaz-7Cerros 66	1.52	8.48
Kavkaz-Torim 73	5.37	-9.87
Kavkaz-Jupateco 73	20.22	-2.03
Kavkaz-Huacamayo "S"	5.26	16.42
Average	5.71	-1.40
Roussalka-Inia 66	26.91	30.41
Roussalka-7Cerros 66	38.54	57.71
Roussalka-Torim 73	31.62	40.18
Roussalka-Jupateco 73	39.64	39.73
Roussalka-Huacamayo "S"	8.33	58.56
Average	29.01	45.32
Yamhill-Inia 66	48.29	27.30
Yamhill-7Cerros 66	46.79	37.06
Yamhill-Torim 73	43.44	26.79
Yamhill-Jupateco 73	43.67	20.70
Yamhill-Huacamayo "S"	7.41	24.03
Average	37.92	27.18
Hyslop-Inia 66	15.80	-10.73
Hyslop-7Cerros 66	6.53	-22.62
Hyslop-Torim 73	10.21	-12.92
Hyslop-Jupateco 73	-3.87	-27.22
Hyslop-Huacamayo "S"	4.38	3.85
Average	6.61	-13.93
W.R. Mace-Inia 66	81.12	57.03
W.R. Mace-7Cerros 66	76.97	67.08
W.R. Mace-Torim 73	61.12	43.89
W.R. Mace-Jupateco 73	57.03	33.21
W.R. Mace-Huacamayo "S"	27.45	49.17
Average	60.74	50.08
Overall Average	28.00	21.45

than the mid-parent value. The F1 values ranged from -3.87 to 81.12 percent fo the mid-parent value with an average of 28.00 percent. The highest values corresponded to crosses where Weique Red Mace was present, followed by crosses with Yamhill and Roussalka. F1 values compared to the winter parent ranged from -27.22 to 67.08 percent with an average of 21.45 percent. Again, the highest value was observed in F1's where Weique Red Mace was involved, followed by Roussalka and Yamhill. The negative values came from crosses where Kavkaz and Hyslop were the winter parents. None of these crosses yielded more than the winter parent with the exceptions of Kavkaz-Siete Cerros 66, Kavkaz-Huacamayo "S" and Hyslop-Huacamayo "S".

Parent-Progeny Standard Regression

To obtain additional information regarding the nature of gene action controlling the traits measured, standardized regression coefficients of F1's on mid-parents were calculated by grouping the spring cultivars with their respective winter parent. The values obtained for the five agronomic characters measured are noted in Table 8.

Regression values were high for plant height in the crosses involving Kavkaz, Roussalka and Hyslop and intermediate for the Weique Red Mace crosses. The values ranged from 39.94 to 98.92 percent.

Parent-progeny values were high for tillers per plant in the crosses with Hyslop and Weique Red Mace, intermediate for Yamhill and low for Roussalka and Kavkaz crosses. These values ranged from -20.92 to 67.41 percent.

For 100 kernel weight, the values were high for Yamhill, Kavkaz, Roussalka and Hyslop crosses and were intermediate for Weique Red Mace.

Table 8. Parent-progeny standard regression in winter x spring crosses using F1 and mid-parent values for the five agronomic characteristics studied expressed as percentage, 1976-77.

Winter Parent Crossed to the Same Group of Spring Wheats	Plant Height	Tillers Per Plant	100 Kernel Weight	Kernels Per Spike	Yield Per Plant
Kavkaz X Spring Parents	93.27	-20.92	62.93	49.57	84.19
Roussalka X Spring Parents	98.92	8.66	62.71	93.87	76.33
Yamhill X Spring Parents	79.68	21.77	90.47	31.09	-2.46
Hyslop X Spring Parents	85.02	67.41	61.76	5.03	79.10
W.R. Mace X Spring Parents	39.94	51.24	34.98	7.39	17.61
Average	79.37	25.63	62.57	37.39	50.96

The range was from 34.98 to 90.47 percent for this trait.

A high estimate was observed for kernels per spike for crosses with Roussalka, intermediate for crosses involving Kavkaz and Yamhill and low for crosses with Weique Red Mace and Hyslop ranging from 5.03 to 93.87 percent.

Regression estimates for grain yield per plant were high for crosses involving Kavkaz, Hyslop and Roussalka and low for those crosses involving Weique Red Mace and Yamhill. The values ranged from -2.46 to 84.19 percent.

Regression estimates on the average were high for plant height, 100 kernel weight and grain yield per plant and intermediate for kernels per spike and tillers per plant. This is the same ranking that was previously noted when comparative performances were presented between F1's and their respective mid-parent and winter parents for these traits.

Study II, 1977-78

Analysis of Variance

In Study II, the same winter and spring parents and F1 winter x spring crosses were utilized plus F1 winter x winter and F2 winter x spring crosses. This resulted in five different genetic groups or populations. An analysis of variance for the five traits studied was computed to detect possible differences among genotypes as well as between and within the five groups formed (Table 9). Differences among all genotypes were highly significant for the five characters. The same was true for between and within groups. When each group was analyzed separately, the winter parents were significantly different ($P = 0.01$) for all the characters with the exception of tillers per plant. Spring

Table 9. Observed mean square values for five agronomic characteristics of winter parents, spring parents, winter x spring Fl's, winter x winter Fl's and winter x spring F2's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Source of Variation	df	Plant Height	Tillers Per Plant	100 Kernel Weight	Kernels Per Spike	Yield Per Plant
Replications	3	43.12	6.64	0.32**	99.03**	177.73**
Genotypes	69	344.15**	14.36**	0.59**	286.46**	280.10**
Between Groups	4	2,086.85**	99.73**	6.67**	1,380.40**	2,454.95**
Within Groups 1/	65	236.91**	9.10**	0.22**	219.14**	146.27**
W/Winter Parents	4	527.89**	3.61	0.35**	369.14**	157.73**
W/Spring Parents	4	187.52**	7.03**	0.57**	82.78	80.49**
W/Winter X Spring Fl	24	286.29**	15.59**	0.18*	356.92**	266.41**
W/Winter X Winter Fl	9	137.97**	6.18	0.07	126.18**	79.30
W/Winter X Spring F2	24	184.36**	4.97**	0.23**	113.96**	60.29**
Reps x Genotypes 2/	207	21.29	3.56	0.07	29.35	45.19
Reps x B/Groups	12	8.67	1.59	0.06	30.37	37.24
Reps x W/Groups 3/	195	22.07	3.69	0.07	29.29	45.68
Reps x W/Winter Parents 4/	12	11.15	1.19	0.01	10.02	9.61
Reps x W/Spring Parents 5/	12	9.29	1.25	0.04	26.87	5.07
Reps x W/Winter X Spring Fl 6/	72	21.58	5.63	0.10	43.68	72.43
Reps x W/Winter X Winter Fl 7/	27	27.52	6.06	0.09	25.96	76.17
Reps x W/Winter X Spring F2 8/	72	24.45	1.67	0.04	19.76	20.26
Total	279					
C.V. %		4.81	15.60	6.17	11.45	26.50

*Significant at the 5 percent probability level.
**Significant at the 1 percent probability level.

1/ Error Term for Between Groups
2/ Error Term for Replications and Genotypes
3/ Error Term for Within Groups
4/ Error Term for W/Winter Parents
5/ Error Term for W/Spring Parents
6/ Error Term for W/Winter X Spring Fl
7/ Error Term for W/Winter X Winter Fl
8/ Error Term for W/Winter X Spring F2

parents were significantly different (P = 0.01) for all the characters with the exception of kernels per spike. F1 winter x spring crosses were significantly different (P = 0.01) for plant height, tillers per plant, kernels per spike and grain yield. A significant difference for 100 kernel weight was also observed at lower probability level (P = 0.05). F1 winter x winter crosses were significantly different (P = 0.01) only for plant height and kernels per spike. Highly significant differences for all traits measured were observed for winter x spring F2 populations.

The coefficient of variation values were low for plant height and 100 kernel weight (4.81 and 6.17 percent, respectively). The coefficient of variation values for kernels per spike, tillers per plant and grain yield per plant were relatively high, 11.45, 15.60 and 26.50 percent respectively.

Mean values for the five winter parents are summarized in Table 10. Kavkaz was the tallest parent being significantly different from the other four parents. Hyslop had the higher tiller number but was not significantly different from the other parents. The highest value for 100 kernel weight was found for Kavkaz. It was not significantly different from Weique Red Mace or Yamhill. Hyslop had more kernels per spike and differed significantly from the other parents. Also, Hyslpp had the highest grain yield, but it was not significantly different from either Yamhill or Kavkaz.

For the spring parents, the mean values are summarized in Table 11. Huacamayo "S" was found to be the superior parent for the five agronomic

Table 10. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for the winter wheat parents grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter Parents	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Kavkaz	110.24 a*	12.82 a	4.60 a	46.82 b	27.92 a
Roussalka	84.30 d	13.29 a	4.08 b	37.81 c	20.80 b
Yamhill	100.62 b	13.32 a	4.42 a	50.29 b	29.91 a
Hyslop	91.69 c	14.67 a	3.91 b	56.10 a	32.48 a
Weique Red Mace	83.01 d	12.07 a	4.50 a	32.20 d	17.63 c
Average	93.97	13.23	4.30	44.64	25.75

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

Table 11. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for the spring wheat parents grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Spring Parents	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Inia 66	82.21 b	7.86 b	3.54 b	36.26 a	10.50 bc
7Cerros 66	89.25 a	8.16 b	3.23 bc	42.31 a	11.95 b
Torim 73	73.76 c	9.58 ab	3.13 c	37.85 a	12.01 b
Jupateco 73	79.10 b	7.36 c	3.09 c	35.74 a	7.98 c
Huacamayo "S"	89.88 a	10.56 a	4.00 a	46.41 a	19.94 a
Average	82.84	8.70	3.40	39.71	12.48

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

characters measured. Significant differences were noted for 100 kernel weight and grain yield per plant. Huacamayo "S", however, was not significantly different from plant height from Siete Cerros 66. This was also true for tillers per plant when compared to Torim 73.

F1 winter x spring mean values (Table 12) indicated that a wide range of variability existed for plant height from 85.29 cm for the cross Roussalka-Torim 73 to 120.35 cm for the cross Kavkaz-Siete Cerros 66. Less variation was noted for tillers per plant which ranged from 8.22 to 15.99. Hyslop-Torim 73 had the highest value but it was not significantly different from 22 out of the 25 crosses. The variation for 100 kernel weight was very small, ranging from 4.22 to 4.98 gm. Kavkaz-Huacamayo "S" had the largest weight but was not significantly different from 18 of the 25 crosses. Kernels per spike ranged from 31.09 to 65.77 with the highest number associated with the Yamhill-Siete Cerros 66 cross. This cross, however, was not significantly different from 11 out of the 25 crosses. Grain yield per plant ranged from 12.48 to 45.07 gm. The highest yielding cross was Kavkaz-Siete Cerros 66.

The mean values for winter x winter F1's are summarized in Table 13. Significant differences for plant height and kernels per spike were detected among the ten winter x winter crosses. Plant height ranged from 93.68 to 114.57 cm with the tallest cross being Yamhill-Kavkaz. This cross was significantly different from five of the ten crosses. The Hyslop-Roussalka F1 was the shortest and was significantly different from six of the ten crosses. The values for kernels per spike ranged from 47.29 to 63.20. The Yamhill-Kavkaz cross had the highest value and was significantly different from five of the ten crosses; Roussalka-

Table 12. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for winter x spring F1's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter X Spring F1's	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Kavkaz-Inia 66	104.64 d-g*	8.47 bc	4.71 a-d	35.96 j	15.09 fg
Kavkaz-7Cerros 66	120.35 a	15.33 a	4.57 a-d	64.65 ab	45.07 a
Kavkaz-Torim 73	97.96 f-h	8.22 c	4.95 a	31.09 j	12.48 g
Kavkaz-Jupateco 73	102.72 e-g	12.51 a-c	4.80 a-c	34.10 j	20.51 e-g
Kavkaz-Huacamayo "S"	118.66 ab	15.92 a	4.98 a	53.38 b-h	42.50 ab
Roussalka-Inia 66	93.19 h	11.74 a-c	4.50 a-d	46.80 hi	24.51 e-g
Roussalka-7Cerros 66	96.54 gh	13.84 a	4.77 a-d	59.04 a-g	38.40 a-c
Roussalka-Torim 73	85.29 i	13.42 a	4.28 cd	48.96 f-h	27.90 b-f
Roussalka-Jupateco 73	91.25 hi	11.75 a-c	4.54 a-d	50.11 e-h	26.60 c-f
Roussalka-Huacamayo "S"	98.03 f-h	14.20 a	4.84 ab	52.39 d-h	36.10 a-e
Yamhill-Inia 66	105.93 c-f	11.49 a-c	4.33 b-d	60.35 a-f	29.93 b-e
Yamhill-7Cerros 66	111.65 b-d	12.86 a-c	4.35 b-d	65.77 a	37.22 a-c
Yamhill-Torim 73	104.64 d-g	13.38 a	4.24 d	63.87 a-c	36.27 a-d
Yamhill-Jupateco 73	107.23 c-e	12.84 a-c	4.50 a-d	56.21 a-h	32.86 a-e
Yamhill-Huacamayo "S"	113.68 a-c	12.64 a-c	4.64 a-d	53.49 b-h	31.67 a-e
Hyslop-Inia 66	97.30 gh	12.71 a-c	4.48 a-d	52.97 c-h	31.28 a-e
Hyslop-7Cerros 66	101.68 e-g	15.87 a	4.24 d	48.59 gh	32.55 a-e
Hyslop-Torim 73	91.95 hi	15.99 a	4.22 d	52.34 d-h	35.85 a-e
Hyslop-Jupateco 73	93.56 h	13.12 ab	4.48 a-d	37.03 ij	21.71 d-g
Hyslop-Huacamayo "S"	98.00 f-h	13.24 a	4.46 a-d	55.36 a-h	34.20 a-e
W.R. Mace-Inia 66	103.60 d-g	11.55 a-c	4.50 a-d	55.96 a-h	28.81 b-f
W.R. Mace-7Cerros 66	104.24 d-g	14.85 a	4.54 a-d	56.02 a-h	38.28 a-c
W.R. Mace-Torim 73	103.02 e-g	13.17 ab	4.47 a-d	60.64 a-e	36.78 a-c
W.R. Mace-Jupateco 73	96.13 gh	14.50 a	4.52 a-d	54.97 a-h	36.26 a-d
W.R. Mace-Huacamayo "S"	107.38 c-e	14.80 a	4.56 a-d	61.86 a-d	41.59 ab
Average	101.94	13.14	4.54	52.48	31.78

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

Table 13. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for winter x winter F1's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter X Winter F1's	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Roussalka-Kavkaz	105.95 abc*	12.70 a	4.58 a	47.29 c	27.37 a
Yamhill-Kavkaz	114.57 a	12.67 a	4.84 a	63.20 a	38.92 a
Hyslop-Kavkaz	108.33 abc	15.14 a	4.61 a	50.23 c	35.34 a
W.R. Mace-Kavkaz	109.36 ab	13.00 a	4.69 a	49.03 c	30.28 a
Yamhill-Roussalka	105.56 abc	13.89 a	4.74 a	59.25 ab	39.07 a
Hyslop-Roussalka	93.68 d	12.48 a	4.55 a	56.13 abc	32.09 a
W.R. Mace-Roussalka	99.26 cd	12.88 a	4.58 a	49.34 c	28.92 a
Hyslop-Yamhill	103.95 bc	11.54 a	4.40 a	61.44 a	31.39 a
W.R. Mace-Yamhill	101.82 bcd	14.74 a	4.81 a	51.49 bc	37.78 a
W.R. Mace-Hyslop	100.51 bcd	15.15 a	4.60 a	54.32 abc	38.29 a
Average	104.30	13.42	4.64	54.17	33.95

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

Kavkaz had the lowest value and was significantly different from three of the ten crosses.

The mean values for the winter x spring F2's are summarized in Table 14. The F2 population of Yamhill-Siete Cerros 66 was the tallest at 108.76 cm. It was significantly different from 19 out of the 25 crosses. Roussalka-Torim 73 with 84.54 cm was the shortest and was significantly different from 18 of the 25 crosses. Values for tillers per plant ranged from 9.80 to 14.28. Hyslop-Huacamayo "S" had the highest value and was significantly different from 14 of the 25 crosses. The lowest value was observed for Kavkaz-Inia 66 which differed significantly from 12 of the 25 crosses. For 100 kernel weight, the cross Kavkaz-Huacamayo "S" had the highest value being significantly different from 23 crosses. Values for kernels per spike ranged from 33.33 to 53.57. Yamhill-Torim 73 which had the highest value was significantly different from ten of the 25 crosses. Kavkaz-Jupateco 73 had the lowest value. For grain yield per plant, Weique Red Mace-Siete Cerros 66 had the highest value, 30.41 gm. It was significantly different from ten of the 25 crosses. The lowest value, 14.43, was for the cross Kavkaz-Jupateco 73.

Analysis of variance and mean values for each characteristic studied indicated that the winter parents differed significantly for each character with the exception of tillers per plant. The spring parents also differed significantly for each character with the exception of kernel weight. On the average, the F1 winter x winter crosses were slightly superior for each trait when compared to the F1 winter x spring crosses. When the magnitude of the ranges are considered, however, winter x spring

Table 14. Mean values for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant for winter x spring F2's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter X Spring F2's	Plant Height (cm)	Tillers Per Plant	100 Kernel Weight (gm)	Kernels Per Spike	Yield Per Plant (gm)
Kavkaz-Inia 66	92.50 d-g*	9.80 e	4.43 bc	34.18 g	15.02 gh
Kavkaz-7Cerros 66	107.19 ab	11.76 b-e	4.58 ab	44.03 c-f	23.54 a-f
Kavkaz-Torim 73	97.06 c-e	11.76 b-e	4.23 b-f	38.03 fg	18.10 e-h
Kavkaz-Jupateco 73	97.82 c-e	9.93 e	4.38 b-d	33.33 g	14.43 h
Kavkaz-Huacamayo "S"	108.31 a	11.08 c-e	4.93 a	42.26 ef	23.21 a-f
Roussalka-Inia 66	90.86 e-h	11.19 c-e	4.22 b-f	43.27 c-f	20.58 b-h
Roussalka-7Cerros 66	95.16 c-e	12.41 a-d	4.31 b-d	48.35 a-e	25.84 a-e
Roussalka-Torim 73	84.54 h	11.97 b-e	4.09 c-g	45.01 b-e	22.11 b-g
Roussalka-Jupateco 73	86.11 gh	11.01 c-e	4.02 d-g	42.89 d-f	19.23 c-h
Roussalka-Huacamayo "S"	91.75 d-h	12.62 a-d	4.45 bc	46.83 a-e	16.38 f-h
Yamhill-Inia 66	100.19 a-d	10.93 de	4.11 c-g	52.60 ab	23.80 a-f
Yamhill-7Cerros 66	108.76 a	11.27 c-e	4.30 b-e	50.84 a-c	26.26 a-d
Yamhill-Torim 73	98.97 b-e	11.99 b-e	3.94 e-g	53.57 a	25.54 a-e
Yamhill-Jupateco 73	101.15 a-c	12.02 b-e	4.03 d-g	45.55 b-e	22.27 b-g
Yamhill-Huacamayo "S"	108.21 a	12.56 a-d	4.43 bc	47.52 a-e	26.56 a-c
Hyslop-Inia 66	98.35 c-e	12.91 a-d	4.17 c-f	46.84 a-e	25.02 a-e
Hyslop-7Cerros 66	97.55 c-e	12.95 a-d	4.08 c-g	49.05 a-e	26.12 a-d
Hyslop-Torim 73	86.44 f-h	13.26 a-c	3.81 g	46.75 a-e	23.63 a-f
Hyslop-Jupateco 73	92.05 d-g	12.85 a-d	3.89 fg	37.13 fg	18.66 d-h
Hyslop-Huacamayo "S"	94.67 c-f	14.28 a	4.22 b-f	46.32 a-e	27.77 ab
W.R. Mace-Inia 66	95.99 c-e	11.46 c-e	4.35 b-d	50.00 a-d	25.22 a-e
W.R. Mace-7Cerros 66	97.08 c-e	13.84 ab	4.33 b-d	50.73 a-c	30.41 a
W.R. Mace-Torim 73	90.44 e-h	11.04 c-e	3.95 e-g	50.36 a-d	22.37 b-g
W.R. Mace-Jupateco 73	92.91 c-g	13.01 a-d	4.22 b-f	48.81 a-e	26.88 a-c
W.R. Mace-Huacamayo "S"	91.90 d-h	12.34 a-d	4.13 c-g	46.00 a-e	23.36 a-f
Average	96.24	12.01	4.22	45.61	22.89

*Duncan's Multiple Range Test. Means with the same letter are not significantly different at the 5 percent probability level.

F1's had a wider range for each trait than the winter x winter F1's.

Heterosis and Inbreeding Depression

Heterosis values and inbreeding depression results for plant height are summarized in Table 15. Expressed in percentage all the F1's were taller than their respective mid-parent value, resulting in a positive heterosis estimate. These values ranges from 6.48 to 31.67 percent with an average of 15.37 percent. Weique Red Mace crosses showed the higher values for plant height. The estimates obtained over the winter parent indicated that all the F1's were taller than the winter parent in each cross, with the exception of Kavkaz when crossed to Torim 73, Jupateco 73 and Inia 66. Again, higher values were found in Weique Red Mace crosses, followed by crosses with Roussalka, Yamhill, Hyslop and Kavkaz. Estimates compared to the winter parent ranged from -11.14 to 29.36 percent with an average of 9.22 percent. Inbreeding depression values were positive for most F1's for plant height, indicating a reduction in the F2 compared to F1 mean values. The exception was with Hyslop-Inia 66 where the value was negative, indicating an increase in plant height in the F2 population. The inbreeding depression values ranged from -1.08 to 14.42 percent with an average of 5.30 percent. The average value for each set of crosses with a common winter parent followed the same ranking as they did for the heterosis estimates over the mid-parent, with the exception of crosses involving Yamhill. In these crosses, a relatively high estimate (18.43 percent) did not result in an inbreeding depression (4.64 percent) of the same magnitude as with the other sets of crosses.

Heterosis and inbreeding depression values for tillers per plant

Table 15. Heterosis as a percentage of the mid-parent (MP), winter parent (WP) and inbreeding depression (ID) for plant height of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Plant Height		
	F1		F2
Cross	MP	WP	ID
Kavkaz-Inia 66	8.74	-5.08	11.60
Kavkaz-7Cerros 66	20.65	9.17	10.97
Kavkaz-Torim 73	6.48	-11.14	0.92
Kavkaz-Jupateco 73	8.50	-6.82	4.77
Kavkaz-Huacamayo "S"	18.59	7.64	8.72
Average	12.59	-1.25	7.40
Roussalka-Inia 66	11.93	10.55	2.50
Roussalka-7Cerros 66	11.25	14.52	1.43
Roussalka-Torim 73	7.92	1.17	0.88
Roussalka-Jupateco 73	11.69	8.24	2.97
Roussalka-Huacamayo "S"	12.56	16.29	6.41
Average	11.07	10.15	2.84
Yamhill-Inia 66	15.87	5.28	4.70
Yamhill-7Cerros 66	17.60	10.96	2.59
Yamhill-Torim 73	20.01	4.00	5.42
Yamhill-Jupateco 73	19.33	6.57	5.67
Yamhill-Huacamayo "S"	19.35	12.98	4.81
Average	18.43	7.96	4.64
Hyslop-Inia 66	11.90	6.12	-1.08
Hyslop-7Cerros 66	12.39	10.90	4.06
Hyslop-Torim 73	11.14	0.28	5.99
Hyslop-Jupateco 73	9.56	2.04	1.61
Hyslop-Huacamayo "S"	7.94	6.88	3.39
Average	10.59	5.24	2.79
W.R. Mace-Inia 66	25.41	24.80	7.35
W.R. Mace-7Cerros 66	21.03	25.58	6.80
W.R. Mace-Torim 73	31.67	24.35	12.21
W.R. Mace-Jupateco 73	18.59	15.81	3.35
W.R. Mace-Huacamayo "S"	24.21	29.36	14.42
Average	24.18	23.98	8.83
Overall Average	15.37	9.22	5.30

are presented in Table 16. All F1's except Kavkaz-Inia 66 and Kavkaz-Torim 73 had a higher tiller number than their respective mid-parent value resulting in a positive heterosis estimate. On the average Weique Red Mace crosses produced more tillers per plant, resulting in higher heterosis estimates over the mid-parent than any of the other winter parents. The range was from -26.61 to 49.18 percent with an average of 19.94 percent. When the F1's were compared with the winter parent some crosses resulted in negative values, indicating the superiority of the winter parents for tillers per plant. All crosses with the spring cultivar, Inia 66, gave negative values. The same was true for the crosses with Jupateco 73, except when it was crossed to Weique Red Mace. Kavkaz-Torim 73, Yamhill-Siete Cerros 66 and Yamhill-Huacamayo "S" were the other crosses with negative values when compared to the winter parent. On the average, only Weique Red Mace crosses exhibited a positive value. The overall range was -35.88 to 24.18 percent with an average of -0.44 percent

Negative values were found for inbreeding depression in four crosses indicating that the F2 had a higher mean value than the F1 for tillers per plant. In general when the heterosis values were high in the F1, so was the inbreeding depression in the corresponding F2.

Heterosis and inbreeding depression values for 100 kernel weight are summarized in Table 17. All the F1 populations were superior in kernel weight to the mid-parent value resulting in positive heterosis estimates. The values ranged from 8.79 to 56.75 percent, with an average of 19.96 percent. On the average, Weique Red Mace crosses were superior in kernel weight (24.39 percent). Most F1's were superior in kernel

Table 16. Heterosis as a percentage of the mid-parent (MP), winter parent (WP) and inbreeding depression (ID) for tillers per plant of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Tillers Per Plant		
	F1		F2
Cross	MP	WP	ID
Kavkaz-Inia 66	-18.09	-33.93	-15.70
Kavkaz-7Cerros 66	46.14	19.58	23.29
Kavkaz-Torim 73	-26.61	-35.88	-36.01
Kavkaz-Jupateco 73	23.98	-2.42	20.62
Kavkaz-Huacamayo "S"	36.19	24.18	30.40
Average	12.31	-5.69	4.52
Roussalka-Inia 66	10.96	-11.66	4.68
Roussalka-7Cerros 66	28.98	4.14	21.65
Roussalka-Torim 73	17.31	0.98	10.80
Roussalka-Jupateco 73	13.75	-11.59	6.30
Roussalka-Huacamayo "S"	19.03	6.85	11.13
Average	18.01	-2.26	10.91
Yamhill-Inia 66	8.50	-13.74	4.87
Yamhill-7Cerros 66	19.74	-3.45	12.36
Yamhill-Torim 73	16.86	0.45	10.39
Yamhill-Jupateco 73	24.18	-3.60	6.39
Yamhill-Huacamayo "S"	5.86	-5.11	0.63
Average	15.03	-5.09	6.93
Hyslop-Inia 66	12.78	-13.36	-1.57
Hyslop-7Cerros 66	38.97	8.18	18.40
Hyslop-Torim 73	31.82	9.00	17.07
Hyslop-Jupateco 73	19.06	-10.57	2.06
Hyslop-Huacamayo "S"	4.91	-9.75	-7.85
Average	21.51	-3.30	5.62
W.R. Mace-Inia 66	15.85	-4.31	0.78
W.R. Mace-7Cerros 66	46.74	23.03	6.80
W.R. Mace-Torim 73	21.61	9.11	16.17
W.R. Mace-Jupateco 73	49.18	20.13	10.28
W.R. Mace-Huacamayo "S"	30.74	22.62	16.62
Average	32.82	14.12	10.13
Overall Average	19.94	-0.44	7.62

Table 17. Heterosis as a percentage of the mid-parent (MP), winter parent (WP) and inbreeding depression (ID) for 100 kernel weight of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	100 Kernel Weight		
	F1		F2
Cross	MP	WP	ID
Kavkaz-Inia 66	15.72	2.39	5.94
Kavkaz-7Cerros 66	16.58	-0.65	-0.22
Kavkaz-Torim 73	28.24	7.61	14.55
Kavkaz-Jupateco 73	24.68	4.35	8.75
Kavkaz-Huacamayo "S"	15.81	8.26	1.00
Average	20.21	4.39	6.00
Roussalka-Inia 66	18.11	10.29	6.22
Roussalka-7Cerros 66	29.97	16.91	9.64
Roussalka-Torim 73	18.56	4.90	4.44
Roussalka-Jupateco 73	26.46	11.27	11.45
Roussalka-Huacamayo "S"	19.80	18.63	8.06
Average	22.58	12.40	7.96
Yamhill-Inia 66	8.79	-2.04	5.08
Yamhill-7Cerros 66	13.58	-1.58	1.15
Yamhill-Torim 73	12.17	-4.07	7.08
Yamhill-Jupateco 73	19.05	1.81	10.44
Yamhill-Huacamayo "S"	10.21	4.98	4.53
Average	12.76	-0.18	5.66
Hyslop-Inia 66	20.11	14.58	6.92
Hyslop-7Cerros 66	18.77	8.44	3.77
Hyslop-Torim 73	19.89	7.93	9.72
Hyslop-Jupateco 73	28.00	14.58	13.17
Hyslop-Huacamayo "S"	12.63	14.07	5.38
Average	19.88	11.92	7.79
W.R. Mace-Inia 66	11.94	0.00	3.33
W.R. Mace-7Cerros 66	17.31	0.89	4.63
W.R. Mace-Torim 73	17.02	-0.67	11.63
W.R. Mace-Jupateco 73	18.95	0.44	6.64
W.R. Mace-Huacamayo "S"	56.75	1.33	9.43
Average	24.39	0.40	7.13
Overall Average	19.96	5.79	6.91

weight when compared to the winter parent in each cross as indicated by the positive value with the exception of five crosses. Roussalka and Hyslop crosses gave greater values when compared to the winter parent (12.40 and 11.92 percent, respectively). The values for all crosses ranged from -4.07 to 18.63 percent. All F2's had lower values than F1's for kernel weight as is indicated by the positive inbreeding depression value. One exception was the Kavkaz-Siete Cerros 66 cross. Inbreeding depression values ranged from -0.22 to 14.55 percent. Yamhill and Kavkaz crosses showed lower inbreeding depression values (5.66 and 6.00 percent, respectively).

On the average, kernels per spike was the yield component that gave the highest heterosis estimates, while at the same time exhibiting the most inbreeding depression (Table 18). Heterosis estimates over the mid-parent were positive in 20 crosses. The values ranged from -26.56 to 73.13 percent with an average of 27.20 percent. Crosses with Weique Red Mace were consistently high in heterosis estimates (61.23 percent). Intermediate estimates were noted for Yamhill and Roussalka crosses (33.55 and 32.77 percent, respectively). Crosses with Kavkaz and Hyslop gave the lowest values (5.77 and 2.70 percent, respectively). When the heterosis estimates were compared to the winter parent, 17 crosses gave positive values. The values ranged from -33.99 to 92.08 percent with an average of 23.50 percent. Here, again, crosses with Weique Red Mace showed the highest values, followed by Roussalka and Yamhill crosses. Three crosses showed negative inbreeding value indicating the superiority of the F2's over F1's mean values for kernels per spike. These crosses were Kavkaz-Torim 73, Hyslop-Siete Cerros 66 and Hyslop-Jupateco 73. On

Table 18. Heterosis as a percentage of the mid-parent (MP), winter parent (WP) and inbreeding depression (ID) for kernels per spike of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Kernels Per Spike		
	F1		F2
Cross	MP	WP	ID
Kavkaz-Inia 66	-13.43	-23.20	4.95
Kavkaz-7Cerros 66	45.07	38.08	31.89
Kavkaz-Torim 73	-26.56	-33.60	-22.32
Kavkaz-Jupateco 73	-17.59	-22.17	2.26
Kavkaz-Huacamayo "S"	14.51	14.01	20.83
Average	5.77	-5.38	7.52
Roussalka-Inia 66	26.37	23.78	7.54
Roussalka-7Cerros 66	47.38	56.15	18.11
Roussalka-Torim 73	29.42	29.49	8.07
Roussalka-Jupateco 73	36.26	32.53	14.41
Roussalka-Huacamayo "S"	24.41	38.56	10.61
Average	32.77	36.10	11.75
Yamhill-Inia 66	39.46	20.00	12.84
Yamhill-7Cerros 66	42.05	30.78	22.70
Yamhill-Torim 73	44.93	27.00	16.13
Yamhill-Jupateco 73	30.68	11.77	18.96
Yamhill-Huacamayo "S"	10.63	6.36	11.16
Average	33.55	19.18	16.36
Hyslop-Inia 66	14.70	-5.58	11.57
Hyslop-7Cerros 66	- 1.25	-13.39	-0.95
Hyslop-Torim 73	11.42	-6.70	10.68
Hyslop-Jupateco 73	-19.36	-33.99	-0.27
Hyslop-Huacamayo "S"	8.01	-1.32	16.33
Average	2.70	-12.20	7.47
W.R. Mace-Inia 66	63.48	73.79	10.65
W.R. Mace-7Cerros 66	50.37	73.98	9.44
W.R. Mace-Torim 73	73.13	88.32	16.95
W.R. Mace-Jupateco 73	61.82	70.71	11.21
W.R. Mace-Huacamayo "S"	57.36	92.08	25.63
Average	61.23	79.78	14.78
Overall Average	27.20	23.50	11.58

the average, Yamhill crosses had higher inbreeding values followed by crosses involving Weique Red Mace.

The greatest heterosis and highest inbreeding depression was observed for grain yield per plant (Table 19). All the heterosis estimates compared to the mid-parent value were positive with the exception of two crosses (Kavkaz-Torim 73 and Kavkaz-Inia 66) indicating the superiority of the F1's for grain yield. High heterosis estimates were noted for the Weique Red Mace crosses (143.23 percent on the average) and specific crosses such as Roussalka-Siete Cerros 66 (134.43 percent) and Kavkaz-Siete Cerros 66 (126.03 percent). Roussalka and Yamhill crosses were of intermediate value. The values ranged from -37.51 to 183.06 percent with an average of 71.55 percent. Heterosis estimates over the winter parent were positive and high with the exception of five crosses indicating the superiority of the F1's for grain yield. Weique Red Mace crosses exhibited the highest values (106.15 percent) followed by Roussalka (47.63 percent), Yamhill (12.30 percent), Kavkaz (-2.83 percent) and Hyslop (-4.19 percent). The values ranged from -55.30 to 135.90 percent with an average of 31.81 percent. Inbreeding depression for grain yield per plant indicated that the F2 Kavkaz-Torim 73 was superior to the F1 as it exhibited a negative inbreeding depression values. The opposite was true for the remaining 24 crosses. The values ranged from -44.87 to 47.77 percent. As in the other characters measured, when heterosis estimates were high compared to the mid-parents, the inbreeding depression was also high in the subsequent generation.

The ten possible F1's between the five winter parents were examined for the expression of heterosis. Results are presented in Tables 20 to

Table 19. Heterosis as a percentage of the mid-parent (MP), winter parent (WP) and inbreeding depression (ID) for grain yield per plant of 25 winter x spring wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Grain Yield Per Plant		
	F1		F2
Cross	MP	WP	ID
Kavkaz-Inia 66	-21.45	-45.95	0.40
Kavkaz-7Cerros 66	126.03	61.43	47.77
Kavkaz-Torim 73	-37.51	-55.30	-44.87
Kavkaz-Jupateco 73	14.26	-26.54	29.69
Kavkaz-Huacamayo "S"	77.53	52.22	45.39
Average	31.77	-2.83	15.68
Roussalka-Inia 66	56.91	17.84	16.03
Roussalka-7Cerros 66	134.43	84.62	32.71
Roussalka-Torim 73	70.08	34.18	20.78
Roussalka-Jupateco 73	84.92	27.93	27.73
Roussalka-Huacamayo "S"	77.13	73.56	26.93
Average	84.69	47.63	24.84
Yamhill-Inia 66	48.10	0.07	20.48
Yamhill-7Cerros 66	77.83	24.44	29.45
Yamhill-Torim 73	73.04	21.26	29.58
Yamhill-Jupateco 73	73.40	9.86	32.23
Yamhill-Huacamayo "S"	27.04	5.88	16.14
Average	59.88	12.30	25.58
Hyslop-Inia 66	45.56	-3.69	20.01
Hyslop-7Cerros 66	46.49	0.22	19.75
Hyslop-Torim 73	61.12	10.38	34.09
Hyslop-Jupateco 73	7.32	-33.16	14.05
Hyslop-Huacamayo "S"	30.43	5.30	18.80
Average	38.18	-4.19	21.34
W.R. Mace-Inia 66	104.76	63.41	12.46
W.R. Mace-7Cerros 66	158.82	117.13	20.58
W.R. Mace-Torim 73	148.18	108.62	42.58
W.R. Mace-Jupateco 73	183.06	105.67	25.87
W.R. Mace-Huacamayo "S"	121.34	135.90	43.83
Average	143.23	106.15	29.06
Overage Average	71.55	31.81	23.30

22 for the five characters measured.

Heterosis estimates for plant height were positive for all the crosses when compared to the mid-parent (Table 20). The same was true when compared to the tallest parent in each cross with the exception of Roussalka-Kavkaz, Hyslop-Kavkaz and Weique Red Mace-Kavkaz. This indicates that the F1 was taller than the tallest parent used in the cross. The values ranged from 6.46 to 18.65 percent when compared to the mid-parent. When compared to the tallest parent, the values ranged from -13.89 to 17.75 percent. The highest heterosis estimate resulted from the cross of the two shortest winter parents (Weique Red Mace and Roussalka).

Positive heterosis estimates for tillers per plant (Table 20) were noted in seven crosses when the F1's were compared to their respective mid-parent. When compared to the highest parent, five crosses gave a positive value. The value ranged from -10.73 to 17.54 percent when compared to mid-parent. When the highest parent is compared, the range for tillering was from -21.34 to 10.66 percent. The Weique Red Mace-Yamhill cross showed the highest value (10.66 percent).

All the F1 populations were superior in kernel weight when mid-parent values are considered (Table 21). The same was true when the F1's were compared to the better parent with the exception of two crosses (Roussalka-Kavkaz and Hyslop-Yamhill). The crosses Hyslop-Roussalka and Yamhill-Roussalka, exhibited the highest heterosis estimates over the mid-parent (13.89 and 11.53 percent, respectively). The Hyslop-Roussalka cross also had the highest kernel weight when compared to the highest parent (11.52 percent). The heterosis estimates ranged from

Table 20. Heterosis as a percentage of the mid-parent (MP) and higher parent (HP) for plant height and tillers per plant of ten winter x winter wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Plant Height		Tillers Per Plant	
Cross	MP	HP	MP	HP
Roussalka-Kavkaz	8.92	-13.89	-2.76	-4.44
Yamhill-Kavkaz	8.67	3.93	-3.06	-4.08
Hyslop-Kavkaz	7.93	-1.73	10.15	3.20
W.R. Mace-Kavkaz	13.18	-0.80	4.46	1.40
Yamhill-Roussalka	14.17	4.91	4.40	4.28
Hyslop-Roussalka	6.46	2.17	-10.73	-14.93
W.R. Mace-Roussalka	18.65	17.75	1.58	-3.09
Hyslop-Yamhill	8.11	3.31	17.54	-21.34
W.R. Mace-Yamhill	10.90	1.19	16.11	10.66
W.R. Mace-Hyslop	15.07	9.62	13.31	3.27
Average	11.21	3.65	1.59	-2.51

Table 21. Heterosis as a percentage of the mid-parent (MP) and higher parent (HP) for 100 kernel weight and kernels per spike of ten winter x winter wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Cross	100 Kernel Weight		Kernels Per Spike	
	MP	HP	MP	HP
Roussalka-Kavkaz	5.53	-0.43	11.76	1.00
Yamhill-Kavkaz	7.32	0.80	30.16	25.67
Hyslop-Kavkaz	8.34	0.22	-2.39	-10.46
W.R. Mace-Kavkaz	3.08	1.96	24.10	4.72
Yamhill-Roussalka	11.53	7.24	34.51	17.82
Hyslop-Roussalka	13.89	11.52	19.54	0.05
W.R. Mace-Roussalka	6.76	1.78	40.95	30.49
Hyslop-Yamhill	5.64	-0.45	15.50	9.52
W.R. Mace-Yamhill	7.85	6.89	24.84	2.39
W.R. Mace-Hyslop	9.39	2.22	31.70	8.01
Average	7.93	3.18	23.07	8.92

3.08 to 13.89 percent over the mid-parent for this trait. When compared to the better parent, they ranged from -0.45 to 11.52 percent for kernel weight.

On the average, kernels per spike was the yield component that responded with the highest heterosis estimates (Table 21) when compared to the mid-parent and higher parent value. Nine F1 populations gave a positive estimate. The Weique Red Mace-Roussalka cross had the highest heterosis estimate. The values ranged from -2.39 to 40.95 percent over the mid-parent. When the better parent was considered, the range for kernels per spike was -10.46 to 30.49 percent.

For the five characters measured, grain yield was found to have the highest heterosis estimates (Table 22). All the estimates of heterosis were higher than the mid-parent value. When compared to the better parent, seven crosses resulted in positive value indicating the superiority of some F1 populations over the parents. The cross Weique Red Mace-Yamhill had the highest mid-parent heterosis estimate (58.94 percent). Weique Red Mace-Roussalka cross was also the highest when compared to the better parent (39.04 percent). The heterosis estimates over the mid-parent ranged from 0.63 to 58.94 percent. When compared to the better parent, the range was from -3.36 to 39.04 percent.

A comparison of the heterosis estimates of winter x spring with the winter x winter F1 populations is summarized in Tables 23 to 25. The heterosis estimates were superior in the winter x spring crosses than winter x winter crosses. The greater differences in mid-parent heterosis values were expressed by grain yield per plant, tillers per plant and kernel weight (71.55 vs 33.44, 19.94 vs 1.59 and 27.20 vs 23.07 percent,

Table 22. Heterosis as a percentage of the mid-parent (MP) and higher parent (HP) for grain yield per plant of ten winter x winter wheat crosses grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	Grain Yield Per Plant	
Cross	MP	HP
Roussalka-Kavkaz	12.36	-1.97
Yamhill-Kavkaz	34.60	30.12
Hyslop-Kavkaz	17.02	8.81
W.R. Mace-Kavkaz	32.95	8.45
Yamhill-Roussalka	54.09	30.63
Hyslop-Roussalka	20.46	-1.20
W.R. Mace-Roussalka	50.51	39.04
Hyslop-Yamhill	0.63	-3.36
W.R. Mace-Yamhill	58.94	26.31
W.R. Mace-Hyslop	52.82	17.89
Average	33.44	15.47

Table 23. Mean and range heterosis values for plant height and tillers per plant for the winter x spring and winter x winter Fl's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter X Spring Fl Wheat Crosses	Plant Height		Tillers Per Plant	
	MP[1/]	WP[2/]	MP	WP
Mean	15.37	9.22	19.94	-0.44
Range	6.48 - 31.67	-11.14 - 29.36	-26.61 - 36.18	-35.88 - 24.18
Winter X Winter Fl Wheat Crosses	**MP**	**HP[3/]**	**MP**	**HP**
Mean	11.21	3.65	1.59	-2.51
Range	6.46 - 18.65	-13.89 - 17.75	-10.73 - 17.54	-21.34 - 10.66

1/ Heterosis as percent of the mid-parent value.

2/ Heterosis as percent of the winter parent value.

3/ Heterosis as percent of the higher parent value.

Table 24. Mean and range heterosis values for 100 kernel weight and number of kernels per spike for the winter x spring and winter x winter F1's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

	100 Kernel Weight		Number of Kernels Per Spike	
Winter X Spring F1 Wheat Crosses	MP[1/]	WP[2/]	MP	WP
Mean	19.96	5.79	27.20	23.50
Range	8.79 - 56.75	-2.04 - 18.63	-26.56 - 73.13	-33.60 - 92.08
Winter X Winter F1 Wheat Crosses	MP	HP[3/]	MP	HP
Mean	7.93	3.18	23.07	8.92
Range	3.08 - 13.89	-0.45 - 11.52	-2.39 - 40.95	-10.46 - 30.49

1/ Heterosis as percent of the mid-parent value.

2/ Heterosis as percent of the winter parent value.

3/ Heterosis as percent of the higher parent value.

Table 25. Mean and range heterosis values for grain yield per plant for the winter x spring and winter x winter F1's grown at Hyslop Agronomy Farm, Corvallis, Oregon, 1977-78.

Winter X Spring F1 Wheat Crosses	Grain Yield Per Plant	
	MP1/	WP2/
Mean	71.55	31.81
Range	-21.45 - 183.06	-55.30 - 135.90
Winter X Winter F1 Wheat Crosses	MP	HP3/
Mean	33.44	15.47
Range	0.63 - 58.94	-3.36 - 30.63

1/ Heterosis as percent of the mid-parent value.

2/ Heterosis as percent of the winter parent value.

3/ Heterosis as percent of the higher parent value.

respectively). The same was true when the heterosis estimates were obtained taking into consideration the winter parent in the winter x spring crosses and the better parent in the winter x winter crosses (grain yield: 31.81 vs 15.47, kernels per spike: 23.50 vs 8.92, and plant height: 9.22 vs 3.65). A wider range was also observed for each trait in the winter x spring crosses.

Parent-Progeny Standard Regression

Parent-progeny regression estimates expressed in percent for the five traits measured for winter x spring crosses are presented in Table 26. Plant height had the highest values. Tillers per plant, kernel weight, kernels per spike and grain yield were found to have intermediate to high value. There was considerable variation within the estimates for each trait depending on cross. However, plant height and kernel weight were more consistent than the other traits when the estimates were obtained from F1 on mid-parent value. In general, the estimates were in agreement when obtained from F1 on mid-parent or F2 on F1 values. The exception was tillers per plant and grain yield, where the regression estimates of F1 on mid-parent value were lower than the F2 on F1.

Regression estimates expressed in percent for winter x winter F1 populations in relation to mid-parent values are presented in Table 27. Highest estimate was observed for plant height. Fairly high estimates were also noted for kernel weight, kernels per spike and grain yield. An unrealistic negative value was recorded for tillers per plant.

Table 26. Parent-progeny standard regression for winter x spring wheat crosses using F1 on mid-parent and F2 on F1 mean values for the five agronomic characters studied, 1977-78.

Winter Parent Crossed to the Same Group of Spring Wheats	Plant Height		Tillers Per Plant		100 Kernel Weight		Kernels Per Spike		Yield Per Plant	
	F1 on MP	F2 on F1	F1 on MP	F2 on F1	F1 on MP	F2 on F1	F1 on MP	F2 on F1	F1 on MP	F2 on F1
Kavkaz x Spring Wheats	97.29	87.44	22.95	48.03	34.99	13.64	78.56	87.47	59.63	88.06
Roussalka x Spring Wheats	98.12	87.61	78.73	99.03	62.10	80.43	69.09	86.70	61.88	93.62
Yamhill x Spring Wheats	92.61	96.80	33.17	58.77	67.66	65.90	-23.61	75.49	-12.74	42.13
Hyslop x Spring Wheats	90.79	85.13	18.65	-13.91	48.50	45.78	52.41	84.45	62.55	82.47
W.R. Mace x Spring Wheats	54.88	5.31	22.49	75.12	59.23	40.50	61.30	-53.22	63.10	- 2.47
Average	86.74	72.46	35.20	53.41	54.50	49.25	47.55	56.18	46.88	60.76

Table 27. Parent-progeny standard regression for winter x winter wheat crosses using F1 on mid-parent values for the five agronomic characters studied, 1977-78.

	Plant Height	Tillers Per Plant	100 Kernel Weight	Kernels Per Spike	Yield Per Plant
F1 on MP	87.85	-13.25	69.26	59.42	51.29

Comparison of Three Populations over Two Years

An analysis of variance for the five characters was computed using the data from both years. The observed mean squares and coefficients of variation values of the winter parents, spring parents and winter x spring F1's are presented in Table 28. There were highly significant differences for the five characters among years. The same was true among the 35 genotypes, between and within the groups (winter and spring parents and winter x spring F1's) and among each group. A significant years x genotypes interaction was also found (P = 0.01) for the five characters measured. The same was true for years x between groups with the exception of grain yield. Years x within groups was highly significant for kernel weight, kernels per spike and grain yield. Plant heigh and tillers per plant were significant, but at a lower probability level (P = 0.05).

Years x within winter parents was significant (P = 0.01) for kernel weight and at a lower probability (P = 0.05) for tillers per plant. The interaction of years and within winter x spring F1's was highly significant for grain yield, kernels per spike and kernel weight. Plant height and tillers per plant were significant at a lower probability level (P=.05).

The coefficient of variation values were low for plant height and kernel weight (3.70 and 5.60 percent, respectively). Relatively high coefficient of variation values were found for kernels per spike, tillers per plant and grain yield (11.34, 16.06 and 23.05 percent, respectively).

Table 28. Observed mean square values for five agronomic characteristics of winter parents, spring parents and the winter x spring F1's grown for two years at Hyslop Agronomy Farm, Corvallis, Oregon, 1976-77 and 1977-78.

Source of Variation	df	Plant Height	Tillers Per Plant	100 Kernel Weight	Kernels Per Spike	Yield Per Plant
Replications within years	6	40.04**	3.83	0.14**	89.56*	123.91*
Years	1	1,886.72**	1,465.28**	37.93**	2,421.97**	27,554.20**
Genotypes	34	864.34**	25.43**	1.83**	603.11**	708.81**
Between Groups	2	5,343.14**	114.33**	18.37**	1,501.59**	4,715.43**
Within Groups	32	584.42**	19.88**	0.80**	546.95**	458.39**
W/Winter Parents	4	865.53**	25.64**	0.56**	517.40**	456.72**
W/Spring Parents	4	439.46**	19.75**	1.26**	281.33**	480.22**
W/Winter X Spring F1	24	561.73**	18.94**	0.76**	596.15**	455.03**
Years x Genotypes	34	34.99**	11.69**	0.25**	108.73**	130.33**
Years x Between Groups	2	236.86**	59.92**	0.95**	348.24**	164.95
Years x Within Groups	32	22.37*	8.67*	0.21**	93.76**	128.17**
Years x W/Winter Parents	4	12.99	13.63*	0.32**	54.54	99.98
Years x W/Spring Parents	4	18.14	1.21	0.10	33.15	91.97
Years x W/Winter X Spring F1	24	24.64*	9.09*	0.21**	110.40**	138.90**
Error	204	12.50	5.28	0.06	31.97	60.37
Total	279					
C.V. %		3.70	16.06	5.60	11.34	23.05

* Significant at the 5 percent probability level.
**Significant at the 1 percent probability level.

DISCUSSION

The major factor influencing the development of superior crop cultivars is the availability of usable genetic diversity, In wheat, serious questions are being raised regarding the possible exhaustion of such variability. This concern is reflected in the yield plateau which seems to have been reached with the release of high yielding spring cultivars like Anza, Siete Cerros 66 and Era and with winter types represented by Gaines, Hyslop and Centurk. The question of the diminishing genetic diversity is further complicated in the breeding self-pollinating species, since the breeder can use only that portion of the total genetic variance which is identified as additive. To minimize these problems, two approaches are being evaluated. The first is to create additional genetic variation through the systematic crossing of winter x spring wheat cultivars. A second is to capitalize on the total genetic variation by developing hybrid wheat in addition to the near pure line cultivars currently being used.

Historically, winter and spring wheat cultivars have evolved in different evolutionary patterns forming to some degree different gene pools. This is due in part to the activities of the plant breeder in emphasizing crosses within either winter or spring types and to the vernalization and winterhardiness requirements of the winter type.

With the discovery of a fertility restoring gene in wheat in the early 1960's, the possibility of developing hybrid wheat became possible. Thus, if winter x spring crosses result in more genetic variability and the breeder of self-pollinated crops could use the total genetic variance including the non-additive portion, possible yield plateaus could be avoided at this point in time.

Five winter and five spring wheat cultivars were used in this study. In addition to growth habit, the ten cultivars were selected because they differ genetically for plant height, grain yield and their components of yield. The conclusions drawn from the results of this study are based on a fixed population of wheat cultivars. These conclusions concern: 1) information on the nature of the gene action influencing height, yield components and yield in winter x spring F1's; 2) comparison of the nature of gene action between winter x spring and winter x winter F1's for plant height, yield and yield components; and 3) the influence of different years on the expression of heterosis in the winter x spring F1 wheat crosses.

The discussion will be presented as Study I and Study II. During the first year (Study I) the nature of the gene action for the traits measured including the winter and spring parents and winter x spring F1's were evaluated. A comparison of the gene action and genetic diversity associated with the winter x spring and winter x winter crosses was obtained during the second year (Study II).

Study I, 1976-77

The results of this study indicated that the yield of the spring parents on a per plant basis was not affected adversely when compared to the winter parents even though they were fall planted. The highest and lowest yielding spring parents yielded as much as the best and the poorest yielding winter parents. A great deal of diversity for grain yield per plant, plant height and number of kernels per spike and a lesser amount for tillers per plant and 100 kernel weight was found among and between the two types of cultivars.

It is generally thought that within limites the greater the genetic diversity between parents, the greater the expression of heterosis. If diverse gene pools have evolved in winter and spring wheats, crosses between them would be expected to result in considerable heterosis. Also, heterosis is generally regarded as a measure of the non-additive portion of gene action and, as such, is a function of dominance and epistatic effects. It was observed that the expression of heterosis depended on the trait and the parents involved in the specific cross. The greatest expression of heterosis was noted for grain yield. Other characters studied, presented in descending order for the expression of heterosis, were 100 kernel weight, plant height, kernels per spike and tillers per plant. Crosses with Weique Red Mace as the winter parent resulted in the highest heterosis estimates for grain yield. The late maturity of these hybrids is responsible for the high heterosis estimates. The same can be stated for the heterosis estimates involving Yamhill crosses. The pedigrees of these two cultivars differ to a large extent in their genetic background when compared to the spring wheat parents.

The heterosis estimate obtained from Roussalka crosses can be explained by the duration of the grain filling period; these hybrids had early flowering and late maturity.

The reason for the lower heterosis values for grain yield associated with Hyslop crosses might be due to the Norin 10-Brevor source of dwarfism, which both Hyslop and the spring wheats have in common. Low heterosis values were also noted for Kavkaz crosses. Examination of the pedigree of Kavkaz reveals the presence of several spring wheats, therefore, some genes may be shared by Kavkaz and the spring wheat parents used in this study.

Plant height is not considered a yield component, but may play an important role in wheat breeding programs for high rainfall or irrigated areas. The heterosis values for this character exceeded the mid- and winter parent values with the exception of one cross. In a hybrid wheat program, the resulting taller F1's could be a serious detriment that must be taken into consideration in selecting potential parents. The taller hybrids may be more susceptible to lodging, when yields are maximized by the use of irrigation and heavy fertilizer application. Roussalka and Hyslop crosses gave a lower expression of heterosis for plant height indicating the importance of using dwarf or semidwarf parents in order to obtain the desired plant height.

A further estimate of the nature of the gene action influencing the traits measured was obtained by using parent-progeny regression. These estimates are a measure of that portion of the total genetic variance which behaves in an additive manner. Parent-progeny regression estimates can assist in determining the degree of selection pressure that should be applied to a given population and in determining how effective selection would be in the early generations.

Parent-progeny regression estimates were high for plant height, kernel weight and grain yield and intermediate for kernels per spike and tillers per plant. Therefore, in addition to the non-additive genetic variation associated with the traits evaluated, there was also a considerable amount of additive gene action. Thus, with the high parent-progeny regression estimates, effective progress could be made through selection following a conventional program involving selfing. Estimates for plant height and kernel weight were high and consistent between crosses; thus, selection can be effective as early as the F2 in a conventional program. However, since both characters were influenced to a large degree by non-additive gene action, it may be necessary to wait until the F3 or F4 generation for effective selection in a conventional program. For kernels per spike and tillers per plant, the regression estimates indicated that selection for both characters should be delayed until later generations. Selection for grain yield per plant also should be delayed until later generations due to the high values for heterosis. Such a delay would permit a loss of the non-additive genetic variance through inbreeding so the additive genetic variance could be better evaluated. Also, sufficient seed could be obtained to conduct replicated yield trials so the environmental influence could be estimated.

Study II, 1977-78

A reduction in grain yield per plant in the second growing season was noted for both parents and winter x spring F1's. This can be attributed, in part, to the high amount of precipitation. The spring cultivars appeared to be more adversely influenced than the winter types. The highest yielding spring parent was superior only to the lowest yielding winter type. The results confirm the genetic diversity noted in Study I for the winter and spring parents and winter x spring F1's. This was true even though the environment was not as favorable for grain yield production during the second year.

On the average, the winter x winter F1 means were slightly superior for each of the characters measured when compared to the F1 winter x spring means. When the range of variability between crosses is considered, however, the F1 winter x spring range was greater for each trait. The winter x spring crosses would be expected to produce more genetic variability than winter x winter crosses. The extent to which such increased variability might be usable for increased grain yield will have to be verified in subsequent generations, if the needs of a conventional program are considered. There was a notable decrease when the mean values of winter x spring F2's were compared to their F1's for the five characters. It was especially true for grain yield and kernels per spike. This decrease was expected and reconfirms the large estimates of heterosis noted in the F1 for these traits. With selfing and the accompanying loss of the non-additive portion, an inbreeding depression would be expected.

The data showed that the crosses involving the winter parents whose genetic backgrounds differed the most from the springs expressed the highest heterosis. The greatest response was found for grain yield per plant followed by kernels per spike, 100 kernel weight and tillers per plant. Crosses with Weique Red Mace as the winter parent plus the specific crosses of Kavkaz-Siete Cerros 66 and Roussalka-Siete Cerros 66 produced the highest heterosis values for grain yield.

In general, the heterosis values were high for plant height, however, low values were obtained with Roussalka and Hyslop crosses, confirming the use of semidwarf or dwarf parents in crosses, if breeders are interested in hybrid wheat production.

When winter x spring crosses were compared to winter x winter crosses, the former had higher heterosis values and wider ranges between crosses. The greatest differences between the types of F1 crosses for heterosis values were found for grain yield, tillers per plant and 100 kernel weight. These data support the conclusion that the amount of heterosis is a function of diversity of the germ plasm used to make crosses. Breeders working on hybrid wheat may wish to look at winter x spring crosses as a means of maximizing heterosis.

Parent-progeny regression estimates indicated that additive gene action was more important for plant height than for grain yield and yield components. The high parent-progeny estimates (additive genetic variance), coupled with the high estimates of heterosis and subsequent inbreeding depression (non-additive genetic variance) in the winter x spring crosses suggest that the systematic crossing of winter x spring cultivars is an effective means of increasing the total genetic variation available to wheat breeders.

Regression values from winter x winter crosses were in general agreement with the winter x spring crosses, except for tillers per plant. A large amount of additive gene action was present for plant height and less for yield components and grain yield per plant.

When the two years are considered, the genotypes responded somewhat differently to the growing seasons. The mean grain yield for the crosses was higher in Study I (1976-77) than in Study II (1977-78), but the expression of heterosis was less. This is in contrast to the general idea that hybrid populations do better under high yielding conditions. No change in the order for the parents was noted between years when the mean values for grain yield were compared. In the ranking of the winter x spring F1 populations many changes were noted when the two years were compared for grain yield. The same happened with kernels per spike, 100 kernel weight and, to a lesser extent, with tillers per plant and plant height. In a breeding program these interactions will present a serious problem if a breeder selects hybrids based on a single year's data. If yield stability is to be obtained, it will be necessary for breeders to determine the genotype-environment interaction for each of the crosses. In general, Weique Red Mace crosses were consistent in both seasons with higher heterosis values for grain yield.

The results of the investigation support the general conclusion that greater diversity between parents results in a larger expression of heterosis. When two gene pools representing winter and spring cultivars are combined through hybridization, substantial heterosis can be expected. It was also observed that a large part of the total genetic variation for the five traits was due to genes which are additive in action both for the winter x winter and the winter x spring crosses. If other factors such as adequate levels of winterhardiness can be achieved, winter x spring crosses will provide additional genetic variability for the wheat breeder. This is true for the development of hybrid wheat and may also be promising for conventional breeding programs.

SUMMARY AND CONCLUSIONS

The objective of this investigation was: 1) to determine the nature of gene action influencing plant yield, yield components and yield in winter x spring and winter x winter F1's; 2) to investigate the influence of different years on the expression of heterosis in the winter x spring F1 crosses; and 3) to compare the extent of heterosis in winter x spring with winter x winter F1's.

Five winter and five spring wheat cultivars were crossed to obtain the F1's and subsequent F2's. The parents plus the winter x spring F1's were planted for two growing seasons at Hyslop Agronomy Farm near Corvallis, Oregon. In the second season the winter x spring F2's and winter x winter F1's were included.

Data were collected on an individual plant basis for plant height, number of tillers per plant, 100 kernel weight, number of kernels per spike and grain yield per plant. An analysis of variance was done on all characters studied to detect possible significant differences among the genotypes and different generations. The group effects (parents, winter x winter F1's, winter x spring F1's and F2's) in the analysis of variance were further divided into component effects to detect differences between and within the groups. Mean values for each group were compared using Duncan's multiple range test.

The predominant type of gene action controlling each character studied was evaluated using heterosis and inbreeding depression estimates as formulated by Matzinger _et al_ (1962) and parent-progeny standard regression estimates using F1 on the mid-parent value and F2 on F1 mean values. Also, in the winter x winter crosses, the hybrid performance was compared to the better parent. The possible influence of years in the expression of the winter x spring F1 crosses was determined. The following conclusions were drawn:

1. More heterosis was found in the winter x spring F1's than in winter x winter F1's.
2. The importance of genetic diversity between the parents for the maximum expression of heterosis was apparent. This was true for both winter x spring and winter x winter crosses.
3. Grain yield per plant had the highest heterosis response. Number of kernels per spike and 100 kernel weight were the highest for the yield components.
4. Those characters which reflected the greatest amount of heterosis likewise showed the most inbreeding depression in the F2 generation. This confirms the importance of non-additive genetic variance in the expression of the heterosis.
5. With the large amount of additive genetic variance present in plant height, selection in early generation would be useful in obtaining the desired plant height in a conventional program. In a hybrid program, special attention will be necessary in selecting dwarf or semidwarf parents because the taller hybrids may be susceptible to lodging.
6. Non-additive gene action is more subject to environmental effects as was noted by the significant interaction of years by winter x spring F1 crosses.
7. In a hybrid wheat program, the use of winter x spring crosses will require more than one year of evaluation due to the high year x

genotype interaction.

8. Winter x spring wheat crosses do present to plant breeders additional genetic diversity for exploitation in hybrid or conventional programs.

LITERATURE CITED

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

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

Bhatt, G. M. 1972. Inheritance of heading date, plant height and kernel weight in two spring wheat crosses. Crop Sci. 12:95-97.

Bhatt, G. M. 1973. Diallel analysis and cross prediction in common bread wheats. Aust. J. Agr. Res. 24:169-178.

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

Briggle, L. W. 1963. Heterosis in wheat - A review. Crop Sci. 3: 407-412.

Briggs, F. N. and P. F. Knowles. 1967. Introduction to Plant Breeding. Reinhold Pub. Corp., New York, N.Y.

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

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

Fedin, M. A. 1976. Heterosis in wheat and its hereditary factors. Proc. Seventh Cong. of Eucarpia, p. 291-302.

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

Fonseca, S. and F. L. Patterson. 1968b. Yield component heritability and interrelationships in winter wheat (*Triticum aestivum* L.). Crop Sci. 8:614-617.

Frey, K. L. and T. Horner. 1957. Heritability in standard units. Agronomy Journal 49:59-62.

Gotoh, T. 1979. Genetic studies on growth habit of some important spring wheat cultivars in Japan, with special reference to the identification of the spring genes involved. Japan J. Breed. 29: 133-145.

Grant, M. M. and H. McKenzie. 1970. Heterosis in F1 hybrids between spring x winter wheats. Can. J. Plant. Sci. 50:137-140.

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.

Johnson, V. A., K. J. Biever, A. Haunold and J. W. Schmidt. 1966. Inheritance of plant height, yield of grain and other plant and seed characteristics in a cross of hard red winter wheat, Triticum aestivum L. Crop Sci. 6:336-338.

Ketata, H., L. H. Edwards and E. L. Smith. 1976. Inheritance of eight agronomic characters in a winter wheat cross. Crop Sci. 16:19-22.

Knott, D. R. 1965. Heterosis in seven wheat hybrids. Can. J. Plant Sci. 5:499-501.

Knott, D. R. and J. Kumar. 1975. Comparison of early generation yield testing and a single seed descent procedure in wheat breeding. Crop Sci. 15:295-299.

Kronstad, W. E. and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat (Triticum aestivum Vill., Host). Crop Sci. 4:616-619.

Liver, R. W. and E. G. Heyne. 1968. Hybrid vigor in hard red winter wheat. Proc. Third Int. Wheat Genet. Symp. p. 431-436.

Lush, J. L. 1945. Animal breeding plans. Ames. Iowa State College Press, Ed. 3.

Matzinger, D. F., T. J. Mann and C. C. Cockerham. 1962. Diallel crosses in Nicotiana tabacum. Crop Sci. 2:383-386.

Mani, S. C. and M. V. Rao. 1975. Heterosis in winter x spring crosses. Ind. J. Genetics 35:330-335.

Mihaljev, I. 1976. Expression of heterosis and combining ability in a diallel wheat cross. Proc. Seventh Cong. of Eucarpia, p. 327-329.

Pinthus, M. J. 1967. Evaluation of winter wheats as source of high yield potential for the breeding of spring wheat. Euphytica 16: 231-251.

Pinthus, M. J. 1973. Winter x spring wheat hybrids: Prospects and preliminary results. Proc. Fourth Int. Wheat Genet. Symp. p. 577-580.

Pugsley, A. T. 1970. A genetic analysis of the spring-wheat habit of growth in wheat. Aust. J. Agric. Res. 22:21-31.

Pugsley, A. T. 1972. Additional genes inhibiting winter habit in wheat. Euphytica 21:547-552.

Rupert, J. A. 1971. Breeding objectives for the 1970's in international programmes. Proc. Inter-regional wheat worker's conference. Oklahoma State University, Stillwater, Oklahoma. Feb. 9-10, 1971.

Sidwell, R. J., E. L. Smith and R. W. McNew. 1976. Inheritance and interrelationships of grain yield and selected yield-related traits in a hard red winter wheat cross. Crop Sci. 16:650-654.

Singh, K. B. and J. K. Singh. 1971. Potentialities of heterosis breeding in wheat. Euphytica 20:586-590.

Snedecor, G. W. and W. C. Cochran. 1967. Statistical methods. Iowa State University Press. Ames, Iowa.

Sun, P. L. F., H. L. Shands and R. A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. Crop Sci. 12:1-5.

Stansfield, W. D. 1969. Schaum's outline series, theory and problems of genetics. McGraw-Hill Book Co., New York.

Walton, P. D. 1971. Heterosis in spring wheat. Crop Sci. 11:422-424.

Warner, J. N. 1952. A method for estimating heritability. Agronomy Journal 44:427-430.

Wells, D. G. and C. L. Lay. 1970. Hybrid vigor in hard red spring wheat crosses. Crop Sci. 10:220-223.

APPENDIX

Appendix Table 1. Pedigree and description of cultivars.

KAVKAZ

Lutescens 314-h-147/Bezostaja 1. A hard red common winter wheat cultivar released by Russia in 1971. Large spikes, cylindrical, white and awnless. Early, tall with high yield potential, poor tillering, large seed with good milling and baking qualities.

ROUSSALKA

Was-Nibay/Sterling B x C54. A hard red common winter wheat variety from Bulgaria, resulted from a cross of Italian and Indian germ plasm. Semidwarf, awned, mid-dense spike, high yielding, early, low tillering potential and medium kernel weight. Resistant to leaf rust (*Puccinia recondita*) and moderately susceptible to stripe rust (*Puccinia striiformis*).

YAMHILL

Heines VII/Redmon (Alba). A soft white common winter wheat cultivar released by Oregon State University in 1969. Late maturity, medium height, high yielding and awnless. Good milling and baking qualities, resistant to stripe rust and powdery mildew (*Erysiphe graminis f. sp. tritici*). Large fertile spikes and medium to large kernels.

HYSLOP

Nord Desprez/Pullman Selection 101^2. A soft white common winter wheat cultivar released by Oregon State University in 1970. Semidwarf, awned, mid-dense spike and high yielding. Resistant to stripe rust and common bunt (*Tilletia caries* and *T. foetida*), moderately resistant to powdery mildew, leaf rust and septoria (*Septoria tritici*). Medium early, large head size, medium kernel weight and good milling and baking quality.

WEIQUE RED MACE

Wheat variety/Rye IB/IR substitution x Hybrid 46. A fixed line resulting from a cross made in the USA of German and British germ plasm. A hard red winter wheat with cylindrical spike, white and awnless. Late maturity, semidwarf with profuse tillering, resistant to shattering and lodging.

INIA 66

Lerma Rojo S-64 x Sonora F-64. A hard red common spring wheat cultivar released by Mexico in 1966. Early maturity, semidwarf, with white awned fusiform spikes and resistant to shattering. Medium size kernel. Resistant to stem rust (*Puccinia graminis f. sp. tritici*) and susceptible to leaf rust. High yield potential and wide adaptation with excellent milling and baking qualities.

SIETE CERROS 66

(Frontana x Kenya 58-Newthatch/Norin 10-Baart)Gabo 55. A hard white common spring wheat cultivar released by Mexico in 1966. Mid-season maturity, semidwarf, with brown awns, oblong to clavate spike and resistant to shattering. Small to medium size kernel. Widely adapted and excellent yield potential, resistant to leaf, stem and stripe rust but is currently susceptible to all three rusts in Mexico. Poor bread-making quality.

TORIM 73

Bluebird x Inia 66. A hard white common spring wheat cultivar released by Mexico in 1973. Midseason maturity, dwarf with white

Appendix Table 1. - continued

awned fusiform spike, resistant to shattering. Small to medium size kernel. High yield potenital and resistant to stem rust and moderately resistant to leaf rust. Good baking qualities.

JUPATECO 73

12300 x Lerma Rojo S-64-8156/Norteno M-67. A hard red common spring wheat cultivar released by Mexico in 1973. Midseason maturity, semi-dwarf, with white, awned, fusiform spike, resistant to shattering. Small to medium size kernel. High yield potential with resistance to stem and leaf rust. Good baking qualities.

HUACAMAYO "S"

Yecora 70 x Sonora 64-NY5207.85/Ciano 67 "S"-7Cerros 66 X Gaboto. A hard red common spring wheat, fixed line from Mexico. Midseason maturity, semidwarf with good straw strength. White, awned fusiform spike, resistant to shattering. Resistant to stripe, stem and leaf rust. High yield potential and profuse tillering.

Appendix Table 2. Summary of climatic data on a per month basis in Corvallis, Oregon for the 1976-77 and 1977-78 growing seasons.

Year	Month	Precipitation (mm)	Temperature Max.	Temperature Min.	Mean (°C)
1976-77	October	31.8	19.1	5.1	12.1
	November	36.1	13.1	3.4	8.3
	December	37.3	6.4	-0.4	3.1
	January	24.4	7.1	-2.3	2.4
	February	75.4	12.5	1.4	7.0
	March	129.3	11.4	1.4	6.4
	April	25.9	17.1	3.1	10.2
	May	87.1	16.5	5.3	10.9
	June	28.7	23.6	8.7	16.2
	July	3.1	26.0	9.5	17.8
	Total	479.1	--	--	--
1977-78	October	65.5	17.8	6.6	12.2
	November	206.0	10.7	3.2	6.9
	December	280.2	9.4	3.8	6.6
	January	186.4	8.1	2.9	5.5
	February	108.7	10.9	4.4	7.7
	March	54.6	15.1	4.7	9.9
	April	25.5	14.3	5.7	10.0
	May	91.7	17.6	7.1	12.3
	June	23.9	23.9	10.6	17.3
	July	7.4	27.1	11.5	19.3
	Total	1,149.9	--	--	--