AN ABSTRACT OF THE THESIS OF

Ira Steven Stein for the degree of Master of Science

in Crop Science presented on January 4, 1984

Title: Potential Reciprocal Differences for Selected Traits in Six Different F_1 Wheat Populations

Abstract approved: Redacted for Privacy

Dr. Warren E. Kronstad

Concerns about the possible reciprocal differences resulting from systematic crossings of winter and spring wheat gene pools prompted this investigation. If traits can be improved by simply reversing the direction of a cross, then identification of the best female parent in a cross would be helpful for breeding programs.

Two reciprocal winter by spring wheat crosses and one reciprocal winter by winter wheat cross were studied under greenhouse conditions. These three populations, coupled with two additional winter x spring crosses were also evaluated in the field. Data were collected on an individual plant basis for heading and physiological maturity date, plant height, tiller number, kernels per spike, 100 kernel weight and grain yield in the greenhouse. Information on anthesis date was also obtained for the material grown in the field.

Overall responses for the traits measured from winter by spring crosses gave little evidence to suggest the widespread occurrence of reciprocal F_1 differences; however, Yamhill/Anza and Yamhill/Siete Cerros produced a relatively high number of reciprocal differences for several traits compared to the other crosses.

Direction of the reciprocal cross was important in obtaining maximum F_1 expression for specific traits. In the Yamhill x Anza F_1,

maximum expression of tiller number and grain yield per plant was obtained while in the Siete Cerros x Yamhill F_1 later heading and anthesis dates and greater 100 kernel weight were observed. No relationship was found in the studies relating the magnitude of parental difference to the occurrence of reciprocal F_1 differences.

Response among the F_1 population for unidirectional heterobeltiosis was insufficient to identify a pattern of occurrence. Heterobeltiosis did occur for only one of the reciprocal F_1s for anthesis date, tiller number, kernels per spike, 100 kernel weight, and yield in five out of the six crosses grown in the field.

Although there were no consistant patterns for reciprocal F_1 differences for the populations evaluated, observations made suggest there are some relationships between the occurrence of reciprocal F_1 differences and the use of specific cultivars in a cross.

Potential Reciprocal Differences for Selected Traits in Six Different F_1 Wheat Populations

by

Ira Steven Stein

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed January 4, 1984

Commencement June 1984

APPROVED:

Redacted for Privacy

Professor of Plant Breeding and Genetics, in charge of major

Redacted for Privacy

Head of Crop Science Department

Redacted for Privacy

Dean of the Graduate School

Date thesis is presented January 4, 1984

Typed by Kathleen Miller for Ira Steven Stein

DEDICATED TO:

my son and daughter,

Andy Hoy and Jessica Rose;

and my family,

Teri and Bob Golden

Lorna and Les Klebe

Hennie Stein

IN MEMORY OF:

Beverly Jean Andrews, my wife

Herman Lewis Stein, my father

ACKNOWLEDGEMENTS

It is with all sincerity and highest admiration that I wish to thank my major professor, Dr. W. E. Kronstad. His encouragement, guidance and understanding has been invaluable and I am deeply indebted to him.

I further want to thank the other members of my committee, Drs. D. C. England, W. L. McCuistion and R. G. Petersen for serving on my graduate committee and reviewing my thesis. A special thanks to Dr. K. E. Rowe for his most valuable suggestions in the analysis of this study.

I have been most fortunate to work with the staff and members of the cereal project. Their interest and input in my study has been beyond measure. The computer instruction from Nan Scott, statistical consulting of Steve Broich, technical field advice from Mary Verhoeven, Ann Corey, Pat Hensleigh and Tom Fairweather, most valuable advice from Dr. R. J. Metzger and his staff, Dale Bargsten and Tom Garbacik, and thesis typing and preparation by Kathie Miller and Kathy McCarthy has made this study possible. I will remember your kindness and I thank you.

My sincere gratitude is extended to my fellow graduate students for their comradeship. A special thanks to those who gave their time and valuable input: Byung Han Choi, Miguel and Elisa Camacho, Cindy Goldstein, Mou Bei-quan, Ricardo Pedretti, Juan Salmeron, Ariel and Maria Lujan Lorenzo, and Zou Yuchun.

Appreciation is extended to Oregon State University for providing financial support and facilities which made research possible.

My heartfelt thanks to all who have given me and my family their warmth and moral support, without which I could not have finished my studies here, including Drs. Lillian and Wendell VanLoan, Dr. Vint and Edith Plath, Dr. William and Ann Mills, John and Phyllis Hagen, Jan and Doug Hare, Marcella and Bernie Brady, David and Marie Carter.

My very special thanks to Adriana Tomas for her help in editing and for arranging to allow me enough time to complete this thesis.

I owe so much, you have all been so gracious.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF APPENDIX TABLES

RECIPROCAL DIFFERENCES FOR SELECTED TRAITS IN SIX DIVERSE F_1 WHEAT POPULATIONS

INTRODUCTION

In most instances conventional wheat breeding programs do not consider direction as to which way crosses are to be made. No reciprocal differences in nuclear constitution is generally assumed when making crosses between wheat cultivars. If reciprocal crosses are made, resulting F_1 seed is bulked in order to increase an already limited population size. However, the cytoplasm inherited from a cross is essentially that of the female parent and since the cytoplasm contains autonomous DNA, it may interact with the nucleus to alter the expression of a particular trait.

In the past breeders have been reluctant to make crosses between winter and spring wheat types. Further, the two gene pools have evolved separately over time due to their ecological requirements. It is possible that distinct cytoplasms have also evolved. Concerns have arisen in breeding programs where there are large scale systematic crossing of winter and spring cultivars regarding the possible reciprocal differences which may occur from different nuclear-cytoplasmic combinations.

Hybrid wheat is again receiving greater attention due to cytoplasmic sterility, genetic restoring genes and, more recently, chemical gametocides. Thus, where the F_1 population is the end product of the breeding program or even in conventional selfing programs, possible reciprocal differences could be a significant factor in determining which way a cross is made for improvement of anyone of a number of traits.

This investigation was undertaken to identify if reciprocal differences do exist when winter and spring cultivars are crossed. Specifically, the objectives of this study were: 1) to identify possible reciprocal differences as a result of the use of specific cultivars in crosses: 2) to identify reciprocal effects based on the magnitude by which the two parents differ: 3) to determine if unidirectional heterobeltiosis occurs between the F_1s of a reciprocal cross.

LITERATURE REVIEW

Reciprocal crosses are ambidirectional crosses made between two plants. On these two plants, plant A and plant B, A is used as the female and B is used as the pollen source for the first cross. In a reciprocal manner, B is the female and A is the pollen source. The progeny (F1's) from reciprocal crosses between two homozygous parents, would have identical heterozygous nuclei, but the cytoplasms would be from the maternal parent.

Differences from reciprocal crosses have long been noted in higher plants (Sager, 1972). Shortly after the theories of Mendel had been rediscovered, a German scientist, Carl Correns, recognized the possibility that two genetics systems might exist, one Mendelian, the other non-Mendelian, presumably in the cytoplasm. He wrote "A consequence of this view is that the mechanism of development of the offspring will be essentially that of the female" (Correns, 1901).

Few investigations on the unequality of reciprocal differences in wheat, *Triticum aestivum* L., have been published. Direction of a cross is not considered in most wheat breeding programs because little is known about the nature or predictability of reciprocal crosses. Moreover, making all reciprocal crosses in a large program would be impractical due to the large increase of crosses made and, subsequently, the additional material that would need to be evaluated. Also since F_1 seed is generally limited, breeders frequently bulk such crosses to obtain larger population sizes. Knowledge of the occurrence of reciprocal differences may help indicate what crosses favor the unequality and what traits are most affected.

The possible importance of different cytoplasm variation in crop production was clearly exemplified by the attack of race T of *Helminthosporium maydis* Nicikado and Miyake on maize hybrids having Texas male sterile cytoplasm (Tatum, 1971). Cytoplasmic male sterility, facilitating hybrid seed production, is another example of the use of cytoplasmic variability. Major grain crops such as *Zea mays* L., *Sorghum vulgare* L. and *T. aestivum* L., have been studied to utilize this characteristic (Kihara, 1951, 1958; Duvick, 1956; Josephson, 1962; Mann, 1973; Stephens, 1954). Wilson and Ross (1962) found the use of *T. timopheevi aestivum* produced cytoplasmic male sterility.

There have been many attempts to identify the mechanisms behind reciprocal differences. The unequality is frequently attributed to extra nuclear inheritance which is largely transmitted from the maternal side via the cytoplasm. An example of this is the work done by Conde et al. (1979) with mitochondrial and chloroplast DNA in an interspecific reciprocal cross within the genus *Zea*.

The question of whether the cytoplasmic extra chromosomes contained in plastids, kinetosomes, mitochondria and centrioles, influences a character like photosynthetic and respiratory rate or pollen sterility, has been investigated by many plant geneticists (Jinks, 1964; Beale, 1966; Durrant, 1965; Iwanaga et al., 1978; Sager, 1972). Jinks (1964) states that some or all of the genes that control a characteristic can have different effects in different cytoplasms. Such genes are said to be plasma sensitive.

Cumulative effects may also be a factor influencing expression of plasma sensitive genes (Law et al., 1978). Working with maize, Bhat and Dhawan (1970), transferred fractions of 25%, 50% and 75% of one variety's genome into the cytoplasm of another. Cytoplasmic effects on yield maturity, plant height and ear height were found to be produced in some relationship to nuclear constitution. It was postulated that when a certain threshold concentration of polygenes affecting a trait is attained in the nucleus, cytoplasmic nuclear interactions are not expressed.

Studies of alloplasmic (nucleus plus alien cytoplasm) lines of common wheat with the cytoplasms of other species of Triticum and Aegilops have demonstrated nuclear-cytoplasmic interaction. Busch and Maan (1978) found differences in heading date by use of various cytoplasms with two lines of spring wheat. Kinoshita et al, (1979) also observed differences in heading date on the Chinese Spring cultivar of wheat in alien cytoplasms. Kofiod and Maan (1980) did not find heading date differences in any alloplasmic line of wheat. Iwanaga et al. (1978) noted differences in respiratory and photosynthetic rates on wheat in seven cytoplasm substitution lines.

In crosses involving only common wheat, investigations have identified some characters that show reciprocal differences, although these are not consistent from cross to cross. The genetic effects of awnedness is reported to be more expressed when genes are introduced from the maternal side (Molchan, 1982). Flour pigment has been investigated in three reciprocal crosses in wheat (Bhatt and McMaster, 1976). The results showed differences in color in reciprocal F_1 and F_2 means and indicated that a breeding program interested in evolving low-pigment wheat types would use the low-pigment parent as the female.

Heteroic effects also may show differences in reciprocal crosses. Hraska (1975), showed F_1 differences in heterosis depended on the direction of the cross in six out of seven wheat crosses . Furthermore, the magnitude of the trait differences were striking with some characteristics, while in others, they were quite small. The smallest effects of heterosis occurred in traits that were quantitatively inherited such as 1000 kernel weight, spike length, spikelets per head and kernels per spike. Other traits that showed F_1 reciprocal differences for heterosis were plant height, plant mass, grain yield and tiller number.

Heading date and plant height differences in wheat were shown in F1's from crosses between six lines by El-Haddad (1974). Barley has also exhibited heading date differences in the progeny of reciprocal crosses (Olsen, 1979).

The various causes of unequality in reciprocal crosses are experimentally difficult to assess. The allelic segregation in nuclear systems is determined by the behavior of chromosomes and the spindle apparatus. However, in cytoplasmic systems the rules of segregation are different from the nuclear ones. A major goal is to identify models to interpret unequality that results from reciprocal crosses. Biometrical analysis models to identify these differences have been proposed (Aksel, 1974; Mather and Jinks, 1971). These models exemplify this complexity.

MATERIALS AND METHODS

To determine if reciprocal differences exists between diverse wheat parents, three winter and two spring habit cultivars were used. The winter cultivars were represented by Yamhill (Ymh), Stephens (Spn) and Maris Hobbit (MH), while Anza (Anz) and Siete Cerros (7C) were the spring types. A description of these cultivars is given in Appendix Table 1.

Reciprocal crosses were made between individual plants representing the parental cultivars. Spikes not used in crossing were bagged to ensure self-pollination. And so, from each pair of parents, seeds of two reciprocal F_1s and two parents were obtained. These were used in the following two studies.

Study I - Greenhouse

Seeds from crosses of Ymh/Anz, Ymh/7C and Ymh/MH were sown on September 2, 1982. The material was planted in vermiculite flats and allowed to germinate for 7 days in the greenhouse. Seedlings were then vernalized for 8 weeks in a growth chamber maintained at 8-10^{o}C and a daylength of 8 hours. Plants were then transplanted into 6-inch pots of silt loam amended with 11 grams of lime and 5 grams of 15-15-15 fertilizer, and put into the greenhouse at 18-24^{o}C and a daylength of 10 hours. After 40 days the light duration was increased to 14 hours, and 15 days later the temperature was increased to 24-30^{o}C.

Seven traits observed on a per-plant basis included:

a) Heading date measured as the number of days from January 1, 1983 until the first spike on the plant fully emerged from the boot. In the Ymh/MH cross, as a result of a change in procedures, heading was measured as the number of days from January 1 until 50% of the heads on a plant fully emerged.

b) Physiological maturity was measured as the number of days from January 1 until complete loss of the green color of the spike and peduncle on the primary tiller.

c) Plant height was measured at harvest as the distance (cm) between the soil surface and the tip of the highest spike, excluding the awns, if present.

d) Tiller number was counted at harvest time as the number of tillers bearing fertile spikes.

e) Kernels per spike was measured as the average number of kernels on the first three tillers.

f) 100 kernel weight (x) was calculated from data collected on the first three tillers as follows:

$$x = \frac{\text{yield (grams) X 100}}{\text{number of kernels}}$$

g) Total grain yield was measured in grams from all plant spikes individually cut and threshed in a head thresher.

Each cross utilized a complete randomized block design with three blocks. The four randomized treatments in each block contained two parents and their two reciprocal F_1s. Twelve plants in each treatment were arranged in two adjacent six-pot rows. There was an 18 cm space between treatments and a total number of 144 F_1s and parents per cross.

The twelve plants were subsamples from each treatment. For each cross, an analysis of variance of each trait was performed. Experimental errors from the three crosses were pooled. t-Values were determined in each cross between parental means, between F_1 means and, where unidirectional heterobeltiosis occurred, between the high parent and higher F_1 or, conversely, between the low parent and lower F_1 depending on which direction produced a favorable combination for the particular trait.

Study II - Field

Reciprocal F_1 seed from six crosses between individual plants were used. Only one of the crosses, Ymh/MH, utilized seed from the same two individual plants. Two crosses, Ymh/Anz and Ymh/7C, were used in both studies, the F_1 seed originated from different pairs of individual plants. Three additional crosses were made: Anz/Spn, 7C/Spn and Anz/MH.

Seeds were hand sown in the greenhouse in 2 1/4 X 2 1/4 inch peat pots, containing a silt loam soil, on October 16, 1982. Seedlings were moved to cold frames after eleven days to harden off. These were transplanted on November 7, 1982 to Hyslop Agronomy Farm, 11 km northeast of Corvallis, Oregon.

The soil, a woodburn silt loam, had been fumigated four weeks earlier with a 66/33 mixture of methyl bromide and chloropicrin (420 kg/ha). A total of 169 kg N/ha was applied in two applications: 34 kg N/ha of urea in March, 1983 and 90 N/ha of urea plus 45 kg N/ha of ammonium chloride in April, 1983. Tilt was applied (20 grams A.I./ha) twice in April to avoid infections of *Septoria tritici* and stripe rust (*Puccinia striiformis*). Malathion dust (6%) was applied to check aphid infestation in May.

In addition to the seven traits measured in Study I, the anthesis date was measured for each individual plant as days from January 1, 1983 until first floret pollen shedding. For all crosses, heading date was measured on the primary tiller. The three primary spikes of individual plants were cut by hand and threshed in the head thresher before recording measurements for kernels per spike and 100 kernel weight . This was done in order to reduce variability due to the use of larger threshers. The large number of plants necessitated the use of the larger Vogel individual plant thresher for the remaining spikes for determining grain yield.

Each cross utilized a complete randomized block design as in Study I, however, four blocks were employed instead of three. Treatment populations contained thirty-two individual plants for each parent and F_1. Each block consisted of four randomized treatments containing two parents and their two reciprocal F_1s. For each block, treatments contained ten plants in a single row with 46 cm between plants and 30 cm between rows. Adjacent rows were planted in a diagonal pattern to provide a more uniform environment. An adjacent row had its first plant 23 cm in front of the row on the left and alternate rows were parallel to each other.

The analysis was similar to that of Study I.

EXPERIMENTAL RESULTS

Results of this investigation are presented based on two studies. The first one involved a greenhouse study with two winter x spring and one winter x winter crosses. Study II, consisting of six crosses, five winter x spring and one winter x winter was grown at the Hyslop Experiment Station. In all F_1s the cultivars used as the female parent will be to the left when crosses are noted. General reference to parents alone will have a slash (/) between cultivars. Tables reflect comparison values only where significant differences are observed.

Study I - Greenhouse Investigation

Identification of Parental Lines Showing Reciprocal Differences

In Table 1 significant differences of parental means are no/ted on the parent with the highest value between the two cultivars. It can be observed that differences between parents were significant for heading date, physiological maturity, plant height and 100 kernel weight for all comparisons. Differences for tiller number and kernels per spike were only found between Ymh and Anz. Likewise, Ymh and 7C and Ymh and MH were different for grain yield.

Table 2 shows significant reciprocal differences, as determined by t-test (Appendix Table 3),for traits in their respective units with values placed on the highest F_1. Larger values were observed for the F_1 Ymh x Anz in plant height, tiller number and 100 kernel weight. The reciprocal, Anz x Ymh, showed a significant difference with a larger number of kernels per spike. Ymh x 7C was significantly different and

Table 1. Differences for seven traits between parental per plant means for plants grown in the greenhouse in 1982-83 (value placed on largest parent).

Parents	t values						
	Heading Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh	28.75**	3.75**	26.42**		17.5**	0.55**	
Anz				6.1**			
Ymh	36.00**	7.03**	14.78**			0.91**	2.840*
7c							
Ymh			11.05**			1.68**	2.78*
MH	7.53**	12.76**					
Standard Error	1.250 (1) 0.809 (2)	0.905	1.940	0.488	3.763	0.156	1.208

*,** Significance at the 0.05 and 0.01 probability levels, respectively, df=18.
(1) From pooled experimental error of Ymh/Anz and Ymh/7C crosses, df=12.
(2) From experimental error for Ymh/MH cross, df=6.

Table 2. Differences, for seven traits, between per plant means of reciprocal Fls grown in the greenhouse in 1982-83 (value placed on largest F1).

Reciprocal Combination	Difference in Reciprocal Means						
	Heading Date	Physiological Maturity	Plant Height (cm)	Tiller Number	Kernels/ Spike	100 Kernel Weight (gm)	Yield/ Plant (gm)
Ymh x Anz			4.28*	1.3**		0.35*	
Anz x Ymh					7.0*		
Ymh x 7C					10.9**		
7c x Ymh	2.19*						
Ymh x MH			3.45*				
Mh x Ymh							
Standard Error	1.250 (1) 0.809 (2)	0.905	1.940	0.488	3.763	0.156	1.208

*,** Significant at the 0.05 and 0.01 probability levels, respectively, df=18.
(1) S.E. for Ymh/Anz and Ymh/7C crosses, df=12.
(2) S.E. for Ymh/MH cross, df=6.

larger than it's reciprocal for kernels per spike, but the opposite was true for heading date with 7C x Ymh being significantly later. In the winter by winter cross, Ymh x MH was significantly taller than MH x Ymh.

In comparisons of differences of parents and reciprocal F_1 differences (Tables 1 and 2) it can be observed that in the cross involving Ymh and Anz, there were significant differences for plant height, tiller number, kernels per spike and 100 kernel weight for the parents and the F_1 populations. Ymh was taller, had more kernels per spike and higher 100 kernel weight while Anz had more tillers per plant. Where Ymh was the female parent in the F_1, significant differences were detected with higher values in plant height, tiller number and 100 kernel weight. The F_1 population when Anz was the female had a significant difference with a larger value for kernels per spike.

In the Ymh/7C cross, Ymh was later than 7C in heading date and no parental difference was detected for kernels per spike or tiller number. The F_1 populations of 7C x Ymh had a significant difference in heading date, with a larger value than its reciprocal. Even though there was no parental difference in kernels per spike, the F_1s were different with Ymh x 7C having a larger value than its reciprocal. Finally, Ymh and MH were different for height and their cross produced a reciprocal difference. The largest value was found when Ymh was the female.

<u>Difference In Magnitude Between Parents and Reciprocal F_1s</u>

Mean values of the seven traits measured for the parents and reciprocal F_1s are presented in Table 3. When compared to Ymh, the spring parents, Anz and 7C were earlier for heading date and physiological maturity, shorter in height and tended to have lower 100 kernel weight and grain yield. Anz had more tillers and fewer kernels per spike than either Ymh or 7C. A comparison between the two winter parents, Ymh and MH, indicates that Ymh was earlier for heading and physiological maturity dates and was taller. Ymh also showed higher values for 100 kernel weight and grain yield.

When the reciprocal F_1s were compared in the three crosses, the one consistent feature was that grain yield was higher than their respective parents. For the other traits measured, few or no consistent differences between the F_1s and their respective parents were observed.

In Appendix Table 4, the mean squares and CV values are presented for the three crosses and for the seven traits measured. Differences were detected for most traits in each of the three crosses. The exceptions were tiller number for the Ymh/7C and Ymh/MH crosses and kernels per spike for the Ymh/MH cross. High CV values were obtained for most traits with the exception of heading date and physiological maturity.

<u>Heterobeltiosis</u>

Comparisons are made in Table 4 between crosses that produced only one F_1 which was higher or lower than the high or low parent respectively. In the Ymh/Anz cross, Ymh being the female parent showed a 0.29 gm increase in 100 kernel weight over the highest parent, Ymh. It is interesting to note that a negative association in kernels per

Table 3. Mean per plant values of seven traits for parents and their reciprocal F1's grown in the greenhouse in 1982-83.

Parents or Reciprocal Combination	Means						
	Heading Date	Physiological Maturity	Plant Height (cm)	Tiller Number	Kernels/ Spike	100 Kernel Weight (gm)	Yield/ Plant (gm)
Ymh	66.39	99.69	85.56	8.2	59.8	4.07	17.31
Anz	37.64	95.94	59.14	14.3	42.3	3.52	16.36
Ymh x Anz	46.06	93.53	77.53	12.0	40.8	4.36	19.24
Anz x Ymh	44.44	93.64	73.25	10.7	47.8	4.01	18.04
Ymh	65.47	100.17	83.28	7.9	57.4	4.27	16.84
7C	29.47	93.14	68.50	7.9	59.6	3.36	14.00
Ymh x 7C	43.75	92.06	82.61	8.5	56.5	4.36	17.77
7C x Ymh	45.94	93.06	82.67	8.8	45.6	4.56	17.17
Ymh	58.50	98.80	84.22	7.9	63.3	4.19	16.75
MH	66.03	111.56	73.17	9.0	71.5	2.51	13.97
Ymh x MH	57.22	101.39	84.64	8.3	63.7	3.82	16.91
MH x Ymh	56.50	100.08	81.19	7.9	65.7	3.76	17.10
Standard Error	1.250 (1) 0.809 (2)	0.905	1.940	0.488	3.763	0.156	1.208

(1) From pooled experimental error of Ymh/Anz and Ymh/7C crosses, respectively, df=18.
(2) From experimental error for Ymh/Mh cross, df=6.

Table 4. Unidirectional heterobeltiosis of seven traits for per plant means of reciprocal F1s grown in the greenhouse in 1982-83.

Reciprocal Combination	Differences Between F1's and Best Parents: Kernels/ Spike	Differences Between F1's and Best Parents: 100 Kernel Weight (gm)
Ymh x Anz		+.29*
Anz x Ymh		
Ymh x 7C		
7C x Ymh	-11.8**	
Ymh x MH		
MH x Ymh		
Standard Error	3.763	0.156

*,** Significant according to t-test at the 0.05 and 0.01 probability levels, respectively df=18.
+ More than highest parent.
- Less than lowest parent.

spike occurred in the Ymh/7C cross. When 7C was the female, it scored an average of 11.8 kernels less than the low parent, Ymh.

Study II - Field Investigation

Identification of Parental Lines Showing Reciprocal Differences

The three crosses used in the greenhouse study were also included in the field investigation. In addition, three other crosses were employed, all being winter by spring crosses (Spn x Anz, MH x Anz and Spn x 7C). Table 5 provides the differences of parental means for the eight traits measured for each pair of parents in the six crosses. Again, as with the tables presented for greenhouse data, the values correspond to the cultivar with the highest value. In heading, anthesis and physiological maturity dates, the later the cultivar the higher the values. Accordingly, in these three traits significant differences are shown for the winter parents, Ymh and MH, because they were later than the respective spring parent. This was also the case for plant height, with the exception of Anz being taller than the winter parent MH. Anza had significantly more tillers than Ymh; however no differences were detected between any of the other cultivars for this trait. In comparison, where 7C and MH were involved they were different from their paired cultivar for kernels per spike. For this trait, 7C was higher in its cross with Ymh and Spn while MH was than Ymh and Anz. Stephens was also significantly higher in kernels per spike when compared to Anz.

The difference between reciprocal F_1 populations for the eight traits measured in their respective units, can be found in Table 6. Here, only those values found to be different, as calculated by t-

Table 5. Differences for seven traits between parental per plant means grown at Hyslop Experimental Station in 1982-83 (value placed on highest parent).

Parents	t-values							
	Heading Date	Anthesis Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh	32.6**	17.40**	8.93**	14.69**			1.18**	15.13*
Anz					5.4*			
Ymh	28.56**	16.46**	9.13**	6.63**			1.07**	24.1**
7C						11.3**		
Ymh				21.12**			0.95**	
MH			1.75**			30.6**		
Spn	27.93**	16.44**	9.03**	10.94**		7.4*	1.91**	19.9**
Anz								
MH	33.40**	16.62**	10.44**			44.5**	0.26*	41.47**
Anz				4.84**				
Spn	27.97**	15.16**	8.44**				0.13**	21.01**
7C						6.9*		
Standard Error	0.98	0.59	0.37	1.86	2.9	3.3	0.13	8.55

*,** Significance at the 0.05 and 0.01 probability levels, respectively, df=54.

Table 6. Differences for eight traits, between per plant means of F1s grown at the Hyslop Experimental Station in 1982-83 (value placed on largest F1).

Reciprocal Combination	Difference in Reciprocal Means							
	Heading Date	Anthesis Date	Physiological Maturity	Plant Height (cm)	Tiller Number	Kernels/ Spike	100 Kernel Weight (gm)	Yield/ Plant (gm)
Ymh x Anz								
Anz x Ymh					5.6*			17.14*
Ymh x 7C								
7C x Ymh	2.50**	1.06*					0.23*	
Ymh x MH								
MH x xYmh								
Spn x Anz								
Anz x Spn								
MH x Anz								
Anz x MH			0.71*					
Spn x 7C								
7c x Spn	2.69**							
Standard Error	0.98	0.59	0.37	1.86	2.9	3.3	0.13	8.55

*,** Significant at the 0.05 and 0.01 probability levels, respectively, df=54.

tests (Appendix Table 5), are identified. From the comparison between Ymh and Anz it can be noted that where Ymh was used as the female parent (Ymh x Anz) larger F_1 values were detected for tiller number and grain yield per plant. In the cross involving Ymh and 7C, differences in heading and anthesis date along with 100 kernel weight were found with a larger value when 7C was used as the female parent (7C x Ymh). When 7C was used as a female with Spn, heading date was also later than its reciprocal. Physiological maturity was found to be later when Anz was used as the female parent with MH as the male.

Difference In Magnitude Between Parents and Reciprocal F_1s

Mean values for the parents and reciprocal F_1s involving the eight traits are provided in Table 7. One additional trait measured in the field study was anthesis date.

For heading, anthesis and physiological maturity dates the spring parent was earlier in every cross. In the winter by winter cross, the two parents Ymh and MH were similar for heading and anthesis, but different in physiological maturity. A similar situation was observed for plant height with the exception of the cross involving the winter parent MH and the spring type Anz.

Maris Hobbit had the highest number of kernels per spike while Spn had the largest 100 kernel weight. With grain yield per plant, the winter types were higher with MH exhibiting the highest value, 106.84 per plant.

When the F_1 populations are compared to their respective parents for heading, anthesis and physiological maturity dates, the values were intermediate between the parents for the winter by spring crosses. No differences in heading and anthesis dates and very small

Table 7. Mean per plant values of eight traits for parents and their reciprocal F1s, grown at Hyslop Experimental Station in 1982-83.

Parents or Reciprocal Combination	Means							
	Heading Date	Anthesis Date	Physiological Maturity	Plant Height (cm)	Tiller Number	Kernels/ Spike	100 Kernel Weight (gm)	Yield/ Plant (gm)
Ymh	147.13	147.87	194.84	105.78	25.1	96.2	5.05	86.19
Anz	114.53	130.47	185.91	91.09	30.5	95.9	3.87	71.06
Ymh x Anz	131.44	138.81	187.16	115.63	37.6	105.0	5.25	121.14
Anz x Ymh	131.84	138.88	187.03	116.31	32.0	104.0	5.13	104.00
Ymh	145.97	146.84	190.97	110.69	28.0	92.3	5.14	93.66
7C	117.41	130.38	181.84	104.06	22.2	103.6	4.07	69.56
Ymh x 7C	133.50	138.75	186.41	122.31	27.4	107.9	5.22	109.30
7C x Ymh	136.00	139.81	186.59	122.22	28.9	111.9	5.45	115.22
Ymh	145.47	146.81	194.03	109.78	25.1	88.0	5.16	77.88
MH	146.03	146.28	195.78	88.66	29.1	118.6	4.21	90.75
Ymh x MH	144.72	145.44	194.41	103.97	29.3	96.1	5.69	101.36
MH x Ymh	144.09	145.03	194.47	105.25	31.0	93.0	5.66	100.92
Spn	143.34	145.78	193.03	103.63	25.7	92.3	5.91	83.23
Anz	115.41	129.34	184.00	92.69	27.3	84.9	4.00	63.33
Spn x Anz	126.22	134.88	187.16	109.09	31.8	103.4	5.16	107.99
Anz x Spn	125.16	134.75	187.19	107.84	33.4	102.5	5.11	108.00
MH	147.59	146.78	196.13	88.88	28.0	134.2	4.52	106.84
Anz	114.19	130.16	185.69	93.72	26.8	89.7	4.26	65.37
MH x Anz	131.16	137.31	187.13	102.34	31.7	116.8	5.00	110.28
Anz x MH	132.31	138.16	187.84	102.22	31.5	118.2	5.10	112.34
Spn	142.91	145.16	192.44	109.34	32.3	92.8	5.79	89.11
7C	114.94	130.00	184.00	110.31	25.2	99.7	4.20	68.10
Spn x 7C	128.00	135.97	186.78	114.69	29.8	104.4	5.73	95.33
7c x Spn	130.69	136.69	186.59	116.06	30.2	103.5	5.81	107.65
Standard Error	0.98	0.59	0.37	1.86	2.9	3.3	0.13	8.55

differences for the physiological maturity date were detected for the winter cross Ymh/MH.

For plant height, the F_1 populations were consistently taller than the tallest parent in all crosses except the Ymh/MH cross where the mean F_1 values were near the tallest parent, Ymh. With kernels per spike and 100 kernel weight, F_1 values tended to be either higher than the highest parent or similar to it, the exceptions being for kernels per spike for Ymh x MH and MH x Anz where in both cases the parent MH was the highest. For tiller number only one cross, Ymh/Anz, had significant differences between means with the F_1s being higher or equal to the spring parent, Anz. The F_1 populations consistently had higher grain yields per plant.

In Appendix Table 6, the mean square, levels of significance and CV values are provided. Only those values where significant differences were found are noted. Differences were detected among the parents and F_1s for most crosses involving the eight traits measured. The exceptions were heading date for the Ymh/MH cross and tiller number for the Ymh/7C, Ymh/MH, MH/Anz and Spn/7C crosses. The CV values were low or intermediate for all the traits except tiller number and grain yield per plant.

Heterobeltiosis

When a comparison is made between reciprocal F_1 populations for heterobeltiosis, several differences can be noted (Table 8). In the Ymh/Anz cross, 7.1 more tillers per plant were observed than the highest parent Anz when Ymh was the female (Ymh x Anz). For the Ymh/7C cross, kernels per spike (8.3) and 100 kernel weight (0.31)

Table 8. Unidirectional heterobeltiosis of eight traits for per plant means of reciprocal F1s grown at the Hyslop Experimental Station in 1982-83.

Reciprocal Combination	Differences Between F1's and Best Parents				
	Anthesis Date	Tiller Number	Kernels/ Spike	100 Kernel Weight (gm)	Yield/ Plant (gm)
Ymh x Anz		+7.1**			
Anz x Ymh					
Ymh x 7C					
7C x Ymh			+8.3**	+0.31**	
Ymh x MH					
MH x Ymh	-1.25*				
Spn x Anz					
Anz x Spn		+6.1*			
MH x Anz					
Anz x MH					
Spn x 7C					
7c x Spn					+18.54*
Standard Error	0.59	2.9	3.3	0.13	8.55

*,** Significant according to t-test at the 0.05 and 0.01 probability levels, respectively df=54.
+ More than highest parent.
- Less than lowest parent.

were greater than the highest parent, 7C and Ymh respectively, when 7C was used as the female (7C x Ymh). In the winter by winter cross, when MH was used as the female with Ymh (MH x Ymh), anthesis date was 1.25 days earlier than the earliest parent MH. Anza used as the female when crossed with Spn was found to exhibit heterobeltiosis for tiller number (6.1) over the high parent, Anz. A larger value (18.54 gm) was obtained over the best parent, Spn, in the cross having 7C as the female (7C x Spn).

DISCUSSION

Wheat breeders generally assume that there are no reciprocal differences when making crosses between two parents, which represent two different homozygous cultivars, therefore no attention is paid to which way crosses are made. Often in conventional breeding programs if reciprocal crosses are made the resulting F_1 seed is bulked in order to increase an already limited population size. With the systematic crosses between such diverse gene pools as winter and spring wheats, concerns have been expressed that possible reciprocal differences might exist. Also, with the advent of cytoplasmic sterility, genetic restoring genes and, more recently, chemical gametocides, F_1 hybrid wheat is again receiving greater interest. Thus, where the F_1 population is the end product of the breeding program or even in conventional selfing programs, possible reciprocal differences could be a significant factor in determining which way a cross is made especially for specific traits.

Variation between reciprocal crosses have been reported for several traits in wheat (Bhat and McMaster,1976; El-Haddad,1974; Hraska,1975; Molchan,1982). However, such investigations have not been numerous and prediction of which crosses may produce reciprocal differences for specific traits is not currently possible. In addition, the question as to whether differences might exist when crossing winter by spring cultivars has not been addressed.

The purpose of this study was to determine if reciprocal differences exist and if so, does the crossing of winter by spring types result in such differences for selected agronomic traits.

Results of the investigation will be discussed as they are related to: 1) possible reciprocal differences as a result of the use of specific cultivars in crosses: 2) possible reciprocal effects based on the magnitude by which the two parents differ: 3) possible unidirectional reciprocal differences resulting in heterobeltiosis. This latter consideration is of particular interest to those involved in the development of hybrid wheat.

Study I. Greenhouse Investigation

Identification of Parental Lines Showing Reciprocal Differences

From the data collected, there appears to be some relationship between the use of specific cultivars and the occurrence of reciprocal F_1 differences. Furthermore, there may be an association of the direction of the cross and the maximum expression of a trait.

The Ymh/Anz cross had a total of four traits that showed reciprocal F_1 differences. In comparison, the other winter by spring cross, Ymh/7C, had two traits while the winter by winter, Ymh/MH, had only one trait where a reciprocal F_1 difference. Differences between the parents Ymh and Anz were the largest among the three crosses for the three traits of plant height, tiller number, and kernels per spike, and so the observed reciprocal difference may be due to some interaction between magnitude of parental difference and use of specific cultivar combinations. This may be questioned, however, in the trait kernels per spike where there was a reciprocal difference for both the Ymh/Anz cross and the Ymh/7C cross. The former had the largest parental difference while the latter showed no parental difference. This is not consistent with the idea of a relationship between magnitude of parental difference and occurrence of reciprocal F_1 differences. Further, this suggests that there is some other phenomenon associated with the use of specific parents and reciprocal F_1 difference occurrence rather than the degree of differences between parents. A possible explanation is that different cytoplasms may exist between certain cultivars.

It could be postulated that if reciprocal F_1s have identical nuclear constitutions, but different maternal cytoplasm, then the difference observed in the F_1s for a trait reflects different nuclear-cytoplasmic combinations. Bhat and Dhawan's (1970) hypothesis that a threshold of polygenes obtained in a nucleus may nullify the cytoplasmic-nuclear effect suggests an explanation for the expression of reciprocal F_1 differences when parents have different cytoplasms and have a large difference for a trait. Large difference between parents would suggest that they were different for a large number of alleles. The F_1s would thus be heterozygous at an equally large number of alleles for quantitatively inherited traits. If these genes expressed themselves in an additive manner, then the F_1, being heterozygous, may fall below this threshold level. Thus the cytoplasmic-nuclear interaction would be expressed. This would all be dependent on the threshold level for a particular trait. For the parents that did not differ in kernels per spike, genetic make up of the two cultivars may be of a nature which results in a genetic constitution of the F_1 nucleus falling below the threshold level of one of the parental cytoplasms. More information is needed with a larger number of crosses to establish this relationship with specific cultivar crosses.

The direction of the cross also appeared to influence which reciprocal F_1 was larger in the Ymh/Anz cross. However, when the female exhibited the greatest expression of a trait between the two parents, the F_1 was not necessarily larger than its reciprocal. Yamhill used as the female when crossed to Anz was greater than its reciprocal for three out of four traits, plant height, tiller number, and 100 kernel weight. The reciprocal (Anz x Ymh) had more kernels per spike. This would suggest that if cytoplasmic nuclear interactions produce reciprocal differences, certain cytoplasms may be best over a number of traits. Further, for plant height, Ymh used as a female in its cross with MH produced a taller F_1 than its reciprocal. This was similar for plant height in the Ymh x Anz F_1. So there is some evidence that for a specific traits, certain cytoplasms may be best. However, for kernels per spike, Anz x Ymh was higher than its reciprocal while Ymh x 7C was higher than its reciprocal. This relationship therefore may be only applicable for crosses where reciprocal differences occur and only for certain traits. Again, more crosses are needed to observe general trends in nuclear-cytoplasmic relations.

Differences In Magnitude Between Parents and Reciprocal F_1s

Two general statements can be made about the parents used in this study. First, there was no clear relationship between the magnitude by which the parents differed and the occurrence of reciprocal F_1 differences for the traits studied. Second, the results suggest, although weakly, that from the populations used, there is some relationship between crossing winter with spring parents and the occurrence of reciprocal F_1 differences for specific traits.

It would be reasonable to assume that if reciprocal F_1 differences were to occur, then their occurrence would be associated with different genetic characteristics of the parents and/or the magnitude of the difference expressed between the parents for a trait. As already stated, the cytoplasm in the F_1 is maternally inherited. Due to different environmental requirements of winter and spring types as well as the historic reluctance of breeders to intercross these types, one might expect that different cytoplasms have also evolved.

Large differences for heading date, 100 kernel weight and grain yield and to a lesser degree for physiological maturity, plant height and kernels per spike were found between the parents in all three crosses. No differences were found in tiller number and 100 kernel weight for two out of three crosses. However, reciprocal differences were found for several traits where either large, small or no differences were observed between parents. For example, in heading date, the only reciprocal F_1 differences came from the winter by spring cross Ymh/7C which had the largest parental difference. With tiller number, the reciprocal difference detected came from the winter by spring Ymh/Anz which was the only cross showing a parental difference. For plant height, reciprocal differences were obtained from two crosses where the largest (Ymh/Anz, winter by spring) and the smallest (Ymh/MH, winter by winter) parental differences were noted. With kernels per spike, reciprocal F_1 differences were obtained with the Ymh/Anz cross having the largest parental difference, and also with Ymh/7C cross which showed no parental difference at all. As for 100 kernel weight, the only reciprocal F_1 difference observed came from the Ymh/Anz cross which had the smallest difference between parents.

For kernels per spike, as discussed earlier, reciprocal F_1 differences occurred for the winter by spring crosses of parents that did (Ymh/Anz), and conversely did not (Ymh/7C) differ for this trait, but no reciprocal differences occurred for the winter by winter Ymh/MH cross. The winter and spring parents Ymh/7C must have differed for this trait in a manner that resulted in the difference of their reciprocal F_1s. If the heterozygous nucleus was identical for both the reciprocal F_1s of the Ymh/7C cross, then a diversity between the parents other than nuclear would be suggested. If different cytoplasms have evolved in winter and spring wheats, reciprocal differences might result from the different cytoplasmic-nuclear combinations. For the traits measured, only one reciprocal difference, plant height, was found in the winter by winter cross whereas from the winter by spring crosses, Ymh/7C had two and Ymh/Anz had four reciprocal F_1 differences. These different cytoplasmic-nuclear combinations from crossing winter by spring types could explain a greater number of reciprocal differences over the winter by winter cross. However, the use of only two winter by spring crosses of diverse parents and one winter by winter cross does not establish a clear argument in favor of reciprocal differences occurring as a result of winter by spring crosses. More evidence is needed from crosses of diverse and similar spring by winter, winter by winter and spring by spring types to support this possible interaction between the nucleus and the cytoplasm based on growth habit.

Unidirectional Heterobeltiosis

There was limited data regarding the expression of heterobeltiosis for reciprocal crosses in this study. Only the Ymh/Anz cross showed a value higher than the highest parent, Ymh, for 100 kernel weight. This was when Ymh was the female parent. A negative response was found in the Ymh/7C cross. When 7C was used as the female, less kernels per spike were produced than the lowest parent, Ymh. No other expressions of heterobeltiosis were detected from the respective reciprocal crosses.

It is accepted that the maximum expression of heterobeltiosis occurs from parents which are genetically widely diverse. In most cases this was true for the F_1s produced from the spring by winter types compared to the winter by winter types. There is simply no evidence to conclude from this study that there is a relationship as to the amount of heterobeltiosis produced and the occurrence of reciprocal differences.

Study II. Field Investigation

Identification of Parental Lines Showing Reciprocal Differences

As in the greenhouse, there appears to be some relationship between the use of specific cultivar or combinations and the occurrence of reciprocal F_1 differences. Direction of a cross may also favor maximum expression of a trait. For example, the Ymh/Anz cross in the field also had two reciprocal differences, one in tiller number and the other in grain yield. The largest number of reciprocal differences were found for the Ymh/7C cross and these were for heading and anthesis date and 100 kernel weight. It is not surprising that crosses or traits that exhibited reciprocal F_1 differences in the greenhouse, did not perform the same way in the field. The traits where similar occurrence of reciprocal differences were not found in both the greenhouse and the field (plant height, kernels per spike, 100 kernel weight, and yield) had correspondingly high CV values. This indicates that these traits are largely effected by the environment and any possible differences were masked by the two different environments of Studies I and II. What is interesting is that the Ymh/Anz and Ymh/7C crosses both showed reciprocal differences in the greenhouse and in the field. Further, each cross had a reciprocal difference that was expressed in the same manner in both environments. Yamhill used as the female in its cross with Anz (Ymh x Anz) had more tillers than its reciprocal. Also 7C used as the female in its cross with Ymh (7C x Ymh) had an earlier heading date than its reciprocal when grown in the greenhouse and field. Both of these traits are quantitatively inherited. The implication is that there are reciprocal F_1 differences for quantitative traits, and the expression of these traits may or may not be environmentally influenced to the same degree as the other traits measured in this study.

Differences In Magnitude Between Parents and Reciprocal F_1s

As in the greenhouse study, large differences between parents were not indicative of possible reciprocal F_1 differences. Large differences for heading date were observed for the combinations Ymh/7C and Spn/7C, with the resulting F_1s reflecting reciprocal differences. In contrast to Study I, equally large parental heading date differences were found in other crosses, but no reciprocal F_1 differences were observed. For tiller number, the one reciprocal difference detected resulted where the parents Ymh and Anz did differ significantly for this trait. This cross, as in the greenhouse study, was the only cross that showed statistical significant difference between parents and between F_1 means. Reciprocal differences for 100 kernel weight and yield were observed in crosses where the parental means were intermediate in contrast to the large and small parental differences found in other crosses for this trait.

No clear relationship was observed between crosses of winter and spring types and the occurrence of reciprocal differences. However, the seven reciprocal differences found in this study involved four winter by spring crosses. No reciprocal differences were found in the winter by spring cross Spn/Anz or the winter by winter cross Ymh/MH. These limited observations do not rule out an association between crosses of winter by spring types and the occurrence of reciprocal differences.

Unidirectional Heterobeltiosis

The relationship between reciprocal crosses and the occurrence of differences in expression of heterobeltiosis between reciprocal F_1s is not clear. It does appear that some effects can be seen in specific crosses for certain traits. In the greenhouse, reciprocal F_1 differences for tiller number were noted for the Ymh/Anz cross, but the F_1s showed no heterobeltiosis. In the field, tiller number was again different between reciprocal F_1s but expression of the Ymh x Anz, F_1 was higher than the highest parent, Anz. In another comparison for tiller number, only when Anz was used as the female in the cross Anz x Spn were more tillers observed than the highest parent, Anz. The use of Anz in its crosses with Ymh and Spn does not indicate one direction which is best; however it does suggest that Anz nuclear-cytoplasmic interactions with these two cultivars promote reciprocal

F_1 differences in the expression of heterobeltiosis.

Only 7C used as the female in crosses with Ymh and Spn showed increase in certain traits over the high parent. With Spn, an increase was noted in grain yield per plant. The use of 7C as the female may therefore be advantageous, however more information is needed for this assessment.

Results from this study provide evidence that breeders may need to pay more attention to which way crosses are made. This is true in the conventional breeding programs and especially where the end product is an F_1 as in hybrid wheat. More reciprocal differences were noted within winter by spring crosses, however, based on the limited number of crosses it would be difficult to make generalizations with regard to winter by spring verses winter by winter crosses. However, the results of this study do strongly suggest that in genetic investigations involving wheat, and especially winter x spring crosses, attention should be paid to the direction in which crosses are made.

SUMMARY AND CONCLUSIONS

The major objectives of this study were: 1) to identify reciprocal F_1 differences resulting from use of specific cultivars in crosses of winter by spring wheat parents; 2) to determine if reciprocal F_1 differences are based on the magnitude by which the two parents differ; 3) to compare reciprocal F_1s with the highest parent to determine if there are possible unidirectional heterobeltiosis for the traits measured.

Two reciprocal winter by spring crosses and one reciprocal winter by winter cross were studied under greenhouse conditions. Five reciprocal winter by spring crosses and one reciprocal winter by winter cross were studied under field conditions. Data were collected on an individual plant basis for heading date, physiological maturity date, plant height, tiller number, kernels per spike, 100 kernel weight and grain yield per plant for the greenhouse investigation. In addition to these measurements, anthesis date was measured in the field. Comparisons of the means of the reciprocal F_1s and the parents were performed on all characters evaluated for each study. A t-test was employed to detect possible differences between reciprocal F_1s, between parents and, where heterobeltiosis occurred between the highest parent and the reciprocal F_1s. The following conclusions drawn were based on the data obtained from the experimental materials used in this study.

1. The data suggests some relationship between the occurrence of reciprocal F_1 differences and the use of specific cultivars in a cross. Yamhill crossed with Anza or Siete Cerros produced F_1s

that differed for more traits than the other crosses.

2. The direction of a cross may influence the maximum expression of a trait between reciprocal F_1s. In the Yamhill/Anza cross, Yamhill used as the female parent showed a greater tiller number than its reciprocal F_1 for both the greenhouse and the field studies. Similarly, when Siete Cerros was used as the female parent in the Yamhill/Siete Cerros cross, a later heading date than the reciprocal F_1 was observed in the greenhouse and in the field.
3. No consistent relationship was found between the magnitude of parental difference and the occurrence of reciprocal F_1 difference for any of the traits investigated. F_1s were unequal in some traits from crosses where the difference in parental means were not only large, but also where there were small or no differences.
4. There were no clear associations between reciprocal F_1 differences and crosses involving winter and spring types. Both greenhouse and field studies, and for all the traits measured, the winter by spring crosses that showed unequal reciprocal F_1s differed in more traits than the winter by winter cross. However, the number of crosses evaluated was limited and only one winter x winter cross (Yamhill/Maris Hobbit) was included in the studies. In the field, this cross did not produce any reciprocal differences in the F_1s but neither did one of the winter by spring crosses (Stephens/Anza).
5. Little evidence was obtained to identify a pattern showing unidirectional heterobeltiosis for specific crosses.

Unidirectional heterobeltiosis was observed from the reciprocal F_1s, but it was not limited to winter by spring crosses nor to crosses with a magnitude of difference between the parents.

REFERENCES

Aksel, R. 1974. Analysis of means in the case of nonequivalent reciprocal crosses in autoganous plants. Theor. Appl. Genet. 45:96-103.

Aksel, R. 1977. Quantitative genetically nonequivalent reciprocal crosses in cultivated plants. In: Genetic Diversity in Plants. IV. Genetics of quantitative characters. Eds. Muhammed, A., Aksel, R., von Borstel, R. C.Plenum Press, New York. p. 269-280.

Allan, R. E., O. A. Vogel and C. J. Peterson. 1962. Seedling emergence rate of fall sown wheat and its association with plant height and coleoptile length. Agron. J. 54:347-350.

Beale, G. H. 1966. The role of the cytoplasm in heredity. Proc. Roy. Soc. (London) Ser. B 164:209-218.

Bhat, B. K. and N. L. Dhawan. 1970. Threshold concentration of plasmon-sensitive polygenes in the expression of quantitative characteristics of maize (Zea mays L.). Theor. Appl. Genet. 40:347-350.

Bhat, B. K. and N. L. Dhawan. 1971. The role of cytoplasm in the manifestation of quantitiative characteris of maize. Genetica 42:165-174.

Bhatt, G. M. and G. J. McMaster. 1976. Variation in pigment control of flour color in bread wheat (Triticum aestivum L). Euphytica 25:685-691.

Busch, R. H. and Maan, S. S. 1978. Effects of alien cytoplasms on agronomic and bread making traits of two spring wheat cultivars. Crop Sci. 18:864-866.

Conde, M. F., D. R. Pring and C. S. Levings III. 1979. Maternal inheritance of organelle DNAs in Zea mays -Zea perennis reciprocal crosses. J.of Heredity (70):2-4.

Correns, E. C. 1901. Die Ergebnisse der neuesten Bastardforschungen fur die vererbungslehre. Ber. Deut. Bot. Ges. XIX:71-94.

Dhaliwal, H. S. 1977. Basis of difference between reciprocal crosses involving Triticum boeoticum and T. urartu. Theor. Appl. Genet. 49:283-286

Durrant, A. 1965. Analysis of reciprocal differences in diallel crosses. Heredity 20:573-607.

Duvick, D. N. 1956. Allelism and comparative genetics of fertility restoration of cytoplasmically pollen sterile maize. Genetics 41:544-565.

Eagles, H. A. 1982. Inheritance of emergence time and seedling growth at low temperatures in four lines of maize. Theor. and Appl. Genet. 62(1):81-87.

El-Haddad, M. M. 1975. Genetical analysis of diallel crosses in spring wheat. Egypt. J. Genet. Cyto. 4:174-188.

Gill, B. S. and J. G. Waines. 1978. Paternal reglulation of seed development in wheat hybrids. Theor. Appl. Genet. 51:265-270.

Hansen, L. A. and J. R. Baggett. 1977. Reciprocal differences for plant and ear characteristics in sweet corn. Hort. Science 12(1):61-62.

Iwanaga, M., Y. Mukai, I. Panayotov and K. Tsunewaki. 1978. Genetic development of the cytoplasm in Triticum and Aegilops. VII. Cytoplasmic effects on respiratory and photosynthetic rates. Japan J. Genetics 53,6:387-396.

Jinks, J. L. 1964. Extrachromosomal Inheritance. Prentice-Hall, Englewood Cliffs, New Jersey.

Josephson, L. M. and H. C. Kinca. 1962. Effects of male sterile cytoplasm on yield and other agronomic characteristics of corn inbreds and hybrids. Crop Sci. 2:41-43.

Kihara, H. 1951. Substitution of nucleus and its effects on genome manifestations. Cytologia 16:177-193.

Kihara, H. 1958. Fertility and morphorlogical variation in the subtitution and restoration backcrosses of hybrids, Tritcum vulgare x Agilop caudata. Proc. Tenth Intern. Cong. of Genet. 2:142-171.

Kinoshita, T., I. Ohtsuka and H. Kiraha. 1979. Alteration of growth habit and variation of heading time induced by the alien cytoplasm in common wheats. Wheat Information Service 50:65-70.

Kofoid, K. D. and S. S. Mann. 1980. Agronomic performance of randomly derived alloplasmic wheats. Wheat Information Service 51:29-32.

Law, C. N., J. W. Snape, A. J. W. Worland. 1978. Cytoplasmic effects on plant characters. Annual Report 1978. Cambridge Plant Breeding Institute. p. 118-121.

Lefort-Buson, M. and Y. Dattee. 1982. Genetic study of some agronomic characters in winter oilseed rape. Agronomie 2(4):323-332.

Maan, S. S. 1973. Cytoplasmic male-sterility and male-fertility restoration systems in wheat. Proc. Symposium on Genetics and Breeding of Durum Wheat. Bari, Italy. p. 117-138.

Mather, K. and J. L. Jinks. 1971. Biometrical Genetics. Cornell University Press. Ithaca, New York.

Molchan, I. M and T. V. Lezzhova. 1981. Genetics of awnedness and the reproduction of variety of winter wheat. Genetika 17(10):1842-49.

Pollmer, W. G., D. Klien and B. S. Dhillon. 1979. Differences in reciprocal crosses of maize inbred lines diverse for protein content. Euphytica 28:325-328.

Sager, R. 1972. Cytoplasmic Genes and Organelles. Academic Press, Inc. New York. 405 pp.

Stephens, J. C. and R. F. Holland. 1954. Cytoplasmic male sterility for hybrid seed production. Agron. J. 46:20-23.

Tatum, L. A. 1971. The northern corn leaf blight epidemic. Sci. 171:1113-1116.

Ward, R. W. 1981. Comparative responses of alloplasmic (Cytoplasm = Triticum timopheevi Zhuk.) and euplasmic wheats (T. aestivum L.em. Thell) to photoperiod and vernalization. Ph.D. Thesis. Kansas State University. Diss.Abst. Order No. 81278886.

Wilson, J.A.,and W.M. Ross. 1962. Male sterility interaction of the Triticum aestivum nucleus and Triticum timopheevi cytoplasm. Wheat Inf. Serv. 14:29-30.

APPENDICES

Appendix Table 1. Pedigree and description of cultivars.

Anza (Anz):	(Lerma Rojo//Norin 10/Brevor/4/Yaktana 54//Norin 10/Brevor/3/Andes*3). Short stature, high yielding spring cultivar. Awned type, semi-hard red grain. From Mexico.
Maris Hobbit (MH):	(Professeur Marchal//Marne/Vogel 9144/4/CI12633/4*Capelle //Heine 110/Capelle/3/Nord Desprez). A semi-dwarf soft red winter wheat from Great Britain with low tiller levels, high spike fertility and moderate seed size.
Siete Cerros 66 (7C):	(Frontana//Kenya 58/Newthatch/3/Norin 10/Baart/4/Gabo 55). A hard white common spring wheat cultivar from Mexico. Mid-season maturity, semi-dwarf. Small to medium size kernel. Widely adapted and excellent yield potential.
Stephens (Spn):	(Nord Desprez/Pullman Selection 101). An awned, standard height, soft white winter wheat from Oregon State University. Medium to high tillering levels, moderate head fertility and a high seed weight.
Yamhill (Ymh):	(Heines VII/Redmond(Alba). A soft white common winter wheat released by Oregon State University. Late maturity, medium height, high yielding and awnless. Large fertile spikes and medium to large kernels. Low tillering.

Appendix Table 2: Summary of meterological data at Hyslop Experimental Farm, Corvallis, Oregon (1982-83).

Month	Temperature (C) Max.	Temperature (C) Min.	Precipitation (mm)	Evaporation (mm)	Radiation (Cal/cm day)
September	42.6	9.6	48.0	114.8	358
October	17.9	5.8	92.5	54.4	230
November	9.7	1.4	140.0	---	118
December	8.2	1.8	268.0	---	78
January	9.0	2.3	175.0	---	79
February	11.2	4.1	261.9	---	135
March	13.5	5.7	223.0	---	186
April	16.1	4.1	76.5	93.5	366
May	20.8	7.0	38.4	127.3	536
June	21.1	17.5	35.3	125.5	476
July	23.3	11.2	64.8	134.1	486
August	26.4	11.9	56.1	158.8	492

Appendix Table 3. t-values of seven traits, for per plant means of reciprocal F1s grown in the greenhouse in 1982-83 (values placed on the largest F1).

Reciprocal Combination	t values						
	Heading Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh x Anz			2.206*	2.692**		2.244*	
Anz x Ymh					1.860*		
Ymh x 7C					2.897**		
7C x Ymh	1.752*						
Ymh x MH			1.778*				
MH x Ymh							
Standard Error	1.250 (1) 0.809 (2)	0.905	1.940	0.488	3.763	0.156	1.208

*,** Significance at the 0.05 and 0.01 probability levels, respectively, df=18.
(1) From pooled experimental error of Ymh/Anz and Ymh/7C crosses, df=12.
(2) From experimental error for Ymh/MH cross, df=6.

Appendix Table 4. Mean squares and coefficients of variance (CV) of seven traits for parents and their reciprocal F1's grown in the greenhouse in 1982-83.

Source	df	Mean Square						
		Heading Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh/Anz	3	5523.958**	299.792**	4407.875**	232.352**	2666.792**	4.370**	53.009
Ymh/7C	3	7887.583**	503.792**	1857.083**	7.824	1412.188*	10.300**	100.924*
Ymh/MH	3	693.406**	1222.625**	1018.438**	10.137	514.917	19.419**	78.766*
Error	18	28.164 (1) 11.786 (2)	14.736	67.674	4.204	254.896	0.437	21.749
CV		8.10 (1) 5.76 (2)	3.930	10.550	22.090	28.430	16.950	27.780

*,** Significant according to F-test at the 0.05 and 0.01 probability levels, respectively, df=18.
(1) From pooled experimental error of Ymh/Anz and Ymh/7C crosses, df=12.
(2) From experimental error for Ymh/MH cross, df=6.

Appendix Table 5. t-values of eight traits for per plant means of reciprocal F1s grown at the Hyslop Experimental Station in 1982-83 (value placed on highest F1).

Reciprocal Combination	t-values							
	Heading Date	Anthesis Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh x Anz					1.947*			2.004*
Anz x Ymh								
Ymh x 7C								
7C x Ymh	2.541**	1.801*					1.705*	
Ymh x MH								
MH x Ymh								
Spn x Anz								
Anz x Spn								
MH x Anz								
Anz x MH			1.909*					
Spn x 7C								
7c x Spn	2.734**							
Standard Error	0.98	0.59	0.37	1.86	2.9	3.3	0.13	8.55

*,** Significance at the 0.05 and 0.01 probability levels, respectively, df=54.

Appendix Table 6. Mean squares and coefficient of variance (CV) of eight traits for parents and their reciprocal F1's grown at the Hyslop Experimental Station in 1982-83.

Source	df	Mean Square							
		Heading Date	Anthesis Date	Physiological Maturity	Plant Height	Tiller Number	Kernels/ Spike	100 Kernel Weight	Yield/ Plant
Ymh Anz	3	5673.833**	1617.000**	541.000**	4431.375**	840.844**	755.000**	13.142**	15078.583**
Ymh 7C	3	4484.417**	1457.333**	444.167**	2599.250**		2276.250**	12.115**	133301.833**
Ymh MH	3		20.750*	18.667**	2698.750**		5848.00**	15.106**	3903.000*
Spn Anz	3	4313.708**	1521.750**	454.333**	1780.708**	428.333**	2490.875**	19.817**	14961.000**
MH Anz	3	5966.583**	1483.583**	708.667**	1412.167**		10929.125**	5.085**	15974.167**
Spn 7C	3	4212.417**	1244.583**	370.000**	343.250**		884.542**	20.041**	8753.271**
Error	54	15.489	5.542	2.213	55.472	132.299	147.178	0.291	1170.611
C.V.		2.96	1.69	0.79	7.02	39.44	11.86	10.75	36.36

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