ESTIMATES OF HETEROSIS AND COMBINING ABILITY IN CROSSES AMONG SEVEN HARD RED WINTER WHEAT VARIETIES

By

YOUNG WOUNG LEE

Bachelor of Agriculture

Korea University

Seoul, Korea

1966

Submitted to the Faculty of the Graduate School
of the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 1969

ESTIMATES OF HETEROSIS AND COMBINING ABILITY

IN CROSSES AMONG SEVEN HARD RED

WINTER WHEAT VARIETIES

Thesis Approved:

E. L. Smith
Thesis Adviser

Harry C. Young

J. Q. Lynd

D. D. Durham
Dean of the Graduate School

ACKNOWLEDGEMENTS

The author wishes to express sincere appreciation to his major adviser, Dr. E. L. Smith, for his advice, guidance and inspirational counsel throughout the period of this investigation.

Sincere appreciation is also expressed to Dr. J. Q. Lynd, and to Dr. Harry C. Young, Jr., for serving on the advisory committee and offering constructive criticism on the manuscript.

The author is deeply grateful to Dr. Robert D. Morrison of the Statistics Department for his time, able assistance in conducting the statistical analysis.

To the Agronomy Department the author is especially grateful for the assistantship and to the Oklahoma Crop Improvement Association for funds for the statistical analysis.

Assistance given by the members of Small Grain's Section in planting and harvesting of this experiment is greatly appreciated.

To the author's wife, Won-Sook, for her loving consideration and patience, encouragement during the course of this study, the author is grateful.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Continued)

CHAPTER I

INTRODUCTION

The discovery of cytoplasmic male-sterility and nuclear genes for restoration of pollen fertility in hexaploid wheat made commercial hybrid wheat production economically feasible and resulted in the initiation of a number of hybrid wheat research programs. Heterosis, particularly for yield, is one of the prerequisities for successful utilization of wheat hybrids on a commercial scale. Recent investigations on heterosis in wheat indicate variable results ranging from little or no hybrid vigor in certain crosses to rather substantial amounts in others. The level of heterosis of the best hybrids so far evaluated appears to be of the same order as that found in hybrid sorghum and hybrid corn.

Of particular importance in a hybrid wheat program will be the identification of the parental lines which will produce hybrids that perform better than the currently available conventional varieties for important agronomic and quality characteristics. The conversion of varieties to male-sterile and restorer lines requires considerable time and effort. Thus it is desirable for the wheat breeder to have an estimate of the value of potential parents before conversion to sterile and restorers is initiated. Therefore, a study of combining ability of varieties is useful in classifying potential parents in terms of hybrid performance.

The primary objectives of this study were: (1) to determine the level of heterosis in crosses of representative hard red winter wheat varieties adapted to Oklahoma, and (2) to estimate general and specific combining ability of these varieties for important agronomic characters.

CHAPTER II

REVIEW OF LITERATURE

Heterosis

A comprehensive review of heterosis in wheat has been reported by Briggle (3). He emphasized that since nearly all of the earlier heterosis studies in wheat have been conducted on rather small populations of spaced plants grown in either field or greenhouse, these data are of limited value as a basis for decisions as to the feasibility of commercial hybrid wheats.

Four wheat varieties and two F_1 hybrids were tested by Briggle et al. (4) for important agronomic characters in a hill-plot experiment. They reported the presence of heterosis for yield and other characters in one hybrid but in the other hybrid only kernel weight showed significant heterosis. The hybrid showing heterosis for yield exceeded the high parent in yield per plot by 17.5, 21.4 and 37.7%, respectively at planting rates of 1, 2, and 4 seeds per hill. They found a significant genotype x seeding-rate interaction for grain yield per hill and plant height but not for other traits.

McNeal et al. (24) evaluated F_1 and F_2 generations of three spring wheat crosses under near solid-seeding for several agronomic and quality characteristics. No positive heterosis was observed. The performance of the F_1 and F_2 populations was intermediate between their respective parents for the agronomic characters while quality characteristics approached those of the best parent. They concluded that closely related parents, providing a rather narrow genetic base, may result in little or no heterosis and emphasized the need of genetic diversity in the development of hybrid wheat.

Brown et al. (6) observed heterosis in a study of inter-class crosses among seven hard and soft winter wheat varieties grown in a hill-plot experiment. Hihg-parent and midparent heterosis was observed for certain agronomic and quality characteristics. The mean yield of the F_1 hybrids ranged from 96 to 131% of the high-parent means. The mean yield of all F_1's was 113% of the high-parent means. It was noted that much less heterosis occurred for components of yield than was observed for grain yield. The mean protein content of the hybrids was 97% of the high-parent and 100% of the midparent values indicating that hybrids may exhibit heterosis for grain yield without suffering a significant decrease in percent protein. Their results suggested that heterosis for grain yield may occur in some wheat hybrids while others show little or no heterosis.

In F_1 and F_2 populations of a tall x semi-dwarf cross evaluated under space-planted conditions, Johnson et al. (15) observed higher yields in the F_1 and F_2 than for either parent. The mean yield of the F_1's was 12.9% above that of the high parent. The F_1 mean for kernel weight was significantly greater than that of either parent, and the F_2 mean for this trait approached that of the high parent. Both the F_1 and F_2 means for number of spikes exceeded that of either parent. No heterosis was observed for number of kernels per spike. They reported that high kernel weight, and to some extent, high spike number accounted for high yield of the hybrid.

Under near-normal field testing procedures Livers and Heyne (21) noted that 18 hybrids averaged 20% over the mean value of 7 parents for yield. The best hybrids yielded 33 and 29% more than the best parent in 1964, 1965, respectively. They concluded that certain hard red winter wheat hybrids grown under near solid seeding could express significant heterosis for yield.

Santiago and Patterson (27) evaluated F_1 and F_2 wheat populations for important agronomic characters and examined the suitability of hill-planting techniques for determining heterosis in early stages of hybrid wheat research when seed is limited. Significant high-parent heterosis was observed for grain yield, kernel weight, and number of spikes in both the F_1 and F_2 generations. The mean yield for all F_1's was 124% of the high-parent average in the 1963 test, and 128% in the 1964 test. The F_2 yields were generally lower than those of F_1's but higher than the parents. The mean yield of all F_2's was 12% better than the high-parent mean under hill-planting and only 2% above the high-parent mean at normal seeding rates. They concluded that the degree of heterosis tended to be overestimated to some extent in hill-planted tests.

Gyawali et al. (9) studied heterosis and combining ability of inter-class F_1 hybrids in a space-planted experiment for important agronomic and quality characteristics. They found that the average yield of all F_1's was 24% greater than the high-parent average. Greatest heterosis for grain yield was found in early x late hybrids. Milling and baking quality prediction tests of soft wheat hybrids were generally intermediate to the parents. They concluded that inter-class diversity is not necessary for expression of heterosis.

McIlrath et al. (23) tested F_1 and F_2 generations of a diallel cross involving two adapted and four foreign varieties representing germ plasm from several different geographic regions in a space-planted experiment. Significant high-parent heterosis was observed for yield and weight per 1000 kernels in only one F_1 hybrid. The mean yield of the F_1's ranged from 45 to 141% of the high-parent means. The mean of all F_1's was 80% of the high-parent means. No heterosis was observed for number of tillers. Significant midparent heterosis was observed in certain F_2 hybrids for yield and yield components but no case of high-parent heterosis was found. Kernel weight and number of kernels per spike were of greatest importance in hybrids which exhibited heterosis for yield.

Combining Ability

The modern use of combining ability analysis starts apparently with the development of the concept of general and specific combining ability by Sprague and Tatum (30). They partitioned the genotypic variance into general and specific combining ability portions and defined the term 'general combining ability' as the average performance of a line in hybrid combination, and 'specific combining ability' as the performance of certain combinations which do relatively better or worse than would be expected on the basis of the average performance of the lines involved.

The diallel analysis has been widely used to estimate general and specific combining ability in cross-pollinated crops such as maize (22) and selfpollinated ones such as tobacco (13) where a sufficient number of pollinations can be made with ease. Also it has been used to some extent to investigate the nature of gene action.

Hayman (10, 11), and Jinks (13), and Jinks and Hayman (14) presented further outlines of the diallel analysis. Griffing (8) gave a complete analysis and numberical example of a diallel cross for studies of combining ability using F_1 progeny with and without reciprocals and parental lines. Littlewood et al. (20) recently developed a computer program for analysis of diallel crosses for the 4 methods and 2 models proposed by Griffing (8). Kempthorne and Curnow (18) presented genetic formulae for general and specific combining ability as (1) Variance of general combining ability ($\sigma^2 g$) = $1/2\ \sigma^2 A + 1/4\ \sigma^2 AA + \cdots$ and (2) Variance of specific combining ability ($\sigma^2 s$) = $\sigma^2 D + 1/2\ \sigma^2 AA + \cdots$. They pointed out that general combining ability variance is due primarily to additive genetic variance while specific combining ability variance estimates primarily non-additive genetic variance.

Little or no work has been reported on combining ability x environment interaction in wheat. This kind of information may be very important particularly for specific combining ability estimates as observed by some workers in other crops. Rojas and Sprague (26) found in maize that the specific combining ability variance included not only the non-additive variation due to dominance and epistasis, but also a considerable portion of the genotype x environment interaction. They also found that specific combining ability variance became of relatively greater importance than the general combining ability variance when the lines under test had been subjected to previous testing and selection. Matzinger et al. (22) noted in maize that specific combining ability x environment interactions were significant in a study of diallel crosses. Kambal and Webster (17) reported that general combining ability variance was more important and more stable than specific combining ability in grain sorghum. Beil and Atkins (2) concluded in grain sorghym that data from either several years testing at a single location or several locations in a signle year are of great value for combining ability evaluations.

At the present time information on combining ability in wheat is rather limited. This is due to the difficulty of obtaining sufficient F_1 seed because of the laborious hand pollination procedures.

Estimates of general and specific combining ability effects were obtained by Kronstad and Foote (19) in a diallel study of 10 winter wheat varieties using Griffing's method of analysis. They found that a large part of the total genetic variation for yield and yield components was associated with general combining ability. Significant specific combining ability variances were observed for plant yield and height but not for yield components.

Brown et al. (6) estimated combining ability in a diallel study of 10 F_1 hybrids derived from crosses involving three hard and two soft winter wheat varieties. They found that most of the genetic variation in yield and other agronomic characters was associated with general combining ability.

Gyawali et al. (9) found general combining ability to be the major component of genetic variation for important agronomic and quality characteristics in a study of winter wheat crosses, although specific combining ability variances were significant for all traits studied except flour yield and micro-alkaline water retention capacity. They found that specific combining ability was more important than previously reported (6, 19) and believed this to be due to selection of experimental material.

McIlrath et al. (23) found highly significant general and specific combining ability variance for all characters measured. General combining ability variances, however, were well in excess of specific combining ability variances for all traits, indicating that the genetic variability in the F_1 populations was predominantly due to additive effects of genes. These results along with those reported by other workers (6, 9, 19) leads to the conclusion that additive genetic effects accounts for most of the total genetic variability in winter wheat for important agronomic characters.

CHAPTER III

MATERIALS AND METHODS

Parent Varieties

Seven varieties and pure-line experimental selections of hard red winter wheat, Triticum aestivum ssp. vulgare (Vill., Host) Mackey, adapted to Oklahoma conditions were selected as parents for crossing. The varieties were chosen to represent a range in genetic diversity for major agronomic characteristics. The pedigree and a brief description of the characteristics of the parents are given in Table I. In certain parts of this report the varieties will be referred to by their abbreviation as shown in this table.

Detailed descriptions of Scout, Triumph 64, Agent, Sturdy and Comanche have been published (1, 5, 16, 28, 29). The other two parents are experimental strains and have not been previously described. Stw 657654 was developed at the Oklahoma Agricultural Experiment Station. It is a selection from a 3*Kaw 61//DS28A/Ponca cross and was first tested in the BCF_3 generation in 1965. The selection carries the DS28A gene which confers resistance to race A of the greenbug (Schizaphis gramium Rond.). Recently, a new strain of the greenbug has been found in Oklahoma wheat fields. Stw 657654 is resistant to the original strain (race A) but is susceptible to the new strain (race B) (31). Stw 657654 is similar to Kaw 61 in maturity, height and yield. However, it is not as winterhardy as Kaw 61. Danne 129-16 (C.I. 13876) is one of the experimental wheat strains bequeathed to the Oklahoma Agricultural Experiment Station by the late Joseph E. Danne. It has been in performance tests conducted by the Oklahoma Agricultural Experiment Station wheat breeding project since 1962. It is similar to Triumph in maturity, test weight, winter-hardness and disease and insect resistance. It has slightly shorter straw than Triumph. During the past six years of testing, C.I. 13876 has exceeded Triumph in grain yield by about 15%.

Field Procedure

Crosses among the 7 parents were made in the greenhouse during February and March of 1967 by the approach method (7) of crossing. At least 120 crossed seeds were obtained for each of 21 crosses. A total of 28 entries consisting of the 7 parents and 21 F_1 hybrids were planted in the field in October 1967, at two locations, Stillwater and Altus, Oklahoma. The test was planted in hill plots in a randomized block design with 3 replicates for each location.

Plots consisted of one row containing 5 hills with 30 cm spacing between hills and between rows. Each hill contained 4 seeds. The experiment was bordered by two hill-planted rows of Scout at Stillwater and two hill-planted rows of the variety Tascosa at Altus to provide uniform competitive conditions for all plots. Fall stands were good except for the variety Agent which showed extremly poor seed emergence in most hills. The number of seedlings in each hill varied from three to four plants and no attempts were made to maintain uniform number of plants for each hill since it was expected that tillering would offset effects due to differences in number of plants per hill.

TABLE I

PARENTAGE, ORIGIN AND AGRONOMIC CHARACTERISTICS OF THE PARENTS USED IN A SEVEN-PARENT DIALLEL CROSS

Variety or Selection	Abbreviation	C.I. or Selection No.	Agronomic Characteristics	Origin	Parentage
Scout	Sut	13546	high yield wide adaptation mid-maturity	Nebraska	Nebred, Hope, Turkey, Cheyenne, Ponca
Triumph 64	Tmp 64	13679	high yield wide adaption early maturity	Oklahoma	Triumph, Danne Beardless, Kanred, Blackhull, Florence
Agent	Ag	13523	leaf rust resistant stiff straw mid-late maturity	Oklahoma	Triumph, *Agropyron elongatum*, *Triticum* spp.
3*Kaw//DS28A/Pnc	7654	Stw657654	greenbug resistant (race A) mid-maturity	Oklahoma	Kaw, Dickinson Selection 28A, Ponca
Sturdy	Sdy	13684	semi-dwarf good quality mid-maturity	Texas	Sinvalocho, Wichita, Hope, Cheyenne, Seu Seun 27
Comanche	Cmn	11673	good quality mid-maturity	Kansas	Oro, Tenmarq
Danne 129-16	13876	13876	high yield good quality early maturity	Oklahoma	Triumph, Danne Beardless, Blackhull, Kanred, Florence

The test at Altus was severely damaged by a hail storm in May, 1968 and no data were obtained for this location. Consequently, all data reported in this study are based on the Stillwater test. All F_1 and parent plants were harvested by pulling all the plants in each hill at maturity; the spikes being bagged to prevent seed loss during storage. Only one missing hill was recorded for the Stillwater test.

Characters Evaluated

All observations were recorded on a per hill basis. The characters studied were: (1) heading date, (2) plant height, (3) number of spikes per hill, (4) 200 kernel weight, (5) average number of kernels per spike, and (6) grain yield.

Heading Date

Heading date was used as a measure of the relative maturity of the parents and hybrids, and was recorded as the number of days from April 1 until the first spike of each hill was completely emerged from the boot.

Plant Height

Measurements were taken in centimeters from the soil surface to the tip of the tallest spike of each hill, exclusive of awns.

Number of Spikes per Hill

This character was determined by a direct count of the number of tillers in each hill bearing fertile spikes.

200 Kernel Weight

This was determined by weighing 200 random kernels from each hill and was expressed in grams per 200 kernels.

Average Number of Kernels per Spike

This was calculated by the following formula:

$$\frac{\text{grain yield (in grams)} \div \text{average weight per kernel}}{\text{total number of spikes per hill}}$$

Grain Yield per Hill

Yield determinations consisted of the weight of threshed, cleaned seed from each hill expressed in grams.

Analysis of Variance

An analysis of variance was conducted only on the data from the population grown at Stillwater for the following traits: heading date, plant height, grain yield, and three components of yield. Calculations were made on a per hill basis. Only one missing hill was recorded in the entire experiment and the average value of four remaining hills was used for the value of the missing hill. Error mean squares for the six characters were computed by using the data from the all parents and crosses. There was a possibility that the analysis of variance was biased due to the poor germination and poor yield performance of the Agent parent. Therefore, a second analysis for yield was conducted with this variety removed. However, since the error mean square of this second analysis was not appreciably different (75.089 vs. 76.244), the original analysis was used.

For subsequent comparisons for heterosis and combining ability, an estimated value for the yield of the Agent parent was used. This value was determined by the following procedure. In a performance nursery adjacent to this test, the yield of Agent was 98.1% that of

Scout. Therefore, the value obtained by taking the product of the average yield of Scout in the diallel test x 98.1 was substituted for the value of the Agent parent and used in subsequent comparisons. Since the yield components of the Agent parent were also affected by poor stands the best hill of Agent in each replication was selected and the average for the 3 replication was computed. Yield component values obtained in this manner were used for subsequent comparison of heterosis and combining ability analysis.

Heterosis Analysis

Heterosis was measured for all F_1 populations with respect to both midparent and high-parent values. Since hybrid means were based on only half as many observations as midparent values adjusted LSD values were used to test each hybrid-midparent contrast. The variance of hybrid-midparent may be defined as (6) EMS ÷ (4) rn, where EMS is experimental error mean square and rn represents the number of observations per treatment mean (25). Thus, in the present case,

$$LSD = t(\alpha, t - 1) \times \sqrt{\frac{6 \text{ EMS}}{4 \text{ rn}}}.$$

Duncan's new multiple range test was used to determine the significant differences among means of the F_1 and parent populations.

Combining Ability Analysis

Estimates of general and specific combining ability effects were obtained for the six agronomic characters by utilizing Griffing's (8) method 4, model 1 diallel cross analysis. Under this model, one set of F_1's is included in a matrix, but neither the parents nor the reciprocal F_1's are used. The genotypes and blocks were regarded as fixed effects.

This analysis provides for partitioning the sum of squares of genotype (crosses) into general and specific combining ability terms associated with p-1 and p(p-3)/2 degrees of freedom respectively, where p represents the number of parents involved in the diallel cross.

General and specific combining ability effects were computed on the Oklahoma State University Computing Center IBM 7040 by utilizing a program developed at the University of Illinois (20).

CHAPTER IV

RESULTS

Heterosis

Growing conditions throughout the extent of this experiment were generally favorable. Rainfall in the spring of the year was above normal and resulted in vigorous growth and taller than normal plants. Average grain yield for all entries in the test was 18.72 grams per hill which is equivalent to 30 bushels per acre. There were no problems with diseases or insects and no winterkilling or lodging occurred. However severe leaf injury was observed in three hybrids, Sut/7654, Sut/13876, and Ag/13876, apparently due to hybrid necrosis as described by Hermsen (12). This hybrid necrosis was believed to have an adverse effect on yield and yield components of these three hybrids as indicated by the negative heterosis that was observed for yield and yield components.

Mean squares from the analysis of variance of six agronomic characters on 21 F_1 hybrids and 7 parents are presented in Table II. Genotype mean squares for heading date, plant height, number of spikes, 200 kernel weight, and grain yield were highly significant and significant differences among genotypes were observed for average number of kernels per spike. In these, and in subsequent analyses, the standard notation for significance is used; * = significance at the 5% level of probability significant, and ** = significance at the 1% level (highly significant).

Parent and hybrid means and hybrid-midparent deviations for the six traits, along with appropriate tests for significance are given in Tables III - VIII. Means of all F_1's for the six characters measured are expressed as the percentage of their respective high-parent and midparent means in Table IX.

In general, the hybrids were earlier than the late parent but slightly later than the earlier parent. There was one notable exception. The Sut/7654 hybrid was nearly 2 days later than the later parent. No hybrid headed significantly earlier than the early parent. However, significant midparent heterosis for earliness was observed in 7 hybrids (Table IX). Four hybrids, Ag/13876, 7654/Cmn, Sut/7654, and Ag/7654 headed significantly later than their respective earlier parents and Sut/7654 was significantly later than its midparent (Table III).

The mean value of the hybrids for plant height ranged from values 16 cm taller than the shortest parent, Sturdy, to values 5 cm taller than the tallest parent, Comanche. Most of the hybrids were within 10 cm of their midparent values for this trait (Table IV). Nine of the 21 hybrids exceeded their high parents in mean plant height, although only one hybrid, Ag/7654, was significantly taller than its taller parent. Significant positive midparent heterosis was observed in 6 hybrids for plant height (Table IX).

None of the hybrids exhibited significant positive heterosis for number of spikes/hill. The mean of all hybrids for this character was 93 and 98% of the high-parent and midparent means, respectively. The greatest number of spikes occurred in the Sut/Ag hybrid which also showed the largest high-parent heterosis for yield. The lowest number of spikes was observed in the Sut/13876 hybrid which was one of the 3 hybrids in which necrosis occurred. Three hybrids, Sut/13876, Tmp 64/Sdy, and Tmp 64/Cmn, were significantly lower in number of spikes than their respective high parents. The Tmp 64/Sdy hybrid was also significantly lower than its midparent (Tables V and IX).

Fourteen of the 21 F_1 hybrids exceeded their respective high parents in 200 kernel weight, although none of the differences was statistically significant (Table IX). The heaviest kernel weight was found in the Ag/Sdy hybrid which also had the highest yield (Table VI). The lowest kernel weight occurred in the Ag/13876 hybrid which also showed hybrid necrosis. Significant positive midparent heterosis for 200 kernel weight occurred in only 5 of the 21 F_1 hybrids, three of which also showed significant positive midparent heterosis for yield. The average for all hybrids for this trait was 103 and 106% of the high-parent and midparent values, respectively (Table IX). No hybrid was significantly lower than its high-parent or midparent for this character.

For number of kernels per spike, 17 of 21 hybrids were higher than their respective midparents and 13 of 21 hybrids were higher than their respective high parents. However, only three hybrids, Tmp 64/Sdy, Ag/Sdy, and Ag/Cmn, showed significant midparent heterosis. Most of the hybrids that exceeded their high parent in yield also exceed their high parent for this trait. The least number of kernels per spike was found in the Sut/7654 hybrid and the Ag/13876 hybrid, both of which also exhibited necrotic symptoms. The range for average number of kernels per spike of the 21 hybrids was from 85 to 114% of the high-parent and 90 to 122% of the midparent. The mean for all hybrids was 103% of the average high-parent value and 108% of the midparent value

(Table IX). No hybrid was significantly lower in number of kernels per spike than its respective high-parent or midparent (Table VII).

Estimates of heterosis for yield were somewhat higher than for the individual components of yield. Thirteen of 21 hybrids were higher than their respective high parents, although none of these differences was statistically significant (Table IX). The largest high-parent heterosis was observed in the Sut/Ag hybrid which was 46% better than its high parent, although this difference was not significant. However, this hybrid was significantly different from its midparent. The highest yielding entry in the test was the Ag/Sdy hybrid which averaged 23.6 grams/hill. This hybrid was 17% better than its high-parent and 33% better than its midparent value. However, the hybrid was significantly different from the midparent only. Eighteen of 21 hybrids were higher than their respective midparents for grain yield. However, in only four of the hybrids, Sut/Ag, Sut/Sdy, Ag/Sdy, and Cmn/13876, was this difference statistically significant. Three of these 4 hybrids also showed significant midparent heterosis for 200 kernel weight. No hybrid was significantly lower in grain yield than its high-parent or midparent. The lowest yielding hybrids were Sut/7654, Sut/13876, and Ag/13876 which were also beset with necrosis (Table VIII). The range for grain yield of the 21 hybrids was 72 to 146% of the high-parent and 81 to 147% of the midparent values. The mean for all F_1's was 105% of the high-parent mean and 114% of the midparent mean (Table IX).

TABLE II

MEAN SQUARES FROM AN ANALYSIS OF VARIANCE OF A DIALLEL CROSS INCLUDING PARENT AND F_1 POPULATIONS

Source of Variation	d.f.	Heading Date	Plant Height	Number of Spikes/Hill	200 Kernel Weight	Average Number of Kernels/Spike	Grain Yield/Hill
Total	419	-	-	-	-	-	-
Replicate	2	8.867	654.073**	695.450**	3.133	40.807	101.138
Genotype	27	288.993**	1105.164**	150.538**	4.556**	98.936*	216.224**
Experimental Error	54	12.667	126.837	45.339	1.175	45.258	75.089
Sampling Error	336	4.587	22.846	34.776	0.394	11.957	30.510

TABLE III

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND HYBRID-MIDPARENT DEVIATIONS FOR HEADING DATE

F_1's and Parents	Rank (earliest to latest)	Heading Date 1/		Hybrid-Midparent Deviation
Tmp 64/Sdy	1	24.3	a	-1.45
Tmp 64	2	25.3	a	-
Sdy	3	26.2	a	-
Tmp 64/7654	4	27.1	a	-0.5
Ag/Sdy	5	27.5	a	-7.15**
Tmp 64/13876	6	27.6	a	-1.0
7654/13876	7	28.1	ab	-1.0
Sut/Sdy	8	28.2	ab	-1.45
Sut/Tmp 64	9	28.3	ab	-0.9
Sdy/13876	10	28.3	ab	1.05
13876	11	28.3	ab	-
Sdy/Cmn	12	28.7	abc	-3.65**
7654/Sdy	13	28.7	abc	1.65
7654	14	28.9	abc	-
Tmp 64/Cmn	15	30.1	abc	-1.8
Tmp 64/Ag	16	30.1	abc	-4.1**
Sut/13876	17	30.3	abc	-0.4
Cmn/13876	18	31.0	bcd	-2.4*
Ag/13876	19	31.6	cd	-4.1**
Sut	20	33.1	de	-
7654/Cmn	21	33.5	de	-0.7
Sut/7654	22	34.8	ef	3.3**
Sut/Ag	23	35.1	ef	-3.0*
Sut/Cmn	24	35.5	ef	-0.3
Ag/7654	25	35.9	efg	-0.6
Ag/Cmn	26	36.7	fg	-4.1**
Cmn	27	38.5	g	-
Ag	28	43.1	h	-

1/ Number of days after April 1st.
*---Exceeds LSD .05 = 2.2.
**---Exceeds LSD .01 = 3.0.

Note: Those means not followed by the same letter are significantly different at p = .05; means followed by the same letter are not significantly different at p = .05.

TABLE IV

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND HYBRID-MIDPARENT DEVIATIONS FOR PLANT HEIGHT

F_1's and Parents	Rank (shortest to tallest)	Plant Height (cm)		Hybrid-Midparent Deviation
Sdy	1	83.3	a	-
Tmp 64/13876	2	99.3	b	-3.6
Tmp 64/Sdy	3	99.5	bc	2.85
Sdy/13876	4	99.6	bcd	7.05
Ag	5	100.6	bcde	-
13876	6	101.8	bcdef	-
Sut/Sdy	7	102.4	bcdef	3.5
7654/Sdy	8	102.8	bcdef	7.4*
Ag/Sdy	9	103.5	bcdefg	11.55**
Tmp 64	10	104.0	bcdefg	-
Sut/Tmp 64	11	104.5	bcdefg	-4.75
Sut/13876	12	104.7	bcdefgh	-3.45
Ag/13876	13	106.1	bcdefghi	4.9
Tmp 64/Cmn	14	107.4	cdefghij	-2.75
7654	15	107.5	cdefghij	-
7654/13876	16	108.7	cdefghij	4.05
Tmp 64/Ag	17	109.2	defghij	6.9
Sdy/Cmn	18	109.8	efghij	10.0**
Tmp 64/7654	19	110.7	fghij	4.95
Cmn/13876	20	113.2	ghijk	4.05
7654/Cmn	21	113.3	ghijk	1.2
Sut/7654	22	114.2	hijk	3.2
Sut	23	114.5	ijk	-
Cmn	24	116.3	jk	-
Sut/Cmn	25	120.1	k	4.7
Ag/7654	26	120.8	k	16.75**
Sut/Ag	27	121.4	k	13.85**
Ag/Cmn	28	121.4	k	12.95**

*---Exceeds LSD .05 = 7.1.
**---Exceeds LSD .01 = 9.6.

Note: Those means not followed by the same letter are significantly different at P = .05; means followed by the same letter are not significantly different at P = .05.

TABLE V

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND HYBRID-MIDPARENT DEVIATIONS FOR NUMBER OF SPIKES PER HILL

F_1's and Parents	Rank (highest to lowest)	Number of Spikes/Hill		Hybrid-Midparent Deviation
Tmp 64	1	31.0	a	-
Sut/Ag	2	29.9	ab	2.7
Sut/Tmp 64	3	29.6	ab	0.4
Tmp 64/7654	4	28.9	abcd	-1.8
7654	5	28.4	abcde	-
Ag/Cmn	6	28.3	abcde	2.8
Ag/7654	7	28.3	abcde	0.7
Sut/Sdy	8	27.9	abcde	0.8
Ag/13876	9	27.7	abcde	3.0
Sut	10	27.5	abcde	-
Ag	11	26.9	abcdef	-
Tmp 64/Ag	12	26.9	abcdef	-2.1
Sut/7654	13	26.7	abcdef	-1.3
Sdy	14	26.7	abcdef	-
Ag/Sdy	15	26.3	abcdef	-0.5
Tmp 64/13876	16	26.1	abcdef	-0.7
7654/13876	17	25.9	abcdef	0.5
Cmn/13876	18	25.7	abcdef	2.4
Sdy/Cmn	19	25.7	abcdef	0.3
7654/Sdy	20	25.1	abcdef	-2.5
Tmp 64/Cmn	21	24.3	bcdef	-3.3
Tmp 64/Sdy	22	24.3	bcdef	-4.6*
Cmn	23	24.1	bcdef	-
Sut/Cmn	24	23.8	cdef	-2.0
Ag/13876	25	23.4	def	-1.3
Sdy/13876	26	23.1	def	-1.5
13876	27	22.5	ef	-
Sut/13876	28	21.3	f	-3.7

*---Exceeds LSD .05 = 4.3.
**---Exceeds LSD .01 = 5.8.

Note: Those means not followed by the same letter are significantly different at P = .05; means followed by the same letter are not significantly different at P = .05.

TABLE VI

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND HYBRID-MIDPARENT DEVIATIONS FOR 200 KERNEL WEIGHT

F_1's and Parents	Rank (highest to lowest)	200 Kernel Weight		Hybrid-Midparent Deviation
Tmp 64/Cmn	1	6.37	a	1.06**
Ag/Sdy	2	6.33	a	0.74*
Sut/Sdy	3	6.32	ab	0.68*
Tmp 64/Sdy	4	6.29	abc	0.61
Sut/Tmp 64	5	6.24	abc	0.57
Tmp 64/7654	6	6.21	abc	0.39
Cmn/13876	7	6.11	abcd	0.99**
Sdy/Cmn	8	6.09	abcd	0.84*
Sut/Ag	9	6.09	abcd	0.51
7654/13876	10	5.97	abcd	0.30
7654	11	5.93	abcd	-
Sut/Cmn	12	5.91	abcd	0.66
7654/Sdy	13	5.88	abcde	0.08
Tmp 64/Ag	14	5.87	abcde	0.25
Tmp 64/13876	15	5.86	abcde	0.30
Tmp 64	16	5.71	abcdef	-
Sdy/13876	17	5.69	abcdef	0.16
Sdy	18	5.65	abcdef	-
Sut	19	5.64	abcdef	-
Sut/13876	20	5.53	abcdef	0.00
Ag	21	5.53	abcdef	-
Ag/7654	22	5.50	abcdef	-0.23
13876	23	5.41	abcdef	-
Sut/7654	24	5.36	bcdef	-0.43
7654/Cmn	25	5.32	cdef	-0.08
Ag/Cmn	26	5.24	def	0.04
Ag/13876	27	4.93	ef	-0.54
Cmn	28	4.86	f	-

*---Exceeds LSD .05 = .68.
**---Exceeds LSD .01 = .92.

Note: Those means not followed by the same letter are significantly different at P = .05; means followed by the same letter are not significantly different at P = .05.

TABLE VII

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID-MIDPARENT FOR AVERAGE NUMBER OF KERNELS PER SPIKE

F_1's and Parents	Rank (highest to lowest)	Average Number of Kernels/Spike		Hybrid-Midparent Deviation
Ag/Sdy	1	28.4	a	4.9*
Tmp 64/Sdy	2	28.1	a	4.2*
7654/Sdy	3	27.9	a	2.9
Sdy/13876	4	27.5	a	2.0
7654/13876	5	27.4	a	3.4
Sdy/Cmn	6	26.8	abc	2.0
Ag/Cmn	7	26.8	abc	4.9*
Sut/Sdy	8	26.7	abc	3.0
Sdy	9	26.4	abcd	-
Cmn/13876	10	25.8	abcde	1.9
Ag/7654	11	25.5	abcde	3.5
Tmp 64/7654	12	24.7	abcde	2.2
13876	13	24.5	abcde	-
Tmp 64/Ag	14	24.3	abcde	3.3
Tmp 64/13876	15	24.3	abcde	1.3
Sut/13876	16	24.2	abcde	1.5
Tmp 64/Cmn	17	23.7	abcde	1.4
7654	18	23.5	abcde	-
Sut/Ag	19	23.4	abcde	2.7
Cmn	20	23.2	abcde	-
7654/Cmn	21	22.8	abcde	-0.6
Sut/Cmn	22	22.8	abcde	0.7
Ag/13876	23	21.5	bcde	-1.0
Tmp 64	24	21.4	bcde	-
Sut	25	20.9	cde	-
Ag	26	20.5	de	-
Sut/7654	27	20.0	e	-2.2
Sut/Tmp 64	28	19.9	e	-1.3

*---Exceeds LSD .05 = 4.2.
**---Exceeds LSD .01 = 5.7.

Note: Those means not followed by the same letter are significantly different at P = .05; those means followed by the same letter are not significantly different at P = .05.

TABLE VIII

PARENTAL AND F_1 MEANS, MULTIPLE RANGE COMPARISONS, AND DEVIATIONS OF HYBRID-MIDPARENT FOR GRAIN YIELD PER HILL

F_1's and Parents	Rank (highest to lowest)	Grain Yield/Hill (gms)		Hybrid-Midparent Deviation
Ag/Sdy	1	23.6	a	5.8*
Sut/Sdy	2	23.4	ab	5.5*
Sut/Ag	3	23.0	abc	7.4**
Tmp 64/7654	4	22.3	abcd	2.8
7654/13876	5	21.2	abcde	3.7
Tmp 64/Sdy	6	21.1	abcde	1.6
Sdy/Cmn	7	21.0	abcde	4.0
7654/Sdy	8	20.5	abcdef	0.3
7654	9	20.2	abcdef	-
Sdy	10	20.2	abcdef	-
Cmn/13876	11	20.0	abcdef	5.7*
Ag/7654	12	20.0	abcdef	2.2
Ag/Cmn	13	19.9	abcdef	5.3
Tmp 64/Ag	14	19.7	abcdef	2.6
Tmp 64/13876	15	19.0	abcdef	2.2
Tmp 64/Cmn	16	18.9	abcdef	1.7
Tmp 64	17	18.8	abcdef	-
Sdy/13876	18	18.5	abcdef	1.0
Sut/Tmp 64	19	18.1	abcdef	0.8
7654/Cmn	20	17.4	abcdef	0.4
Sut	21	15.7	bcdef	-
Sut/Cmn	22	15.5	cdef	0.7
Ag	23	15.4	cdef	-
13876	24	14.8	def	-
Sut/7654	25	14.7	def	-3.3
Sut/13876	26	14.3	ef	-1.0
Cmn	27	13.8	ef	-
Ag/13876	28	13.2	f	-1.9

*---Exceeds LSD .05 = 5.4.
**---Exceeds LSD .01 = 7.3.

Note: Those means not followed by the same letter are significantly different at P = .05; those means followed by the same letter are not significantly different at P = .05.

TABLE IX

PERFORMANCE OF 21 F_1 HYBRIDS EXPRESSED AS PERCENT OF HIGH-PARENT AND MIDPARENT MEANS FOR SIX CHARACTERS

Hybrid	Heading Date		Plant Height		Number of Spikes/Hill		200 Kernel Weight		Average No. of Kernels/Spike		Yield/Hill	
	%HP 1/	%MP	%HP 2/	%MP	%HP 3/	%MP 4/	%HP	%MP	%HP	%MP	%HP	%MP
Sut/Tmp 64	83	94	91	96	93	99	109	110	93	94	96	105
Sut/Ag	83	94*	106	113*	112	114	109	110	112	113	146	147*
Sut/7654	105	112	100	103	93	95	90	92	85	90	72	81
Sut/Sdy	85	97	89	104	102	103	107	113*	101	113	116	130*
Sut/Cmn	92	99	103	104	87	92	105	112	98	103	99	103
Sut/13876	92	99	91	97	78*	85	98	100	99	107	91	94
Tmp 64/Ag	70	88**	105	107	87	93	104	105	114	116	105	115
Tmp 64/7654	91	98	103	105	93	97	105	107	105	110	110	114
Tmp 64/Sdy	93	94	93	103	78*	84*	107	112	106	117*	105	108
Tmp 64/Cmn	72	94	92	98	78*	88	112	121**	102	104	101	116
Tmp 64/13876	98	103	96	97	84	97	104	106	99	106	101	113
Ag/7654	83	98	112*	116**	100	102	93	97	109	116	99	112
Ag/Sdy	64	79**	103	113*	98	98	113	114*	108	121*	117	133*
Ag/Cmn	85	90**	104	112**	105	111	95	100	116	122*	129	136
Ag/13876	73	89**	104	105	87	95	89	90	88	96	86	87
7654/Sdy	99	106	96	108*	88	91	100	103	106	112	102	102
7654/Cmn	87	98	97	106	99	105	90	98	97	99	86	102
7654/13876	94	97	101	104	91	102	102	106	112	114	105	121
Sdy/Cmn	75	89**	94	110**	100	101	109	116*	102	108	104	124
Sdy/13876	100	104	98	108	87	94	102	104	104	111	92	106
Cmn/13876	81	93*	97	104	107	110	113	118*	100	102	135	140*
Mean	86	96	99	105	93	98	103	106	103	108	105	114

Significantly (*) or highly significantly (**) different than its high parent or its midparent based on LSD.

1/ HP = later parent. 2/ HP = taller parent.

3/ %HP = Percent of high parent. 4/ %MP = Percent of midparent.

Combining Ability

Since differences among hybrids were highly significant for 6 characters (Table X), Griffing's diallel analysis method 4, model 1 which eliminates parents and utilizes only one set of F_1's was conducted for all characters measured.

Combining ability mean squares and the relative magnitude of general to specific combining ability for the six traits are shown in Table XI. Highly significant general combining ability variances were observed for all traits. Specific combining ability variances were also highly significant for all traits except number of spikes/hill which was significant at the 5% level of probability. The genetic variability for heading date and plant height was largely accounted for by general combing ability. The ratios of general to specific combining ability variance for these traits were 14:1 and 17:1, respectively. The components of yield; number of spikes, kernel weight, and kernels/spike had larger variances for general combining ability than for specific combining ability. The ratio was 2:1, 2:1 and 5:1, respectively. The ratio of general to specific combining ability variance for yield was nearly 1:1 which suggests that non-additive genetic effects were as important as additive effects for this trait.

The diallel analysis for combining ability provides an estimate of general combining ability effects of parents and specific combining ability effects of individual crosses. The general combining ability effects of individual parental lines along with the corresponding standard errors for each character are presented in Table XII. For heading date, Triumph 64 and Sturdy had the greatest negative general combining ability effects (earliness) which was desirable in this case. The

Sturdy, Triumph 64, and C.I. 13876 parents had the greatest significant negative general combing ability effects for plant height. High negative effects are desirable in this case since it indicates shortness of straw. Sturdy had the highest positive general combining ability effect for yield while C.I. 13876 and Scout had the greatest negative general combining ability effects for this trait. Agent had the highest general effect for number of spikes per hill while C.I. 13876 had the largest negative effect for this trait. Triumph 64 and Sturdy had significantly greater positive general combining ability effects for kernel weight than the other five parental lines. Agent and C.I. 13876 had the greatest negative effects for this trait. Sturdy had, by far, the greatest positive effect for kernels/spike while Scout had the greatest negative effect for this trait. Considering general combining ability effects of all traits Sturdy and Triumph 64 appeared to be the best parents in this set.

Estimates of specific combining ability effects associated with individual crosses for each of the six characters are presented in Table XIII. Shown also in this table are standard errors for comparison of effects of two crosses having one parent in common. Significant negative (earliness) specific combining ability effects were observed in six crosses for heading date. Three of these crosses involved the semi-dwarf parent, Sturdy. The greatest negative (shortness) effect for plant height was found in the 7654/Cmn hybrid which is interesting since both parents had high positive general effects for this trait. The Ag/13876 and Ag/Sdy hybrids also had high negative specific effects for plant height. Five of the 21 hybrids exhibited significant positive specific combining ability effects for yield. The greatest positive effect for yield occurred in the Sut/Ag hybrid which also had positive effect for the three yield components. Other hybrids with high positive effects for yield were Sut/Sdy, 7654/13876, and Cmn/13876. The largest negative effect was found in the Ag/13876 and Sut/7654 hybrids which also had the greatest negative effects for kernel weight and kernels/spike. This may be explained in part by the fact that these two hybrids were affected by hybrid necrosis.

TABLE X

MEAN SQUARES FROM ANALYSIS OF VARIANCE OF DATA FROM F_1 HYBRIDS

Source of Variation	d.f.	Heading Date	Plant Height	Number of Spikes/Hill	200 Kernel Weight	Average Number of Kernels/Spike	Yield/Hill
Total	314	-	-	-	-	-	-
Replicates	2	22.193**	476.953**	457.069**	2.853**	33.539	139.063**
Hybrids	20	183.943**	854.398**	79.636**	2.559**	97.357**	131.133**
Reps x Hybrids	40	11.341**	112.515**	40.420	1.360**	50.913**	86.930**
Sampling Error	252	4.611	24.795	36.018	0.438	11.513	33.365

TABLE XI

OBSERVED MEAN SQUARES FOR GENERAL COMBINING ABILITY, SPECIFIC COMBINING ABILITY AND ERROR FOR SIX CHARACTERS AND THE RATIO OF GENERAL TO SPECIFIC COMBINING ABILITY

Character	G.C.A. 1/	S.C.A. 2/	Error	G.C.A./S.C.A.
Heading Date	35.177**	2.444**	0.307	14:1
Plant Height	166.296**	10.038**	1.653	17:1
Number of Spikes/Hill	8.128**	4.093*	2.401	2:1
200 Kernel Weight	0.282**	0.122**	0.029	2:1
Average Number of Kernels/Spike	14.419**	3.096**	0.768	5:1
Yield/Hill	10.743**	7.881**	2.224	1:1

The degrees of freedom associated with G.C.A., S.C.A., and error are 6, 14, and 252, respectively.
1/ G.C.A. = General Combining Ability.
2/ S.C.A. = Specific Combining Ability.

TABLE XII

ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR SIX CHARACTERS

Character	Sut	Tmp 64	Ag	7654	Sdy	Cmn	13876	S.E. $(\hat{g}_i-\hat{g}_j)$
Heading Date	1.70	-3.36	2.82	1.12	-3.37	2.40	-1.31	0.35
Plant Height	2.64	-5.32	5.64	3.26	-7.92	6.22	-4.52	0.78
No. Spikes/Hill	0.46	0.05	1.41	1.10	-0.93	-0.28	-2.27	0.96
200 Kernel Weight	0.05	0.34	-0.24	-0.19	-0.29	-0.03	-0.21	0.10
Avg. No. Kernels/Spike	-2.45	0.85	0.11	-0.20	3.23	-0.13	0.29	0.56
Yield/Hill	-1.36	0.66	0.71	0.03	2.47	-0.60	-1.91	0.90

TABLE XIII

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR SIX CHARACTERS

Hybrid	Heading Date	Plant Height	Number of Spikes/Hill	200 Kernel Weight	Avg. No. Kernels/Spike	Yield/Hill
Sut/Tmp 64	-1.45	-1.81	1.74	0.00	-1.68	-0.53
Sut/Ag	0.57	4.02	2.83	0.41	0.82	4.33
Sut/7654	1.41	-0.70	-1.19	-0.39	-2.18	-3.33
Sut/Sdy	-0.70	-1.32	2.17	0.11	1.06	3.04
Sut/Cmn	0.79	2.24	-2.53	0.02	0.49	-1.81
Sut/13876	-0.62	-2.42	-3.02	-0.16	1.51	-1.70
Tmp 64/Ag	0.10	-0.12	-1.14	-0.08	0.20	-0.97
Tmp 64/7654	-1.21	3.66	1.17	0.20	0.86	2.35
Tmp 64/Sdy	0.42	0.74	-1.40	-0.19	0.81	-1.34
Tmp 64/Cmn	0.44	-2.50	-2.04	0.19	-0.19	-0.42
Tmp 64/13876	1.70	0.04	1.67	-0.12	0.01	0.91
Ag/7654	1.35	2.90	-0.41	0.07	0.67	-0.08
Ag/Sdy	-2.49	-3.22	-0.38	0.43	0.17	1.10
Ag/Cmn	0.94	0.54	0.98	-0.35	1.91	0.52
Ag/13876	-0.43	-4.12	-1.89	-0.48	-3.78	-4.90
7654/Sdy	1.34	-1.64	-1.27	-0.07	0.01	-1.32
7654/Cmn	-0.57	-5.18	0.76	-0.32	-1.76	-1.37
7654/13876	-2.32	0.96	0.94	0.52	2.41	3.75
Sdy/Cmn	-0.94	2.40	0.71	-0.03	-1.17	-0.17
Sdy/13876	2.37	3.04	0.17	-0.24	-0.08	-1.31
Cmn/13876	0.66	2.50	2.13	0.48	0.73	3.25
S.E. $(\hat{S}_{ij}-\hat{S}_{ik})$	0.70	1.56	1.93	0.21	1.13	1.80

CHAPTER V

DISCUSSION

Heterosis

In commercial hybrid wheat production one of the most important considerations is the level of heterosis that must be obtained in order to make hybrid seed production economically feasible. Heterosis, particularly for yield, is the primary consideration in any effort to manipulate parents for F_1 hybrid usefulness. However, cases where the F_1 hybrid maintains the desired level of productivity in yield while other important characters such as flour quality, earliness, insect and disease resistance are incorporated, may be useful.

One of the primary objectives of this experiment was to evaluate hybrid performance in relation to parental performance for six agronomic characters of winter wheat. Although four F_1 hybrids showed significant midparent heterosis for yield none exhibited significant high-parent heterosis for this character. Some combinations resulted in negative heterosis for yield and yield components possibly due to hybrid necrosis. The average grain yield of all F_1's was only 5% greater than the mean of the high parents (Table IX). Other recent heterosis studies conducted under space-planted, hill-planted or nearly normal seeding rate indicate that heterosis of about 25% over the high parent is common (Table XIV). However much less heterosis was observed in this experiment. With regard to heterosis for yield, the results of this experiment are somewhat similar to those of McIlrath (23). In comparison with other studies, the rather low degree of heterosis obtained in this study, and also in McIlrath's (23) study, conducted in Oklahoma may be due to: (1) choice of parent, (2) different techniques, or perhaps environmental differences. Additional studies on performance of hard red winter wheat hybrids under Oklahoma conditions are needed.

In the utilization of hybrid vigor in commercial hybrid wheats, only that vigor in excess of the better parent or best conventional variety is of practical significance. Under the conditions of this study it appears that the amount of heterosis is not great enough to encourage a hybrid breeding program with the particular parental combinations studied. However, these parents were not selected on the basis of combining ability and further studies utilizing parents previously selected for high general combining ability may result in higher levels of heterosis.

Although two of 21 hybrids produced yields that were 46% and 35% above the high parent, they were not significantly different from their respective high parents in this trait. This could be due to the high experimental error observed for yield. Such variability was believed to result from high interaction between hills within plots.

High experimental error may be due in part to an unequal number of plants per plot. In this experiment, four seeds were planted in each of the five hills in each plot and the number of plants per hill after germination ranged from 3 to 4. It was assumed that the performance of the hills having three plants was comparable with those of four plants since tillering should offset the reduction in number of plants. The observed high coefficient of variability (47%) for yield suggests that the assumption that tillering would take care of the varying number of plants per hill failed. It also suggests that more accuracy of measuring the expression of heterosis can be gained by designing hill experiments such that each hill has an equal number of plants. In addition, more replications should be considered as a means of increasing precision.

In this experiment the best hybrid, Ag/Sdy, yielded 23.6 gram/hill, which was 17% better than the highest yielding variety in the test. The wheat grower will be concerned with the amount of heterosis in relation to the best commercial varieties already available. The best hybrid in this study was 39% better than the mean of all parents and 17% better than the best yielding parent, Sturdy. If it is assumed that heterosis of about 25% over the best parent is the expected level of heterosis that is necessary for successful commercial hybrid wheat production then the level of heterosis exhibited by the best hybrid in this test is not sufficient. This would be particularly true if the degree of heterosis was overestimated to some extent from hill-plot data as was suggested by Santiago and Patterson (24). However, other hybrid combinations or tests conducted in other years or at other locations in the state might result in different degrees of heterosis. Also different field designs and techniques would no doubt influence estimates of heterosis. In conclusion, the results from this study indicate that although the level of heterosis for yield was rather low, certain parents and hybrid combinations are worthy of further examination for hybrid wheat programs.

TABLE XIV

HETEROSIS IN WHEAT: RESULTS OBTAINED BY DIFFERENT WORKERS

Source of Data	Number of Hybrids	Yield (% HP) Range	Mean
Lee (Present Study)	21	72 - 146	105
Briggle et al. (5)	2	119 - 137	128
Brown et al. (6)	16	96 - 131	113
McIlrath et al. (23)	15	45 - 141	80
Santiago and Patterson (27)	21	68 - 171	124
Gyawali et al. (9)	21	86 - 176	124

% HP = Percent of High Parent.

Combining Ability

The results obtained from the combining ability study suggest that a large part of the total genetic variability for heading date, plant height and three components of yield was due to additive gene action. The present results are therefore in good agreement with those of Brown et al. (6), Kronstad and Foote (19), Gyawali et al. (9) and McIlrath et al. (23), who also found that the predominate type of gene action governing these characters was additive.

It is interesting, however, to note that a much smaller general to specific combining ability ratio (nearly 1:1) was observed for yield. This indicates that specific combining ability portion of the genotypic variance was equally as important for this trait as general combining ability. This relatively high proportion of specific combining ability is due to dominance and epistatic gene effects. Specific combining ability may also be associated with geneotype x environment interaction as has been reported by several workers in corn (22, 26). This result, however, may be expected since all of the parental lines have been highly selected on the basis of their performance per se and are commonly used as parents in variety improvement programs throughout the hard red winter wheat growing region of the United States.

The pattern of general and specific combining ability variances for yield and yield components found in this study is in agreement with the results presented by McIlrath et al. (23) and by Gyawali et al. (9) except for kernel weight. No specific combining ability was detected for this trait by Gyawali et al. (Table XV). The results obtained in this study for general combining ability were generally consistant with those of other workers. Less agreement was noted for the results on specific combining ability for yield and yield components. Brown et al. (6) did not detect significant variances due to specific combining ability while Kronstad and Foote (19) found significant variances for specific combining ability for yield only. The differences might be due to the selection of experimental material or sampling variation.

On the basis of estimates of general combining ability effects for earliness, height, yield and average number of kernels per spike Sturdy was the best parent among those of the set studied. Agent had the second largest positive general combining ability effect for yield. Therefore, a cross between Agent and Sturdy, both of which had high individual general combining ability effects for yield would appear to be most promising in producing high yielding progeny. Furthermore, it is interesting to note that each of them showed large individual general combining ability effects for both plant height and heading date. Their hybrid also showed significant negative specific combining ability effects for both characters (Table XIII).

In the study reported, observed mean squares for specific combining ability for all characters were highly significant. These results indicated that non-additive genetic variance could play an important role for yield, yield components, height, and heading date for particular parental combinations. However, the level of heterosis observed was rather low for all characters indicating that non-additive gene effects were apparently not too important. The fact that only five of the 21 possible hybrids exhibited significant specific combining ability effects for yield even though the specific combining ability variance observed for this character was highly significant indicates that the importance of non-additive effects may have even overestimated.

TABLE XV

SIGNIFICANT DIFFERENCES DUE TO GENERAL AND SPECIFIC COMBINING ABILITY VARIANCES FOR YIELD AND YIELD COMPONENTS OBTAINED BY VARIOUS AUTHORS

Source of Data	Yield	Kernel Weight	Kernel Number	Spike Number
Lee (Present Study)				
G.C.A. 1/	**	**	**	**
S.C.A. 2/	**	**	**	**
McIlrath et al. (23)				
G.C.A.	**	**	**	**
S.C.A.	**	**	**	**
Kronstad and Foote (19)				
G.C.A.	**	ns	**	**
S.C.A.	**	ns	ns	ns
Brown et al. (6)				
G.C.A.	**	**	--	**
S.C.A.	ns	ns	--	ns
Gyawali et al. (9)				
G.C.A.	**	**	--	**
S.C.A.	**	ns	--	**

** = $p < .01$; ns = nonsignificant; -- = not reported.
1/ G.C.A. = General Combining Ability.
2/ S.C.A. = Specific Combining Ability.

CHAPTER VI

SUMMARY

Heterosis and combining ability for heading date, plant height, yield and certain yield components were examined in the F_1 generation of a diallel cross of 7 hard red winter wheat varieties adapted to Oklahoma. The test was planted in hill plots in a randomized complete block design with three replicates on the Agronomy Research Station at Stillwater in 1967-68. Plots consist of 5 hills spaced 30 cm apart and data were obtained on an individual hill basis.

Heterosis was evaluated in relation to high-parent and midparent values and estimates of general and specific combining ability variances and effects based on F_1 data were obtained to determine the relative importance of additive and non-additive effects of genes controlling character expression.

In general, the hybrids were earlier than the late parent and later than earlier parent. No hybrid headed significantly earlier than its earlier parent. However, significant negative midparent heterosis for heading date was observed in 7 hybrids. Nine of the 21 hybrids were taller than their taller parent, however only one hybrid showed significant high-parent heterosis for this trait. Positive midparent heterosis for plant height was significant in 6 hybrids. None of the hybrids exhibited significant high-parent heterosis for yield or for any of the yield components, although 13 hybrids exceeded their respective high parent for yield. The mean yield of the hybrids ranged from 72 to 146% of the high-parent values and 81 to 147% of the midparent values. The mean yield for all hybrids was 105% of the high-parent mean and 114% of the midparent. Significant midparent heterosis was observed in the Sut/Ag, Sut/Sdy, Ag/Sdy, and Cmn/13876 hybrids for yield; in the Sut/Sdy, Tmp 64/Cmn, Ag/Sdy, Sdy/Cmn, and Cmn/13876 hybrids for 200 kernel weight; in the Tmp 64/Sdy, Ag/Sdy, and Ag/Cmn hybrids for average number of kernels/spike. No significant positive midparent heterosis was found for number of spikes. Three hybrids, Sut/13876, Tmp 64/Sdy and Tmp 64/Cmn were significantly lower than their high-parents for this trait. The Tmp 64/Sdy hybrid was also significantly lower than its midparent. The best hybrid, Ag/Sdy yielded 23.6 grams/hill and also had the largest number of kernels/spike.

The diallel analysis for combining ability indicated that a large part of the total genetic variation for all characters was associated with general combining ability, although significant specific combining ability variances were also observed for all traits measured. On the basis of general to specific combining ability ratios it appeared that non-additive genetic effects were as important as additive effects for yield.

Sturdy had the greatest general combining ability effects for heading date (negative), plant height (negative), yield and average number of kernels/spike. The greatest positive general combining ability effects for kernel weight occurred in Sturdy and Triumph 64 while Agent exhibited the largest negative general effects for this trait. Agent had the highest positive general effects for number of spikes while C.I. 13876 showed the largest negative effect for this trait. Considering general combining ability effects of all traits Sturdy and Triumph 64 appeared to be the best parents.

Six hybrids showed significant negative (earliness) specific combining ability effects for heading date. Three of these hybrids involved the semi-dwarf parent, Sturdy. Significant negative (shortness) specific combining ability effects were observed in 7 hybrids. The greatest negative effect was found in the 7654/Cmn hybrid for this trait. Only five hybrids, Sut/Ag, Sut/Sdy, 7654/13876, Cmn/13876, and Tmp 64/7654 exhibited significant positive specific combining ability effects for yield. The greatest effect for this trait was observed in the Sut/Ag hybrid which also had positive effect for the three yield components. The largest negative effect was found in the Ag/13876 and Sut/7654 hybrids which also had the greatest negative effects for kernel weight and kernels/spike.

LITERATURE CITED

1. Atkins, I. M., K. B. Porter, and O. G. Merkle. 1967. Registration of Sturdy wheat. Crop Sci. 7:406.

2. Beil, G. M., and R. E. Atkins. 1967. Estimates of general and specific combining ability in F_1 hybrids for grain yield and its components in grain sorghum, Sorghum vulgare Pers. Crop Sci. 7:225-228.

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

4. ____________, R. J. Daum, and H. Stevens. 1964. Expression of heterosis in two wheat crosses. Crop Sci. 4:220-223.

5. ____________. and L. P. Reitz. 1963. Classification of Triticum Species and of Wheat Varieties Grown in the United States. USDA Tech. Bull. 1278

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

7. Curtis, B. C., and L. I. Croy. 1958. The approach method of making crosses in small grains. Agron. J. 50:49-51.

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

9. 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.

10. Hayman, B. I. 1954a. The analysis of variance of diallel crosses. Biometrics 10:235-244.

11. ____________. 1954b. The theory and analysis of diallel crosses. Genetics 39:789-809.

12. Hermsen, J. G. Th. 1963. Hybrid necrosis as a problem for the plant breeder. Duphytica 12:1-16.

13. Jinks, J. L. 1954. The analysis of heritable variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:767-788.

14. ____________, and B. I. Hayman. 1953. The analysis of diallel crosses. Maize Genetics News Letter 27:48-54.

15. 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.

16. ______________, J. W. Schmidt, A. F. Drier, and P. J. Mattern. 1955. Registration of Scout wheat. Crop Sci. 5:485-486.

17. Kambal, A. E. and O. J. Webster. 1965. Estimates of general and specific combining ability in grain sorghum, Sorghum vulgare Pers. Crop Sci. 5:521-523.

18. Kempthorne, O. and R. N. Curnow. 1961. The partial diallel cross. Biometrics 17:229-250.

19. 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.

20. Littlewood, R. K., S. G. Carmer, and C. N. Hittle. 1964. A computer program for estimating combining abilities in relation to diallel crossing systems. Crop Sci. 4:662-663.

21. Livers, R. W., and E. G. Heyne. 1966. Field performance of Kansas wheat hybrids in 1964, 1965, and 1966. Agron. Abs. pp. 11.

22. Matzinger, D. F., G. E. Sprague, and C. C. Cockerham. 1959. Diallel crosses of maize in experiments repeated over locations and years. Agron. J. 51:346-350.

23. McIlrath, W. O., E. L. Smith, and A. M. Schlehuber. 1968. Heterosis and combining ability in a diallel cross among common wheat varieties of diverse origin. Agron. Abs. pp.14.

24. McNeal, F. H., D. E. Baldridge, M. A. Berg, and C. A. Watson. 1965. Evaluation of three hard red spring wheat crosses for heterosis. Crop Sci. 8:85-88.

25. Morrison, R. D. Personal communication. 1968.

26. Rojas, B. A., and G. F. Sprague. 1953. A comparison of variance components in corn yield trials: III. General and specific combining ability and their interaction with locations and years. Agron. J. 44:462-466.

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

28. Schlehuber, A. M., and J. W. Johnson. 1965. Registration of Triumph 64 wheat. Crop Sci. 5:605.

29. Smith, E. L., A. M. Schlehuber, H. C. Young, Jr., and L. H. Edwards. 1968. Registration of Agent wheat. Crop Sci. 8:511-512.

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

31. Wood, E. A. Jr. Personal communication. 1968.

VITA

Young Woung Lee

Candidate for the degree of

Master of Science

Thesis: ESTIMATES OF HETEROSIS AND COMBINING ABILITY IN CROSSES AMONG SEVEN HARD RED WINTER WHEAT VARIETIES

Major Field: Agronomy

Biographical:

Personal Data: Born in Seoul, Korea, November 6, 1943, the son of Chung K. and Hyun S. Lee.

Education: Attended elementary school and graduated from Kyung-Bock High School, Seoul, Korea, in 1962; received the Bachelor of Agriculture Degree from Korea University, with a major in Agronomy, in February, 1966; completed requirements for the Master of Science degree in May, 1969.

Professional Experience: Graduate Research Assistant in the Department of Agronomy, Oklahoma State University, Stillwater, U. S. A., from February, 1967, to March, 1969.