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Heterosis and combining ability in winter wheat (Triticum aestivum L.)

Krishna K. Gyawali

To the Graduate Council:

I am submitting herewith a thesis written by Krishna K. Gyawali entitled "Heterosis and combining ability in winter wheat (Triticum aestivum L.)." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

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Vice Provost and Dean of the Graduate School

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December 5, 1966

To the Graduate Council:

I am submitting herewith a thesis written by Krishna Kumar Gyawali entitled "Heterosis and Combining Ability in Winter Wheat (*Triticum aestivum* L.)." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

Calvin O. Qualset
Major Professor

We have read this thesis and recommend its acceptance:

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Accepted for the Council:

Hilton A. Smith
Vice President for Graduate Studies and Research

HETEROSIS AND COMBINING ABILITY IN WINTER WHEAT

(*TRITICUM AESTIVUM* L.)

A Thesis

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Krishna K. Gyawali

December 1966

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ABSTRACT

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A diallel cross involving seven parents and 21 hybrids was adopted to study heterosis and combining ability in wheat. F_1 hybrids and parents were compared in space-planted experiments in two years. Ten hybrids gave significantly higher yield than the highest parent in the cross. The range for all hybrids was -13.8 to 75.9 per cent over the highest parent. Heterosis was obtained from hybrids within the soft red winter wheat group as well as from hybrids derived from hard red and soft white winter wheats. Heterosis was observed for all characters measured in some of the crosses. Greatest heterosis was observed in hybrids derived from crossing late and early maturity parents, a fact that could be important for the commercial utilization of hybrid wheat since it will be difficult to produce hybrid seed from parents that differ in time of anthesis. Heterosis was not observed in hybrids involving closely related parents indicating that genetic diversity is required for the expression of significant heterosis.

Significant general and specific combining ability effects were obtained for yield and agronomically important traits. Tenn. 9, an experimental line, contributed positive general and specific combining ability effects for most characters. This study indicated that certain hybrids should be studied for heterosis under conditions of commercial production.

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CHAPTER I

INTRODUCTION

The main objective of any plant breeding program is to increase the yielding capacity and quality of the crops involved and thereby increase production efficiency. The total output of a crop is influenced by genetic and environmental factors. Improvement in both of these components is necessary to maximize production. Genetic improvement provides a more permanent advance, but it must be coupled with improved environmental conditions through better management practices. In many species, crosses of inbred lines or populations result in a higher yield of the F_1 than the average of the parents or even above the best parent. This phenomenon is known as heterosis. Heterosis has been used to great advantage for increasing yield and stability of performance of several agricultural species.

The original success in utilizing heterosis by means of hybrid varieties was with cross-pollinated species, notably maize (*Zea mays* L.) and onion (*Allium cepa* L.). The discovery of cytoplasmic male sterility and nuclear genes for restoration of pollen fertility contributed to the interest in the utilization of heterosis in the self-pollinated species as in sorghum (*Sorghum vulgare* Pers.). Interest was renewed in the potential use of heterosis in wheat, a self-pollinated species, with the discovery of cytoplasmic male sterility (Kihara, 1951; Fukasawa, 1953) and genes for restoration of pollen fertility (Schmidt *et al.*, 1962; Livers, 1964).

The present study was undertaken to determine whether sufficient heterosis for grain yield could be realized in wheat for commercial production. Also in this investigation, several wheat varieties were characterized for general and specific combining ability for several agronomically important traits.

CHAPTER II

REVIEW OF LITERATURE

Many references are available pertaining to theories of heterosis and estimates of heterosis in various crops, for example corn, onion, sorghum, and sugarbeets (*Beta vulgaris* L.). This chapter will deal primarily with heterosis in wheat, as well as combining ability in several crops including wheat.

Heterosis in Wheat

Because of the distinct success in the practical approach towards the development of hybrid corn, many attempts were made to measure and utilize heterosis in wheat. Early workers had difficulty in obtaining adequate hybrid seed for testing purposes. Attempts were made to find methods by which large amounts of hybrid seed could be produced. Rhoades (1931) discovered cytoplasmic male sterility in maize. After pollen fertility restoring genes were found, methods of producing large quantities of hybrid seed became practicable during the 1950's. Meanwhile, the possible application of cytoplasmic male sterility in self-pollinated crops was under study. Kihara (1951) and Fukasawa (1953) discovered cytoplasmic male sterility in wheat and this discovery gave a new impetus to the study of sterility mechanisms in wheat. Schmidt *et al*. (1962) discovered a genetic fertility restoration mechanism and found that this mechanism was environmentally sensitive. Livers (1964a) found that two dominant genes (*Rf*$_1$ and *Rf*$_2$) are required to give full fertility restoration to cytoplasmic male sterile wheat.

Freeman (1919) was the first to find that heterosis occurred in wheat. Griffee (1921) studied the comparative vigor of hybrid wheat and the parents. Rosenquist (1931) also detected heterosis in wheat. Varenica (1946) found that hybrids yielded from 63 to 172 per cent of the mean of the parents, but in a naturally cross-pollinated source, hybrid performance ranged from 6 to 80 per cent of the mean of the parents. Palmer (1952) found a 31.6 per cent increase in yield of the hybrids over the highest yielding parent.

In a more recent study Lupton (1961) found yield levels that were both lower and higher than the average of the parents and some of the crosses yielded 44 per cent more grain than the highest yielding parents. Schmidt *et al*. (1962) reported grain yields 3 per cent below to 31 per cent above the average of the parents. Gandhi *et al*. (1961) found heterosis for several characters but not for yield. McNeal *et al*. (1965) studied agronomic and quality characters of the parents and the F_1 and F_2 generations of three crosses. They did not detect differences between the F_1 and F_2 populations for yield; both generations were below the highest parent. They concluded that closely related parents would not produce heterosis and emphasized the need for diverse genotypes for hybrid wheat production. Briggle *et al*. (1964) found expression of heterosis in the cross Blackhawk x Kharkof for yield and other characters, but in Wabash x Purkof, only heterosis for kernel weight was significant. They found a significant interaction of genotypes with planting rates and believed it to be chance variation. Fonseca (1965) found 87 per cent heterosis over the mid-parent and 72 per cent over the highest parent for the best cross in his study. He combined close-planted and hill-planted experiments to evaluate planting techniques. Some interactions of genotypes with seeding rates were observed. Bitzer (1965) found a range in heterosis from 0 to 70 per cent more than the superior parent for yield. Knott (1965) found that the differences in yield between space-planted and row-planted hybrids were nonsignificant. He found that hybrids yielded 22.5 per cent more than the parental means and concluded that high yielding F_1 hybrids could be obtained from crosses involving high yielding parents. Johnson et al. (1966) studied tall x semi-dwarf hybrids and found that high kernel weight and to some extent high spike number accounted for high yield of the hybrids. Shebeski (1966) found that three of 14 hybrids yielded significantly more than the higher parent of the crosses. His data were from close-planting. Livers and Heyne (1966) studied field performance of hybrids and found yield increases of 20 per cent greater than the average of the parental varieties. The best cross yielded 33 and 29 per cent more than the best variety for 1964 and 1965, respectively. They concluded that wheat hybrids could express significant heterosis under commercial production conditions.

The milling and baking characteristics of hybrid wheat (F_2 seed) have been studied. Fonseca (1965), studying soft wheat, found that the quality of most hybrids was about the same as the mid-parent. Flour yield was very similar to that of the parents. Heyne and Finney (1965), using hard wheat, found that the quality of hybrids was superior to the poor quality parents but not superior to the better parent indicating partial dominance of the superior parents. Several hybrids studied by Shebeski (1966) expressed heterosis over the better parents for protein content. He concluded that hybrids produced acceptable milling and baking qualities.

Even if economical levels of heterosis are demonstrated it will be necessary to develop methods of obtaining sufficient quantities of hybrid seed for planting. Thus, the cross-pollinating potential of parents must be established in addition to the expression of heterosis. Wilson and Ross (1962) obtained 71 per cent seed set on sterile plants placed in the field between strips of wheat at flowering time. Porter et al. (1965) presented data on sterile lines planted at normal planting rates and found that seed set ranged from 9 to 91 per cent and was highest when the flowering time of the pollinator and the female parent was the same. Patterson and Bitzer (1966) found that seed set was reduced about 10 per cent for each day difference in flowering time between the female and pollinator. Livers (1964b) found that cytoplasmic male sterile heads exposed to the pollinator at various distances had an average of 29 and 35 per cent seed set in 1963 and 1964, respectively.

Combining Ability

The study of combining ability of parents in hybrid combination is useful to isolate better parents for hybrid production. It is known that the appearance, yield, or adaptation of the parents is not always a good indication of the performance of the parents or lines in hybrid combination. Sprague and Tatum (1942) defined the combining ability of an inbred line as the performance of the line in hybrid combination. They recognized two types of combining ability: (1) general combining ability as the average performance of a line in hybrid combinations, and (2) 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. They pointed out that specific combining ability effects could be due to Mendelian segregation and various types of gene interaction.

Maize. Rojas and Sprague (1952) found that the specific combining ability variance included not only the nonadditive deviation due to dominance and epistasis, but also a considerable portion of the genotype x environment interaction. Matzinger et al. (1959) noted that specific combining ability x environment interactions were significant in a study of diallel crosses. Also, general combining ability x years, general combining ability x years x locations and specific combining ability x locations interactions were significant. Federer and Sprague (1947) indicated that the lines x tester interaction could be an important factor in the evaluation of inbred lines. Purdey and Crane (1965) reported that general combining ability variance was more important than specific combining ability variance for endosperm fill. The general combining ability effects were significant for seed weight, seed volume, and specific gravity while specific combining ability effects were significant for seed weight and seed volume.

Cotton. White and Richmond (1963) studied crosses between various *Gossypium hirsutum* L. types and found that the variance for general combining ability was significant for all characters measured except fruiting index. Specific combining ability variance was significant for four characters including yield. There were no significant reciprocal effects. Miller and Marani (1963) reported that in *G. hirsutum* genetic variance was due mainly to general combining ability. Specific combining ability effects were also significant but were not consistent from year to year. Hawkins *et al*. (1965) ranked the *G. hirsutum* varieties used in their study for general combining ability and concluded that the ranking for general combining ability in crosses was the same as the performance of the varieties themselves. Parent varieties should have a good combination of characters and diverse origin for consideration as parents in a hybrid cotton program.

Grain sorghum. Niehaus and Pickett (1966) reported that in grain sorghum specific combining ability was important in determining grain yield. General and specific combining ability variances were significant for all characters measured in the F_1, but in the F_2 generation heads per row was not significant for general combining ability and for specific combining ability grain yield, seeds per head, heads per row and threshing percentage were nonsignificant. Kambal and Webster (1965) found that potential male and female parent lines could be evaluated by using three or four tester lines. Both general and specific combining ability were important in determining yield, but general combining ability was more important and stable over years.

Tobacco. Matzinger *et al*. (1962) reported that there was a significant but small amount of heterosis in tobacco (*Nicotiana tabacum* L.) variety crosses. General combining ability effects were important and no significant specific combining ability effects were found. Only two genotype x environment interactions among 60 were significant. Marani and Sachs (1966) reported that there was significant heterosis for the yield of cured leaves and on the average 21 per cent higher than the parental varieties. They concluded that general combining ability effects were more important than specific combining ability for yield and quality characteristics. Similar results were found by Chaplin (1966).

Wheat. Combining ability in wheat has been determined by several workers and will be considered in more detail in a later section. Kronstad and Foote (1964) found that a large portion of the genotypic variance was due to general combining ability. Significant specific combining ability variance was observed for grain yield and plant height. Fonseca (1965) and Bitzer (1965) also found that general combining ability for yield and yield components was significant. Bitzer (1965) did not find significant specific combining ability effects while Fonseca (1965) demonstrated significant specific combining ability for yield, kernel weight, and spike number. Patterson and Bitzer (1966) concluded that the best hybrid might result from crossing high yielding parents. Brown *et al*. (1966) found highly significant general combining ability for all traits measured while significant specific combining ability effects were detected only for per cent protein. They concluded that the major portion of genetic variation in winter wheat was due to general combining ability. Shebeski (1966) assessed the combining ability of a number of spring wheat varieties. He used a heterozygous tester in an attempt to evaluate wheat varieties for combining ability. The same trend for the performance of parents for combining ability was found by using the parental array means and by crossing with a common tester.

CHAPTER III

MATERIALS AND METHODS

The varieties used as parents in this study were selected to represent a wide range of winter wheat types. Five of the varieties used (Table 1) are soft red winter types while Genesee is a soft white and Triumph is a hard red winter type. In addition to differences in kernel color and hardness the varieties differ in time of maturity and plant height. These two characters may be of importance in selecting parents for use in production of hybrid varieties. Throughout this thesis the abbreviations given in Table 1 will be used to designate the parental varieties. The parentages of these varieties were quite diverse with the exception of the three varieties from Indiana. Monon is a selection from the cross of a Knox sib and Purdue 4127A4-12-1. Knox and Knox 62 are closely related since Knox 62 was obtained from Knox^5 x (Purdue 4781A7-26-2 x Purdue 4126A9-16-1-1-3) in a backcrossing program to introduce hessian fly resistance from P.I.94587 (Table 1). The parentage of Tenn. 9 is not known precisely, but Fulcaster, a variety selected in Tennessee, may occur in its parentage. Tenn. 9 is an experimental line developed by C. D. Sherbakoff at the University of Tennessee. It is classed as a soft wheat, but its kernel hardness is somewhat intermediate to the hard and soft types. Since Seneca has Fulcaster in its parentage it may be somewhat related to Tenn. 9. Further information on

Table 1. Parentage, origin, market class, relative maturity, and relative height of the parents used in the study of heterosis and combining ability

Variety		Relative maturity	Relative height	Market class[a]	Origin	Varieties in parentage
Seneca, C.I.12529[b]	(S)	late	tall	SRW	Ohio	Portage, Fulcaster
Monon, C.I.13278	(M)	early	short	SRW	Indiana	Trumbull, Fultz Sel., Minhardi, Wabash, Purplestraw, Chinese, Michigan, Amber, Kawvale, Hungarian, W38, Fairfield, Hope, Hussar
Knox, C.I.12798	(K)	early	short	SRW	Indiana	Chinese, Michigan Amber, Purplestraw, Minhardi, Wabash, Fultz Sel., Trumbull
Knox 62, C.I.13701	(K62)	early	short	SRW	Indiana	Knox, P.I.94587 (durum), Hope, Hussar, Kawvale, Hungarian, Fairfield, W38
Tenn. 9	(T9)	late	tall	SRW	Tennessee	Unknown
Triumph, C.I.12132	(T)	early	short	HRW	Oklahoma	Blackhull, Kanred, Florence
Genesee, C.I.12653	(G)	late	tall	SWW	New York	Yorkwin, Honor, Forward

[a] SRW, soft red winter; SWW, soft white winter; HRW, hard red winter.

[b] Accession number of the Crops Research Division, U. S. Department of Agriculture.

the parental varieties used in this study, except Tenn. 9, is given by Briggle and Reitz (1963).

Two experiments were conducted to determine combining ability of the seven parental varieties and heterosis in the F_1 generation. The parental varieties were intercrossed in all combinations (21 hybrids) excluding reciprocals. Sufficient quantities of seed were obtained for space-planted tests. The experiments were conducted at the University of Tennessee Plant Science Farm, at Knoxville in 1965 and 1966. The plantings were made on 15 and 20 October 1964 and 1965, respectively. The replicated experiments consisted of a seven parent diallel cross with the seven parents included.

In the 1965 experiment, the entries (parents and F_1s) were planted in a somewhat systematic design where the parents occurred throughout the experiment but all plants of a particular cross occurred in adjacent rows. The number of replications was not the same for all hybrids and parents (harmonic mean number replications = 6.6). Statistical analyses of parental performances indicated no differences between portions of the experimental area (50 ft. x 60 ft.) so comparisons among hybrids were considered valid. The experimental unit was a one-row plot ten feet long with one foot between rows and plants within rows.

In the 1966 experiment, the entries were planted in a randomized complete block design and replicated four times. As in 1965 the experimental unit was a single row plot ten feet long, but plants and rows were spaced 18 inches apart. Eight plants per plot were established; Monon occurred at the ends of each row to minimize border effects.

The seeding rate was two seed per hill and the hills were thinned to one plant on 21-22 March, 1966. Barley yellow dwarf virus infected plants were discarded. Hail damage in this experiment after heading time (29 May) prevented the collection of grain yield and kernel weight data.

The following characters were studied: heading date, measured as the number of days from 31 March when the first head emerged completely from the flag leaf sheath; number of spikes per plant; plant height (in.) to the apex of the tallest culm in the plant; kernel weight (mg.), determined from 1,000 kernels; number of spikelets per spike, determined from ten spikes per plot; length of spike (cm.) from ten spikes per plot; and yield (g./plant), calculated after harvesting the entire row in bulk. Plot means were calculated for all characters and used in the statistical analyses.

The analyses of variance were computed by conventional methods for a randomized complete block design for the 1966 data and a completely randomized design with unequal number of replications for 1965. All traits measured in 1965 and 1966 were subjected to the diallel cross combining ability analysis, using Griffing's (1956) method 2, model 3, where parents and F_1's were included but not reciprocal crosses. The genotypes were regarded as fixed and blocks as random effects. Genotype sums of squares were orthogonally partitioned into general (gca) and specific combining ability (sca) terms. Appropriate F ratios were computed for tests of significance. The general and specific combining ability effects were computed by using the methods devised by Griffing

(1956). Heterosis was calculated as per cent increase of the F_1 hybrids over the mid-parent and highest parent for each trait.

CHAPTER IV

RESULTS AND DISCUSSION

The mean performance of the hybrids and parents is given in Table 2 for the 1965 and 1966 experiments. Summaries of the analyses of variance for each character in 1965 and 1966 are presented in Table 3. Mean squares for genotypes for all characters in the 1965 and 1966 experiments were highly significant. Since highly significant genotype mean squares were obtained, mean squares for general and specific combining ability were calculated and are also presented in Table 3. General combining ability effects were significant for all characters measured in the 1965 and 1966 experiments, while specific combining ability effects were significant for all characters except kernel weight in 1965 and spikelet number and plant height in 1966. However, specific combining ability effects for plant height were significant in 1965.

Heterosis

Heterosis measured as a per cent increase of the F_1 hybrids over the mid-parent and highest parent was computed for all characters (Table 4). The average performance of all parents and hybrids and the average mid-parent and highest parent heterosis for all characters measured in 1965 and 1966 are given in Table 5. Heterosis for yield was much larger than heterosis for other characters. Hybrids with T9 as a parent generally produced the greatest heterosis for most characters.

Table 2. Performance of seven wheat parents and their F_1 hybrids for seven characters in 1965 and 1966

Parent or hybrid	Yield,[a] g./plant 1965	Kernel wt., mg. 1965	Spike no./plant 1965	Spike no./plant 1966	Number spikelets/spike 1966
S	16.2	36.0	21.0	36.9	21.8
M	17.9	28.7	24.6	46.6	18.4
K	16.6	30.5	26.2	44.2	19.6
K62	19.6	30.7	30.6	47.4	18.4
T9	15.5	34.8	20.6	46.2	24.4
T	16.2	35.6	24.2	45.0	17.5
G	19.7	34.0	22.3	38.0	24.0
S x M	20.6	37.1	24.6	46.3	21.0
S x K	23.5	37.9	23.3	42.3	21.2
S x K62	20.4	37.1	25.5	37.8	20.6
S x T9	20.7	35.9	25.4	44.8	23.6
S x T	24.6	36.3	27.4	49.4	20.2
S x G	24.1	37.0	25.0	37.3	22.9
M x K	21.0	31.0	27.9	46.8	18.5
M x K62	18.0	32.0	22.1	53.0	18.5
M x T9	26.0	36.6	26.2	49.2	21.6
M x T	16.9	34.5	26.1	52.1	19.1
M x G	18.4	35.6	25.6	45.2	20.8
K x K62	16.9	31.7	26.7	46.8	18.8
K x T9	28.5	38.0	27.4	54.5	20.8
K x T	21.6	35.6	28.5	53.1	18.4
K x G	26.9	35.8	29.4	46.1	20.8
K62 x T9	27.5	34.9	34.2	50.8	20.4
K62 x T	21.2	36.0	29.4	53.1	18.7
K62 x G	23.3	36.9	24.8	47.8	20.2
T9 x T	28.5	40.6	26.3	50.2	20.8
T9 x G	20.6	41.2	18.3	45.0	24.0
T x G	24.7	43.0	17.8	44.9	20.6
SE[b]	2.4	3.3	2.1	1.2	0.6

Table 2. (Concluded)

Parent or hybrid	Spike length, cm. 1966	Plant height, in. 1965	Plant height, in. 1966	Heading date, days past 31 March 1965	Heading date, days past 31 March 1966
S	11.2	43.9	56.6	36.5	43.4
M	9.6	39.0	40.8	28.3	28.6
K	10.2	42.8	43.0	27.7	30.4
K62	10.0	43.7	46.2	28.0	30.4
T9	14.4	47.4	57.2	35.7	41.1
T	9.2	42.8	42.2	28.0	30.3
G	12.2	45.1	54.5	36.4	43.3
S x M	12.1	44.2	46.8	30.6	35.1
S x K	11.8	46.0	49.2	29.0	34.8
S x K62	12.1	46.2	47.6	31.0	33.6
S x T9	13.6	49.4	59.2	35.2	41.6
S x T	11.7	46.6	48.8	32.5	34.0
S x G	12.4	49.0	56.2	36.0	41.2
M x K	9.6	44.6	42.8	27.8	28.2
M x K62	10.1	43.3	44.2	28.1	28.8
M x T9	12.1	46.8	51.0	32.0	33.3
M x T	10.2	42.4	48.2	27.6	28.6
M x G	11.1	41.0	49.8	33.0	35.0
K x K62	10.5	42.8	42.0	28.3	29.2
K x T9	12.1	50.5	51.4	30.0	33.1
K x T	10.6	45.8	44.5	27.2	26.8
K x G	11.4	51.2	50.6	20.0	33.0
K62 x T9	11.2	49.2	50.6	30.3	32.8
K62 x T	10.5	44.2	49.3	27.0	27.9
K62 x G	11.3	47.9	50.6	31.3	32.5
T9 x T	11.4	53.3	50.5	30.0	35.8
T9 x G	13.4	54.1	56.9	34.0	39.6
T x G	11.2	49.1	50.2	29.5	34.0
SE[b]	0.5	1.4	2.4	0.4	0.9

[a]Multiply by 1.35 to convert to bushels per acre.

[b]Standard error of difference between any two means.

Table 3. Mean squares from the analyses of variance for genotypes, combining ability, and error[a] in 1965 and 1966

Character	Year	Genotypes	Combining ability		Error
			general	specific	
Yield	1965	15.54**	7.84**	17.74**	3.04
Kernel wt.	1965	10.52**	21.95**	7.25	5.57
Spike no.	1965	12.72**	18.81**	10.98**	2.28
	1966	83.80**	234.27**	40.80**	2.73
Spikelet no.	1966	14.61**	62.57**	0.90	0.82
Spike length	1966	6.15**	23.65**	1.16**	0.51
Plant height	1965	13.20**	35.68**	6.78**	0.96
	1966	101.95**	402.88**	15.95	11.16
Heading date	1965	13.48**	40.00**	5.23**	0.11
	1966	96.22**	345.98**	8.40**	1.69

[a]The degrees of freedom associated with error mean squares for 1965 and 1966 are 160 and 81, respectively.

$^{**}P < 0.01$.

Table 4. Heterosis: Per cent increase of the F_1 hybrids over the mid-parent (MP) and highest parent (HP) for seven characters in 1965 and 1966

Hybrid	Yield MP	Yield HP	Kernel weight MP	Kernel weight HP	Spike number MP		Spike number HP	
	1965	1965	1965	1965	1965	1966	1965	1966
S x M	20.8	15.1	8.0	3.1	7.9	10.8**	0.0	-0.8
S x K	43.3**	41.6**	14.0	5.2	-1.3	4.3	-11.2	-4.3
S x K62	14.0	4.1	11.2	3.1	-1.2	13.4**	-16.7	0.8
S x T9	30.6*	27.8*	1.6	-0.3	22.1*	17.8**	12.0*	-3.1
S x T	51.8**	51.8**	1.4	0.8	21.2*	20.7**	13.2	9.8**
S x G	34.5*	22.3	5.7	2.8	15.4	-0.4	12.1	-1.9
M x K	21.7	17.3	4.7	1.6	9.4	3.1	6.8	0.3
M x K62	-4.0	-9.2	7.7	4.2	-19.9	12.6**	-27.8*	17.4**
M x T9	55.7**	45.2**	15.2	5.2	15.9	5.8*	6.5	5.4*
M x T	-0.9	-5.6	7.3	3.1	7.0	13.7**	6.1	16.3**
M x G	-2.1	-4.6	13.6	4.7	9.2	6.8*	4.1	-3.0
K x K62	-6.6	-13.8	3.6	3.2	-6.0	2.1	-12.8	-1.4
K x T9	77.6**	71.7**	16.4	9.2	17.1	20.8**	-10.5	8.0**
K x T	31.7*	30.1*	7.7	0.0	13.1	19.2**	-6.9	18.1**
K x G	48.2**	36.5**	11.0	5.3	21.2*	12.2**	-3.9	4.3
K62 x T9	56.7**	40.3**	6.6	0.3	33.6**	8.6**	11.8	7.2**
K62 x T	18.4	8.2	8.6	1.1	7.3	16.1**	-3.9	13.1**
K62 x G	18.6	18.3	14.1	8.5	-6.2	12.0**	-19.0*	0.8
T9 x T	79.8**	75.9**	15.3	14.0	17.4	10.0**	8.6	8.5
T9 x G	17.0	4.6	19.8*	18.4	-14.7	6.7*	17.9	-2.8
T x G	37.0**	25.4*	23.6*	20.8*	-23.4	8.2*	-26.4**	0.0
Mean		123.95		105.4			93.4	

Table 4. (Concluded)

Hybrid	Spikelet no. MP	Spikelet no. HP	Spike length MP	Spike length HP	Plant height MP		Plant height HP		Heading date MP		Heading date HP	
	1965	1965	1966	1966	1965	1966	1965	1966	1965	1966	1965	1966
S x M	0.4	-3.7	16.1**	7.7	6.6	-3.8	-3.8	-17.2**	-5.6**	-2.4**	-15.2	-19.0**
S x K	2.2	-2.8	9.6*	4.7	6.1	-1.4	4.8	-13.2**	-9.7**	-5.8*	-20.6**	-21.6**
S x K62	2.2	-3.6	13.8**	7.4	5.4	-7.4	5.2	-15.9**	-3.9*	-9.0**	-15.1**	-22.6**
S x T9	2.2	-3.4	6.2*	-5.4	8.2*	4.0	4.2	3.4	-2.5	-1.5	-3.6*	-4.1*
S x T	3.0	-7.2	14.4**	4.2	7.5	-1.2	6.2	-13.8**	0.8	-7.7	-11.0**	-21.6**
S x G	0.0	-4.6	5.8	1.6	10.1*	1.1	8.6	-0.8	-1.2	-4.9**	-1.4	-5.0**
M x K	-4.4	-5.9	-3.2	-6.2	9.0*	1.8	4.2	0.8	-0.8	-3.6	-1.2	-7.5*
M x K62	6.2	0.4	3.1	1.3	4.7	1.4	5.7	4.6	-0.2	-2.6	-0.8	-5.6
M x T9	1.0	-11.6**	0.8	-15.9**	8.3*	4.0	-1.3	-10.8**	0.0	-4.4	-10.4**	-19.0**
M x T	6.2**	3.8	8.2	6.1	3.6	16.3**	-0.9	14.4	-2.0	-3.1	-2.5	-5.9
M x G	-2.8	-12.9**	1.4	-9.5*	-2.8	4.4	-9.9*	-8.8*	2.0	-2.8	-9.4**	-19.2**
K x K62	-4.6	-4.6	4.2	-1.5	-1.0	-5.9	-2.1	9.2	1.6	-4.0	1.1	-4.9
K x T9	-5.2**	-15.2**	-2.0	-16.0**	12.0**	2.7	6.5	10.0**	-5.4**	-7.6**	-16.0**	-19.6**
K x T	-1.2	-6.5	8.6	-0.4	7.0	4.4	7.0	3.4	-2.4	-11.4**	-2.9	-11.7**
K x G	-4.5	-13.4**	2.0	1.6	16.5**	4.0	13.5**	-7.0	-37.6**	-10.6**	-45.1**	-23.9**
K62 x T9	-5.2	-16.9**	-7.4	-21.9**	8.0*	-2.0	3.8	-11.4**	-4.9**	-8.5**	-15.2**	-20.4**
K62 x T	4.1	1.4	9.6	5.5	2.2	11.5*	1.2	6.6	3.6*	8.4**	-3.6*	-8.6**
K62 x G	-4.9	-15.9	1.8	7.7	7.8	0.4	6.2	-7.2	-2.8	-11.9**	-14.0**	-25.0**
T9 x T	-1.2	-15.3**	-2.6	-20.2**	18.2**	1.6	12.4**	-11.6**	-5.8**	0.1	-14.0**	-13.0**
T9 x G	-1.2	-2.2	0.5	-6.9	16.9**	2.0	14.1**	-0.4	-5.7**	-6.2**	-6.6**	-8.6**
T x G	-0.6	-13.9**	4.6	-8.4*	11.7**	3.7	8.8*	8.0*	-9.4**	-7.8**	-19.0**	-21.6**

* .01 < P < .05; ** P < .01 based on least significant difference.

Table 5. Average performance of parents and hybrids and average heterosis for all hybrids for seven characters in 1965 and 1966

Character	Year	Average for all		Per cent heterosis	
		parents	hybrids	mid-parent	highest parent
Yield, g./plant	1965	17.4	22.5	30.7	23.9
Kernel wt., mg.	1965	32.9	36.4	10.6	1.1
Spike no./plant	1965	24.3	25.8	6.6	-15.7
	1966	43.4	48.0	10.3	1.1
No. spikelets/spike	1966	20.6	20.4	-0.4	-16.1
Spike length, cm.	1966	11.0	11.4	4.4	-79.7
Plant height, in.	1965	43.5	47.0	8.0	-0.8
	1966	48.6	49.5	1.5	-13.4
Heading date, days past 31 March	1965	31.5	30.0	-4.8	-17.8
	1966	35.4	33.2	-6.0	-23.4

Yield. Briggle (1963) reviewed the early studies on heterosis in wheat and pointed out that most of the studies were made using spaced plants which may not give results which are useful since wheat is not grown commercially under space-planted conditions. The present study is no exception since spaced plants were also used. In fact, special precautions were taken in the 1966 experiment to eliminate competition effects by using 18-inch spacing between plants. In the 1965 experiment the average yield of the parents was 23.4 bushels per acre compared with 30.3 for the hybrids. This yield level is lower than desired, but unless large plant density x genotype interactions occur the best hybrids in this study should also be good with a high planting rate.

For yield, the 1965 experiment produced a range of heterosis values of -13.8 to 75.9 per cent over the best parent. These results are comparable to other recent studies on heterosis in wheat (Table 6). Two crosses of the present study (K x T9, 71.7 per cent; T x T9, 75.9 per cent) gave exceptionally large estimates of heterosis. Fonseca (1965) also found values in this range. It is not likely that such large increases will be found with commercial seeding practices, since such results probably occurred due to sampling variation. Comparison of these results with other studies with space-planted materials indicate the same general trend, i.e., heterosis of about 25 per cent over the best parent is common, but many crosses do not produce heterotic hybrids. The results from space-planted tests are believed to be useful for preliminary evaluation of hybrids so that more promising combinations may be studied in detail. In two recent studies (Livers and Heyne, 1966;

Table 6. Heterosis[a] in wheat: results obtained for yield and yield components by different authors

Source of data	No. hybrids	Character			
		Yield	Kernel weight	Spike number	Kernel number
Gyawali	21	-13.8 to 75.9	-0.3 to 20.8	-27.8 to 13.2	------------
Bitzer (1965)	15	-11.5 to 32.2	-10.8 to 6.7	-18.0 to 12.0	-18.5 to 22.4
Fonseca (1965)	21	-3.9 to 70.8	-1.4 to 14.9	-35.8 to 33.8	-22.8 to 11.5
Brown *et al*. (1966)	16	-4.0 to 31.0	-4.0 to 10.0	-19.0 to 19.0	------------
Gandhi *et al*. (1961)	11	-49.4 to 35.2	-29.3 to 5.5	-48.2 to 55.6	------------
Knott[b] (1965)	7	-2.1 to 33.5	------------	------------	------------
Briggle *et al*.[c] (1964)	2	19.2 to 37.2	1.6 to 4.9	5.2 to 12.8	0.6 to 7.3
Shebeski (1966)	10	-12.4 to 30.2	-19.9 to 9.3	-8.2 to 22.5	-5.0 to 3.1

[a]Per cent over highest parent.

[b]Results computed as per cent over Thatcher parent mean.

[c]Results computed from large seed data.

Shebeski, 1966) seeding rates and testing methods more closely approximating commercial practices were used. The results of these experiments were quite similar to the space-planted tests in that yield increases for the hybrids of about 30 per cent over the best parents have been observed.

If heterozygosity per se is required for the maximum expression of heterosis (East, 1936), the results indicate that as the genotypic diversity of the parental lines increased, the heterotic response for yield of the hybrid increased. The parents most closely related, K and K62, did not produce a heterotic F_1 as expected. M is a selection from the cross Knox sib x Purdue 4127A4-12-1 and since K62 is a backcross derivative where Knox was the recurrent parent M, K, and K62 probably have many genes in common. The hybrids from these parents would not be expected to produce heterotic F_1's and this was observed in this study.

When genotypic diversity is considered among the hybrids in the SRW, SWW, and HRW market classes, the average performance of the hybrids as percentage increase over the average of the parents was as follows:

SRW x SRW	27.2 per cent
SRW x HRW	29.7 per cent
SRW x SWW	30.2 per cent

These results indicate that heterosis could be obtained within the SRW class of wheat. One of the hybrids between the SRW and HRW classes (T9 x T) expressed the greatest vigor but the second highest hybrid, K x T9, is a SRW x SRW hybrid. Among the SRW x HRW hybrids K62 x T and

M x T did not show heterosis. A similar result was found by Brown et al. (1966) for the latter cross. The hybrid K x T was also included by Brown et al. (1966) and they found 16 per cent heterosis over the highest parent and 40 per cent over the mid-parent; only heterosis over the mid-parent value was significant. The results of the present study are similar since K x T produced 31.7 and 30.1 per cent higher yield than the mid- and highest-parent, respectively. It can be concluded that heterosis is expected for this hybrid. In the SRW x HRW hybrids a wide range of heterosis may be expected; -0.9 to 79.8 per cent over the mid-parent and -5.6 to 75.9 per cent over the highest parent was observed in this study. Among the five SRW x SWW hybrids, two (S x G and K x G) expressed significant heterosis.

Time of anthesis of the parents must coincide for successful hybrid seed production (Patterson and Bitzer, 1966). Assuming adequate pollen dispersal hybrid seed could be produced from early x early or late x late crosses, but early x late hybrids would require methods of modifying heading time to successfully produce hybrid seed. The parents used in this study provided a range of heading time so that comparisons of the performance of hybrids in various maturity groups could be made. The average of the hybrids exceeded the mean of the parents for maturity group crosses by the following amounts:

early x early	10.6 per cent
early x late	40.2 per cent
late x late	25.2 per cent

If K x K62, not expected to be a heterotic cross, is excluded from the early x early comparison the per cent increase for this group is 13.5. It should be remembered, however, that three of the four early parents are closely related. On the average, early x late hybrids gave greater heterosis which would be difficult to utilize on a commercial scale.

Yield components. Two traits, kernel number and spike number, were studied. Heterosis for kernel weight was for crosses between commercial classes and between early and late maturing parents (Table 4, page 20). Within the SRW class, K x T9 gave the greatest response although it was not significant. All hybrids, except S x T9 and K x T, exceeded the highest parent, but only two of 21 hybrids were significantly higher than the mid- or highest parent.

The expression of heterosis for spike number was not consistent over years. Some of the hybrids which expressed negative values over the highest parent in 1965 exhibited positive responses in 1966 and vice versa. This apparent genotype-environment interaction may be due to the difference in spacing between plants in the two years or to an environmental effect associated with years. Heterotic response was observed among the hybrids between market classes. Vigor could also be obtained for the traits within the SRW class but only from late x early hybrids.

Other traits. The other traits measured in this study--number of spikelets, spike length, plant height, and heading date--are agronomically important. The hybrids generally produced fewer spikelets per spike and shorter spikes than the average of the parents as indicated by the predominance of negative estimates of heterosis (Table 4). Tallness of the hybrids was generally found; however, for commercial production shorter types are more desirable since they allow production with high soil fertility without losses due to lodging. T9 hybrids were high yielding but they were also quite tall so benefits from heterosis for yield may not be realized if lodging is a problem.

Hybrids were generally earlier than the mean of their parents (negative values for heterosis) and some were earlier than the earliest parent. Early varieties have been desirable since they sometimes escape leaf and stem rust damage. However, the hybrids with the highest production were from early x late or late x late crosses with maturity being later than the desirable time of maturity of M and K. Disease resistance will likely be necessary for high yields of grain if late maturing hybrids are to be used.

Combining Ability

Parental array means (Table 7) and general combining ability (gca) effects (Table 8) were calculated for all characters in 1965 and 1966. For yield S, M, K62, and T contributed negative estimates while K, T9, and G contributed positive gca effects, but only the effects for T9 and M were significant. T9 expressed positive gca effects for all characters except spike number in 1965; however, kernel weight and spike number were nonsignificant. For kernel weight G contributed positive effects but M, K, and K62 had significant negative effects. For spike number K62 showed significant positive effects while G and S contributed significant negative effects; T was significantly positive only in 1966.

Table 7. Means of parental arrays for seven characters measured in 1965 and 1966

Character	Year	Parent						
		S	M	K	K62	T9	T	G
Yield, g./plant	1965	22.3	20.2	23.1	21.2	25.3	22.9	23.0
Kernel weight, mg.	1965	36.8	34.4	35.0	34.8	37.8	37.6	38.2
Spike no./plant	1965	25.2	25.4	27.2	27.1	26.3	25.9	23.4
	1966	44.6	48.8	48.2	50.0	49.1	50.6	44.4
Spikelet no./spike	1966	21.6	19.9	19.7	19.5	21.8	19.6	21.6
Spike length, cm.	1966	12.2	10.8	11.0	10.9	12.2	10.9	11.8
Plant height, in.	1965	46.9	43.7	46.8	45.0	50.6	46.9	48.7
	1966	51.2	47.1	46.7	47.4	53.2	46.1	52.4
Heading date, days past 31 March	1965	32.4	29.8	21.1	29.3	31.9	29.0	30.6
	1966	36.7	31.4	30.8	30.8	36.0	31.2	35.8

Table 8. Estimates of general combining ability effects for seven characters for the parental genotypes

Character	Year	Parental genotypes							Standard error
		S	M	K	K62	T9	T	G	
Yield, g./plant	1965	-0.43	-1.50*	0.16	-0.41	1.40*	-0.03	0.80	0.54
Kernel wt., mg.	1965	1.00	-2.23*	-1.48*	-1.58*	1.36	1.44	1.46*	0.72
Spike no./plant	1965	-1.12*	-0.17	0.26	2.28*	-0.47	0.07	-1.97*	0.46
	1966	-3.65*	1.25	0.36	2.23*	1.35	2.06*	-3.60*	0.80
No. spikelets/spike	1966	0.96*	-0.90*	-0.76*	-1.16*	1.72*	-1.29*	1.42*	0.14
Spike length, cm.	1966	0.61	-0.70*	-0.46	-0.56	1.32*	-0.72*	0.52	0.14
Plant height, in.	1965	0.00	-3.21*	-0.30	-0.91*	3.21*	-0.24	1.48*	0.30
	1966	2.93*	-3.36*	-3.12*	-1.97*	4.38*	-2.06*	3.20*	0.52
Heading date, days past 31 March	1965	2.68*	-0.82	-2.82*	-1.23	2.20*	-1.48	1.50	1.02
	1966	4.09*	-2.70*	-2.77*	-2.76*	3.10*	-2.52*	3.51*	0.20

*Exceeds 2 x standard error.

For spikelet number S, T9, and G expressed significant positive effects while M, K, K62, and T contributed significant negative effects. Plant height was consistent over years in the expression of positive and negative effects but S, K, and T did not express significant effects in both years. Similarly, for heading date S, T9, and G expressed positive (late maturity) effects while M, K, K62, and T produced negative gca effects.

Observed mean squares for gca were larger than the mean squares for specific combining ability (sca) except for yield (Table 3, page 19). This indicated that the major type of gene action in this population was the additive type. When the seven parents were categorized (Table 8) T9 expressed significantly positive effects for all characters except kernel weight and spike number and was the only parent which contributed significant positive effects for yield. G also had good gca although the effects for all characters were not significant. The most closely related parents (M, K, and K62) expressed negative values for gca effects except for K for yield and spike number, K62 for spike number, and M for spike number in 1966. Bitzer (1965) studied M and K62 for gca effects and found that both varieties expressed negative values for yield. K62 had the largest significant positive gca effect while S and G had the largest significant negative gca effects for spike number. M and T9 were not consistent over years for spike number.

Specific combining ability effects were computed (Table 9) for those characters which expressed significant mean squares for sca in Table 3. For yield, K x G produced the largest positive effects whereas K x K62 produced the largest negative sca effects. The sca effects were

Table 9. Estimates of specific combining ability effects for five characters in 1965 and 1966

Hybrid	Yield, g./plant	Spike no./plant		Spike length, cm.	Plant height, in.	Heading date, days past 31 March	
	1965	1965	1966	1966	1965	1965	1966
S x M	-1.26	0.48	1.88	0.77	1.27	-1.64	-0.06
S x K	2.50	-2.36	-0.24	0.23	0.16	-1.24	-0.40
S x K62	-0.04	-1.08	2.44	0.59	0.79	-0.84	-1.53
S x T9	-1.54	1.58	0.26	0.07	0.04	-0.07	0.64
S x T	3.78	3.04	4.17	0.44	0.70	0.91	-1.34
S x G	2.46	2.70	-2.29	-0.16	1.38	1.43	0.16
M x K	1.06	1.30	-1.63	-0.56	1.98	1.06	-0.32
M x K62	-1.37	-5.42	2.68	-0.04	1.28	-0.22	0.42
M x T9	4.82	1.44	-0.26	-0.15	0.66	0.24	-0.85
M x T	-2.84	0.79	1.95	0.22	-0.28	-0.46	-0.02
M x G	-3.98	2.34	0.76	-0.26	-3.41	1.94	0.38
K x K62	-4.12	-2.37	-2.67	0.19	-2.13	1.98	0.90
K x T9	5.66	1.09	5.97	-0.33	1.44	0.24	-1.12
K x T	0.20	1.65	3.66	0.39	-0.20	1.12	-1.68
K x G	6.21	4.60	2.48	-0.06	3.88	-9.06	-1.59
K62 x T9	5.23	6.98	0.43	-1.01	0.76	-1.04	-1.39
K62 x T	0.36	1.63	2.49	0.40	-0.78	-0.67	-0.67
K62 x G	1.63	-0.92	2.36	-0.14	1.19	0.66	-2.05
T9 x T	5.86	1.30	-0.10	-0.13	4.19	-1.10	1.37
T9 x G	-2.88	-4.66	-0.36	0.31	3.27	-0.08	-0.80
T x G	2.66	-5.70	-0.40	-0.14	1.72	-0.90	-0.80
SE[a]	1.56	1.36	0.74	0.32	0.88	0.30	0.58

[a]Standard error.

generally large for hybrids with T9 as a parent. S x M and T9 x T produced the largest positive sca effects for spike length and plant height. For spike number, K62 x T9 produced the largest positive sca effect in 1965 whereas K x T9 was the largest in 1966.

Since observed mean squares for sca were highly significant for most characters particular parental combinations must be considered in selecting parents for hybrid production. K x G gave the largest sca effects among all hybrids (Table 9). T9 in combination with other parents, except S, contributed larger sca effects than other parental combinations. The results indicated that nonadditive variance could be expected for yield, spike number, spike length, and heading time. Mean squares for sca were not significant for spikelet number and kernel weight. Plant height was not stable over years and in 1966 the mean square for sca was not significant. The information obtained concerning sca effects could be very useful for selecting parents for hybrid wheat production.

For comparison, significance of gca and sca effects obtained by various workers are presented in Table 10. The results obtained in this study for gca were generally consistent with the results of other workers. More variation was found for the results on sca. The present results were consistent with those of Fonseca (1965), except for kernel weight. Bitzer (1965) and Brown et al. (1966) did not detect sca effects and Kronstad and Foote (1964) found that only sca effects for yield were significant. The differences might be due to the selection and choice of experimental material or sampling variation.

Table 10. Significance of general and specific combining ability effects for yield and yield components obtained by various authors

Source of data	Yield	Yield components		
		Kernel weight	Kernel number	Spike number
Gyawali				
gca	**	**	--	**
sca	**	NS	--	**
Kronstad and Foote (1964)				
gca	**	NS	**	**
sca	**	NS	NS	NS
Bitzer (1965)				
gca	Φ	**	**	NS
sca	NS	NS	NS	NS
Fonseca (1965)				
gca	**	**	**	**
sca	**	**	NS	**
Brown *et al*. (1966)				
gca	**	**	--	**
sca	NS	NS	--	NS

Φ $.05 < P < .10$; ** $P < 0.01$; NS, Nonsignificant.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Among the seven parental genotypes used in this study were five soft red winter wheats (Knox, Knox 62, Monon, Seneca and Tenn. 9), one hard red winter variety (Triumph) and one soft white winter variety (Genesee). These varieties differ in important agronomic characters such as time of maturity and plant height.

Two experiments were conducted in 1965 and 1966 to evaluate the F_1 performance of the 21 hybrids obtained from intercrossing the seven parental genotypes and to estimate the importance of general and specific combining ability. Both experiments were space-planted using seed produced by hand pollination. Yield, kernel weight, spike number, plant height, and heading date were determined in the 1965 experiment. In addition to these characters spikelet number and spike length were determined in 1966, but no yield and kernel weight data were obtained because of hail damage.

Heterosis for yield, measured as a percentage increase over the mid-parent and highest parent, was significant for 10 hybrids (range: -13.8 to 75.9 per cent over the highest parent). Heterosis was observed for kernel weight in only two crosses, but heterosis for increased spike number was observed in several crosses. A wide range of heterosis was observed for all of the agronomically important traits measured in this study. Heterosis was obtained from hybrids within the soft red winter wheat market class as well as from hybrids with parents from different market classes. Greater heterosis was observed in late x early maturity than in late x late and early x early hybrids. Since hybrids involving parents of different maturity groups would be difficult to produce additional studies with a large sample of genetically diverse parents that have the same time of anthesis are necessary to determine if heterosis within maturity groups is economically feasible. Heterosis was not observed between closely related parents indicating that genetic diversity is required for the expression of heterosis.

General and specific combining ability effects were evaluated using Griffing's diallel cross analysis method 2, model 3. General combining ability was significant for all characters measured while specific combining ability effects were significant for yield, spike number, spike length, heading date, and plant height. Tenn. 9 contributed positive general combining ability effects for all characters measured. It was the only parent which contributed highly significant general combining ability effects for increased yield. Tenn. 9 in combination with other parents, except Seneca, contributed larger specific combining ability effects than the other parental combinations. Further studies are warranted to determine its usefulness in hybrid wheat production.

Results from this study have indicated that certain parents and hybrid combinations are worthy of further examination for F_1 yield potential.

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LITERATURE CITED

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