HETEROSIS AND COMBINING ABILITY ESTIMATES
OF HYBRIDS INVOLVING SELECTED RESTORER
AND MALE STERILE WINTER WHEATS

By

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CHAPTER I

GENERAL INTRODUCTION

The discovery of cytoplasmic male sterility and a genetic system for fertility restoration in wheat has stimulated interest in the possibility of producing commercial wheat hybrids and has led to a number of studies concerning the extent to which heterosis is manifested in wheat hybrids. Since release of information on these systems in late 1962, hybrid wheat research has become a field of great interest and activity.

Many problems have developed concerning hybrid wheat which must be solved before hybrid wheat can be economically feasible. Research is being conducted by a number of research centers in an effort to solve these problems. The amount of pollen produced, how far it is transported, its viability, and the stigma receptiveness of the male sterile lines are of great importance in determining the procedures necessary for seed production blocks (5, 40).

Selection of suitable parents is of major importance in hybrid wheat production. The development of suitable restorer lines is necessary before commercial hybrid wheat can be grown. A restorer line must provide good pollen fertility restoration in the hybrid as well as produce sufficient pollen to pollinate the male sterile line. Conversion of male sterile lines appears to be a relatively straight forward procedure involving a back crossing scheme. Borlaug (3) considers good combining ability of the male sterile parent essential to the production of a commercial hybrid. In many instances high yielding varieties perform very poorly when used as parents for hybrids. Although not all hybrids exhibit superior performance, many hybrids have exceeded their better parent in yield and other agronomic characters (28). The economics of hybrid wheat production requires that hybrids display a certain amount of heterosis before they can be commercially successful.

Nearly all of the previous studies concerning heterosis and combining ability in wheat involved handmade crosses between two normal wheat varieties and were conducted using space plants or thinly seeded plots. This study was undertaken to determine the heterosis and combining ability, both general and specific, of selected male sterile and restorer wheat hybrids and to conduct tests in nursery plots using solid seeding conditions. Information was obtained for the following characters: yield, tiller number, kernels/spike, kernel weight, heading date, plant height and test weight. In addition, seed set percentages were determined as an estimate of the degree of fertility restoration. Complete quality analysis was conducted to determine the influence of the male sterile cytoplasm on quality characteristics.

CHAPTER II

REVIEW OF LITERATURE

Male Sterile and Restorer Systems

The recent discovery of cytoplasmic male sterility and a genetic mechanism for fertility restoration provided the necessary tools for exploration into the feasibility of hybrid wheat for commercial production. These tools were necessary to provide a means of producing substantial amounts of crossed seed from a normally self pollinating crop such as wheat.

Cytoplasmic induced male sterility in wheat was first reported by Kihara (22) and Fukasawa (13, 14). Wilson and Ross (55) were able to substitute the nucleus of *Triticum aestivum* into three sterile cytoplasms, *Aegilops caudata* L., *Aegilops ovata* L., and *Triticum timopheevi* Zhuk. Of the three sterile cytoplasms, *T. timopheevi* was the most promising. Fewer deleterious effects were observed in the material involving the *T. timopheevi* cytoplasm and more meiotically stable wheat types were produced.

Genotypes capable of restoring fertility in the presence of male sterile cytoplasm were discovered in 1962 by Schmidt, Johnson, and Mann (47) and J. A. Wilson as cited by Livers (27). Fertile plants from the population designated as Nebraska 542437 gave fertile hybrids when used as pollinators for male sterile sister strains. This wheat population has a winter growth habit. Reports of other restorer materials from other sources throughout the world are presently available.

In general, in crop plants possessing a cytoplasmic-genetic sterile system, the fertility restoration occurs by the action of one or more dominant genes. In corn, different sterile cytoplasms require different gene systems for fertility restoration. Plants having the T (Texas male sterile) cytoplasm require two complementary dominant genes, Rf_1 and Rf_2 (12). A single dominant gene, Rf_3, is required for fertility restoration in the S (Connecticut sterility-inducing) cytoplasm (10). A number of genes have been identified which express partial fertility in these sterile systems (2, 6). In sorghum, one dominant restorer gene appears to be present with other modifying genes of varying degrees of expression necessary for good restoration in certain environments (17, 36). Fertility restoration in pearl millet appears to be the result of one major dominant gene although some effect by modifiers has been observed (11).

Preliminary genetic investigations indicate that fertility restoration in wheat is simply inherited and most investigators (47, 27, 45, 32) suggest that complimentary genes are involved in the expression of fertility restoration. Livers (27), working with the Nebraska 542437 wheat material, classified F_2 testcross plants according to the microscopic appearance of the pollen as normal, partially fertile, and sterile. From these observations he concluded that two factors were responsible for fertility restoration. Johnson et al. (20) reported that the Nebraska 542437 material contained one lot, lot 1, which contained two major genes for fertility restoration. Much more research is needed to increase the knowledge and understanding of the cytoplasmic sterility and fertility restoring systems in wheat. Rodriguez et al.

(45) stated that a genetic system for fertility restoration which involves a single dominant gene would simplify the development of wheat hybrids.

Investigations concerned with the degree of restoration indicate that the genetic system will not restore complete fertility to the sterile x restorer hybrids. McCuistion (32) examined the degree of restoration to male sterile Bison exhibited by various restorer selections from the Nebraska 542437 population. He observed restoration of 75 percent and better on the majority of the testcross progeny involving most of the restorer selections. He concluded that environmental conditions influenced the degree of fertility restoration. Wilson and Ross (54) studied 124 hexaploid wheat varieties for pollen-restoring chromogenes. The sterile cytoplasm used for testing these varieties was *Aegilops ovata*. They concluded that no single variety of wheat tested has the complete pollen-restoring character and most of the hexaploid wheat varieties appear to lack the full compliment of restoring genes necessary for the production of pollen-fertile hybrids.

Heterosis

Recent discoveries of cytoplasmic male sterility and the fertility restoration system have engendered much interest as to the feasibility of a commercial hybrid in common wheat. For hybrid wheat to be successful, heterosis for grain yield must be sufficient to provide an economic return. Reitz (42) calculated the amount of heterosis required to reach the "break-even" point at various extra seed costs for hybrid seed at different production levels. If the market price of wheat were $2.00 per bushel and the additional cost of hybrid seed were $5.00 per acre, a hybrid would have to produce a 25 percent increase in yield over conventional "pure line" varieties at the 10-bushel per acre yield level. Under the same financial situation, it would require only a 6 percent increase in yield at the 40-bushel per acre level. Roberts (43) stated that current economics will not permit the farmer to pay more than five to ten dollars for 50 pounds of hybrid seed.

Briggle (4) reviewed the work on heterosis in wheat and cited instances of yield increases of 100 percent over the mean yield of the parents. Similar increases were reported on other agronomic characters. He pointed out that virtually all heterosis studies involving wheat have been carried out under space-planting and involve rather small populations. Patterson and Betzer (39) reported yield increases over the better parent in intercrosses involving six and seven parental wheat lines. Briggle et al. (7) conducted heterosis studies under conditions believed to permit accurate evaluation of hybrid potential without growing them in the conventional manner. Two crosses using winter wheat were made, Blackhawk x Karkof and Wabash x Perkof. F_1 plants were placed in hills at the rate of one, two and four seeds per hill. Heterosis was noted on the Blackhawk x Karkof F_1's for yield, 1000 kernel weight, weight of grain per spike, number of kernels per spike, and plant height. No heterosis for the previous traits was observed on the Wabash x Perkof F_1's. Brown et al. (9) observed heterosis in a study of crosses among hard and soft winter wheats. Yielding capacity of the hybrids ranged from 96 to 131 percent of the high parent means. They also noted that heterosis for yield was not accompanied by a reduction in grain protein. Wells and Lay (51) working with spring wheat observed yields ranging from 14 percent less than the high parent to 82 percent above the high parent. Gyawali et al. (16) observed yields ranging from 86 to 176 percent of the high parent. These studies point out that considerable heterosis for yield occurs in some wheat hybrids but not in others.

Johnson et al. (19) observed populations of a cross between two varieties which varied greatly in several characteristics. Heterosis for grain yield, kernel weight, and spikes per plant was present. Higher yields and more spikes were observed in both the F_1 and F_2 generations than for either parent. Livers and Heyne (28) observed heterosis for yield comparable to that in other crops. McNeal et al. (34) evaluated F_1 and F_2 generations for agronomic and quality traits. The performance of the F_1 and F_2 generations was usually found to be intermediate between the parents for both agronomic and quality traits. Parental lines involved in this study represented a rather narrow gene base. McIlrath (33) found that hybrids from lines of diverse origin resulted in more heterosis than hybrids from parents with a narrow gene base. These results imply the necessity of genetic diversity for expression of heterosis in wheat.

Glover and Smith (15) examined the F_1 and F_2 generations of a cross between four male sterile lines and one common restorer. The F_1, F_2, restorer line, and the normal counterpart of the sterile lines were solid seeded in a replicated yield trial. Significant high parent heterosis for yield was observed on the F_1 and F_2 generations involving one male sterile line. The yielding capacity of the F_1 and F_2 generations was 132 percent and 118 percent of the high parent respectively. There was no difference observed among the F_1, F_2, or mid-parent values involving the remaining male sterile lines. These results indicate that heterosis is expressed in some male sterile x restorer wheat hybrids and not in others.

Hand made hybrids were tested in yield trials by Merkle et al. (35) and the results indicated that wheat hybrids are capable of yielding significantly better than the best yielding varieties grown in the area. Their data indicated that the major factor which contributed to the increased yields on the hybrids was the average number of seeds per spike. They were unable to find any significant difference between the hybrids and the standard varieties in 100-kernel weight or the number of tillers. McIlrath (33) concluded that heterosis for both seed weight and kernels per spike were the contributing factors in hybrids exhibiting heterosis for yield.

Combining Ability

Numerous investigations have been conducted in recent years in an effort to determine the relative importance of the different types of gene action influencing the variability in quantitative characters in self-pollinated crops. Both diallel analyses and analyses based on early segregating generations of crosses between pure lines have been employed. In general, it has been found that additive gene action is of major importance in the expression of quantitative characters (31, 44, 30, 41, 37, 52, 38, 21, 26), although some instances of important non-additive effects have been noted (25, 18).

Whitehouse et al. (53) observed the F_1 and F_2 generations of a diallel cross among four spring wheat varieties for yield and components of yield. The yield components were found to be primarily effected by additive genetic effects with slight dominance effects in the F_1 generations for seed per spikelet and spikelets per head. Non-allelic interactions strongly influenced yield in both the F_1 and F_2 populations, although there was little evidence of non-additive influence in separate analyses of the components of yield. Lupton (29) found gene interactions influencing yields in a diallel study involving F_1 and F_2 populations from crosses among six winter wheat varieties. In contrast to Whitehouse et al. (53), Lupton found components of yield were also influenced by gene interactions, although these interactions could be traced to specific varieties. After eliminating the arrays of crosses involving these varieties, he found 1000-kernel weight to be controlled predominately by additive gene action, but grains per head and heads per plant were inherited largely by dominance.

Gyawali et al. (16) evaluated hand crossed F_1's and the parents of a seven-parent diallel cross in space-planted tests. Soft red, soft white, and hard red winter wheat varieties composed the parental lines. Combining ability effects were measured for grain yield, kernel weight, spikes per plant, heading date, and plant height. In addition, several quality characteristics were evaluated. General combining ability was significant for all characters studied, both agronomic and quality. Specific combining ability was significant for grain yield, kernel weight, spikes per plant, heading date, pearling index, and micro-AWRC (alkaline water retention capacity).

General combining ability variances were found to be considerably greater than specific combining ability variances for all traits except kernel weight in a diallel study by Kronstad and Foote (23) which involved 10 winter wheat varieties. Significant specific combining ability. McIlrath (33) also concluded that total genetic variability in the F_1 populations was predominately due to additive effects of genes.

Quality

The incorporation of exotic *T. timopheevi* cytoplasm into bread wheats has caused concern as to its effect on quality characteristics. The yield increase anticipated from hybrid wheat should not be obtained at the expense of reducing the milling and baking quality of the wheat crop. More information on the effects of the exotic cytoplasm and restoration factors on wheat quality is necessary. Industrial quality considerations were not so important in the development of corn and sorghum hybrids, since both of these cereals are used primarily as feed grains. The situation is different in wheat, as this cereal is used almost entirely for human consumption. In recent years it has become standard policy to evaluate milling and baking quality characteristics of all new experimental wheats in cooperative tests in governmental and industrial laboratories. Only those wheats which meet the requirements of industry and are acceptable to the farmer are increased and released for production.

Several studies have been conducted to study the effects of the exotic cytoplasm on wheat quality. A preliminary study by Wilson and Villegas (56) indicated that *T. timopheevi* cytoplasm had no adverse affect on several grain and dough handling characteristics which they studied in male sterile, restorer, and experimental hybrid lines. Rodriguez et al. (45) found that for most grain and dough characteristics the hybrids were intermediate between the two parents. They noted that some hybrids produced loaves which were larger and had better texture and color than either of their parents. They also pointed out that hybrids involving wheats with inferior baking quality often had baking characteristics as good or better than the better parent. McNeal et al. (34) found that the quality of F_1 and F_2 grain from hard red spring wheat crosses usually approached the quality of the better parent.

Rooney et al. (46) examined male sterile and hybrid lines to determine the effect of the *T. timopheevi* cytoplasm. They concluded that the quality was not adversely affected by the exotic cytoplasm. Abbott (1) conducted milling and baking quality analysis on several male sterile x restorer hybrids and concluded that the quality characteristics were equal to or better than Triumph, which is the principal wheat variety grown in Oklahoma. Shebeski (48) determined the combining ability of several hard red spring varieties for yield and quality and found among two varieties with high quality one which was an excellent combiner for quality; the other was quite poor.

CHAPTER III

MATERIALS AND METHODS

Materials

The material used in this study consisted of eight F_1 hybrids developed from crosses of four cytoplasmic male sterile lines with two fertility restoring lines. All male sterile lines had the T. timopheevi cytoplasmic male sterile system. The genetic system for fertility restoration of the restorer lines was also derived from T. timopheevi.

The two restorer lines were derived from selections made at Stillwater from the Nebraska 542437 restorer population which was obtained from Dr. J. C. Craddock[1] in July of 1963. The pedigree of Nebraska 542437 is as follows: T. timopheevi x (Hussar - Hard Federation)^2 x (Comet - Hussar - Hard Federation) x Nebred. The population consisted of two lots of seed, designated as lot 1 and lot 2. Reports from Nebraska (20) indicated that lot 1 had two major genes for restoration while lot 2 had a single major gene with possible minor genes associated. The F_2 generation of these two lots were grown at Stillwater in 1964 with lot 1 as plot 5892 and lot 2 as plot 5893. Individual F_3 plant selections were made from each plot and the resulting populations from these selections carried the selection number of Stw 645892 and Stw 645893 plus the plant selection number. In all, some 70 F_3 plant

[1]Dr. J. C. Craddock, USDA, ARS, CRD, Beltsville, Maryland.

selections were made and the two selections used in this study were Stw 645892-25 and Stw 645893-25.

The choice of the two restorer lines for use in this study was based on degree of fertility restoration and agronomic characteristics as determined in previous tests conducted at the Oklahoma Agricultural Experiment Station. These two restorer lines represented the best lines considering both restoration ability and agronomic traits. Also, the two selections represented the two lots, 1 and 2, which supposedly represent two types of gene systems for fertility restoration. Both restorer lines have white chaff, are of mid-season maturity, mid-tall and produce yields which are only slightly below varieties presently being grown in Oklahoma. Each of these lines have provided adequate fertility restoration when testcrossed to male sterile Bison.

Male sterile lines used in this study were chosen primarily for the availability of seed. The four sterile lines selected yielded sufficient seed, when grown in crossing blocks with restorer lines, to provide adequate amounts for replicated field trials. The male sterile lines which were used included Bison, Tascosa, Agent, and C.I. 13678. The normal counterpart of these sterile lines represents a range of characteristics and a rather large area of adaptation. Bison is a Kansas Experiment Station released variety with white chaff, is early to mid-season in maturity, short to mid-tall, and susceptible to leaf and stem rust (8). Tascosa was developed by the Texas Experiment Station and was released in 1959. It is early, short, brown, glumed, and is also susceptible to both leaf and stem rust (8). Agent was released by the Oklahoma Research Station in 1967 as a forage type wheat which is resistant to all known races of leaf rust. It is described by Smith et al. (49)

as being mid-season in maturity, mid tall, with white glumes. The last line, C.I. 13678, has a pedigree of Norin 16/C.I. 12500[2] and is an early maturing, semi-dwarf experimental line.

The male sterile cytoplasm in each of the sterile lines was from *T. timopheevi*. The male sterile Bison was developed by Wilson and Ross, as indicated by Briggle (4) using a back-cross system of *T. timopheevi* x Bison with Bison used recurrently as the male parent. The remaining male sterile lines were developed in a similar fashion using male sterile Bison as the source of the male sterile cytoplasm. This procedure was conducted in the greenhouse, therefore, the amount of available seed was limited.

Hybrid seed used in this study was harvested from rows of the male sterile line grown adjacent to rows of the restorer in isolated field crossing blocks. Each isolated crossing block had a single restorer line for the pollinator. The four male lines were included in each block. To insure pollination of the male sterile lines by the selected restorer line, the crossing blocks were isolated by a distance of approximately 200 meters. Cross pollination was accomplished by allowing wind-blown pollen from the restorer line to pollinate the male sterile lines. Four male sterile x restorer hybrids were produced in each of the two crossing blocks.

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[2]C.I. 12500 = NB 60 x Mediterranean x Hope

Methods

Nursery tests of F_1 hybrids, parents, and check varieties were conducted at Stillwater and Goodwell, Oklahoma in 1968 and 1969. The nursery at each location consisted of four 2.5 meter rows per plot replicated three times. Seeding rate was approximately seven grams per row (equivalent to 1 bu/A)[3]. Because of limited amounts of hybrid seed, the two center rows of the hybrid plots were planted with F_1 seed and the two outside rows were planted with B-line parent. The nursery plots were planted with a four-row tractor-driven cone planter. This same procedure was used for all small grains performance nurseries. The test at Goodwell was grown under irrigation, those at Stillwater under dryland conditions. Fertilizer application was the same as for all other performance nurseries, and included a pre-plant application of P_2O_5 in the fall and a top dressing of nitrogen in the spring. Entries included in the test were the eight hybrids, the two restorer parents, the normal counterpart of the four sterile parents, and two check varieties, Kaw 61 and Triumph 64. The entries are listed in Table I and designated as to the nursery location.

Characters under study were grain yield expressed as grams per plot, tiller number/50cm^2 obtained by counting tillers in two-25cm^2 areas in each plot, kernel weight expressed as grams/200 random kernels, kernels per spike obtained by counting kernels from 25 random heads in each plot, test weight expressed as kg/hl, plant height in cm, and

[3]This is the approximate seeding rate used in commercial production.

TABLE I

HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS IN 1968-1969

Hybrid, Parent or Check Variety	C.I. or Sel. No.	1968 Stw	1968 GdwI	1969 Stw
Agent[1]	13523	X	X	X
Bison	12518	X	X	X
Kaw 61 (ck)	12871	X	X	X
Tascosa	13023	X	X	X
Tmp 64 (ck)	13679	X	X	X
Nr16/C.I. 12500	13678	X	X	X
R-5892-25[2]	Stw645892-25	X	X	X
R-5893-25	Stw645893-25	X	X	X
A-Agent/R-5892-25[3]	H67x262a	X	X	X
A-Agent/R-5893-25	H67x268a	X	X	X
A-Bison/R-5892-25	H67x261a	X	X	X
A-Bison/R-5893-25	H67x267a	X	X	X
A-Tascosa/R-5892-25	H67x265a	X	X	X
A-Tascosa/R-5893-25	H67x271a	X	X	X
A-C.I. 13678/R-5892-25	H67x264a	X	X	X
A-C.I. 13678/R-5893-25	H67x270a	X	X	X

[1]B-line parent; the normal counterpart of the male sterile line.

[2]The R designates the restorer line.

[3]The A designates the male sterile line.

heading date expressed as days from April 30. A randomized complete block design with three replications was used and statistical analyses were conducted on these seven characters. Comparisons of the hybrids and their parents were made to study the heterosis expressed by the hybrids. Comparisons were made with both the high parent and the mid-parent value. The normal counterpart of the male sterile lines were used as a measure of the male sterile parent. Means were compared by the Least Significant Difference method with "t" values taken from tables in Steel and Torrie (50).

Estimates of general and specific combining ability were calculated for all seven characters. The method used to determine combining ability followed the method described by Kambal and Webster (21) for data obtained on grain sorghum hybrids. Analyses of variance involving only the hybrids was utilized in this method.

Seed set percentages were calculated and used as a means for estimating fertility restoration in the hybrids. This was done by taking 25 heads from each entry in each replication and counting the number of kernels per spike and the number of florets per spike. All lateral florets were counted, and each central floret containing a seed was also counted. The number of seed divided by the number of florets gave the seed set percentage. Fertility restoration was estimated by the seed set of the hybrids expressed as a percentage of the seed set of the normal varieties.

Complete quality analysis was conducted on the hybrids in an effort to determine if any adverse effects in quality characteristics resulted from the incorporation of the *T. timopheevi* cytoplasm. Quality characters examined were wheat protein, flour protein, percent flour yield, corrected absorption percentage, average mixing time, loaf volume, corrected loaf volume at 13% protein, grain and texture, and external loaf score. Quality analysis was conducted in 1968 on a composite of seed from the nursery in 1969 by the Wheat Quality Laboratory at the Oklahoma Agricultural Experiment Station. As a result of the composite analysis in 1968, statistical analyses were not performed.

The system of nomenclature used in this text follows the ABR system of sorghum workers. The male sterile lines are referred to as A-lines, the normal counterpart of the male sterile lines are the B-lines, and restorer lines are R-lines. This system of nomenclature is the one most commonly found in reports concerning hybrid wheat.

CHAPTER IV

RESULTS AND DISCUSSION

Fertility Restoration

A major problem facing hybrid wheat is adequate fertility restoration in male sterile x restorer hybrids. Seed set percentages were calculated on the hybrids and parental lines to estimate the fertility restoration obtained in the hybrids. Seed set percentages may not be a direct measure of fertility restoration since some cross pollination may occur. In an effort to examine the effect of cross pollination on seed set, a few heads were randomly selected before anthesis from the hybrid rows. One half were bagged and the others tagged. Examination of the heads indicated that very little difference in seed set was present between bagged and non-bagged heads. In view of these findings, cross pollination was considered to be of slight importance to seed set on the hybrids, indicating that seed set was a fair measure of fertility restoration.

Seed set percentages were calculated on the hybrids, the restorer lines, the B-line counterpart of the sterile lines, and on the check varieties. Restoration was determined by comparing the seed set of the hybrids with the seed set obtained from the parental lines. This method was used since the parental lines failed to maintain 100% seed set. The mean seed set of the hybrids was 90% of the mean of the parental lines. Means of the hybrids, the R-lines, the B-lines and the parental average are presented in Table II. Appendix Table XVIII presents seed set percentages for the hybrids, parents, and check varieties.

TABLE II

MEAN SEED SET PERCENTAGES OF HYBRIDS, R-LINES, B-LINES, AND THE PARENTAL AVERAGE

Line	Seed Set Mean (%)
Hybrid	79.6
R-Lines	87.8
B-Lines	89.0
Parental Average	88.6

Hybrids were grouped by the A-line parent and by the R-line parent to determine if some male sterile lines were more easily restored than others and if one restorer was more effective than the other. Comparisons were made using these two groupings, and the means are compared in Table III. It was indicated by these comparisons that the male sterile lines Agent and Bison might be slightly easier to restore than Tascosa or C.I. 13678. Hybrids involving the R-line, R-5892-25, appeared to be slightly better restored than those involving R-5893-25.

Overall, fertility restoration in the hybrids appeared to be sufficiently high so as not to introduce bias into the studies on heterosis and combining ability.

TABLE III

MEAN SEED SET PERCENTAGES OF HYBRIDS GROUPED BY A-LINE AND R-LINE

A-Line	Ave. of Hybrids (%)
A-Agent	83.4 a[1]
A-Bison	82.9 a
A-Tascosa	76.4 b
A-C.I. 13678	76.0 b
R-5892-25	80.8 a
R-5893-25	78.7 b

[1]Means followed by the same letter are not significantly different at the .05 level.

Analysis of Variance

Two tests in 1968 and one in 1969 were combined as three different environments and analyzed for seven characters. The seven characters analyzed were grain yield, tiller number, kernel weight, kernels/spike, test weight, heading date, and plant height. Tiller number, kernel weight, and kernels/spike were analyzed in an effort to determine the yield component or components responsible for any heterosis in yield expressed by the hybrids. The sources of variation and the mean squares for each of these seven characters analyzed are presented in Table IV. Highly significant differences were observed for all sources of variation on all the characters. The standard notation for significance used in these and all subsequent analyses is *= significance at the 5% level of probability and **= significance at the 1% level. Comparisons were made on the means of all entries and these comparisons are presented in Appendix Tables XVIII - XXIV.

Heterosis

Heterosis, in relation to both mid-parent and high-parent values, was examined for all characters analyzed. Appendix Table XXV presents the hybrids as the percent of mid-parent and high parent. Heterosis was determined by comparing the means of the hybrids with the means of the better parental line and the average of the two parents.

Four hybrids exhibited significant mid-parent heterosis for grain yield, three of which were significant for high-parent heterosis. The fourth hybrid, although not significantly superior to its high yielding parent, did exhibit a 9% increase in yield over its better yielding parent. The four hybrids exhibiting heterosis included all hybrids involving Agent and C.I. 13678. With the exception of A-Tascosa/R-5892-25, which yielded significantly below the mid-parent values for yield. Comparisons of the hybrids and their parents are illustrated in Figure 1.

Yield increases above the higher yielding parent ranged from 9% to 18% for the four hybrids exhibiting heterosis for this trait. Although these hybrids yielded considerably better than their high-parents, they were not significantly better than the highest yielding check variety in

TABLE IV

MEAN SQUARES FROM COMBINED ANALYSES OF VARIANCE OF DATA FROM HYBRIDS AND PARENTS GROWN IN THREE ENVIRONMENTS

Source of Variation	d.f.	Yield	Tiller Number	Kernel Weight	Kernels per spike	Test Weight	Heading Date	Plant Height
Total	143							
Environments	2	7191.42**	7177.14**	0.62**	3334.68**	111.94**	271.52**	1005.78**
Blocks in environments	6	256.01**	1254.01**	0.84**	33.39**	1.60**	25.55**	35.75**
Genotypes	15	130.06**	739.99**	2.67**	115.53**	22.99**	68.90**	34.55**
Genotypes x environments	30	94.90**	851.80**	0.33**	21.67**	4.46**	5.57**	9.92**
Error	90	23.90	46.92	0.12	8.17	0.65	1.97	2.45

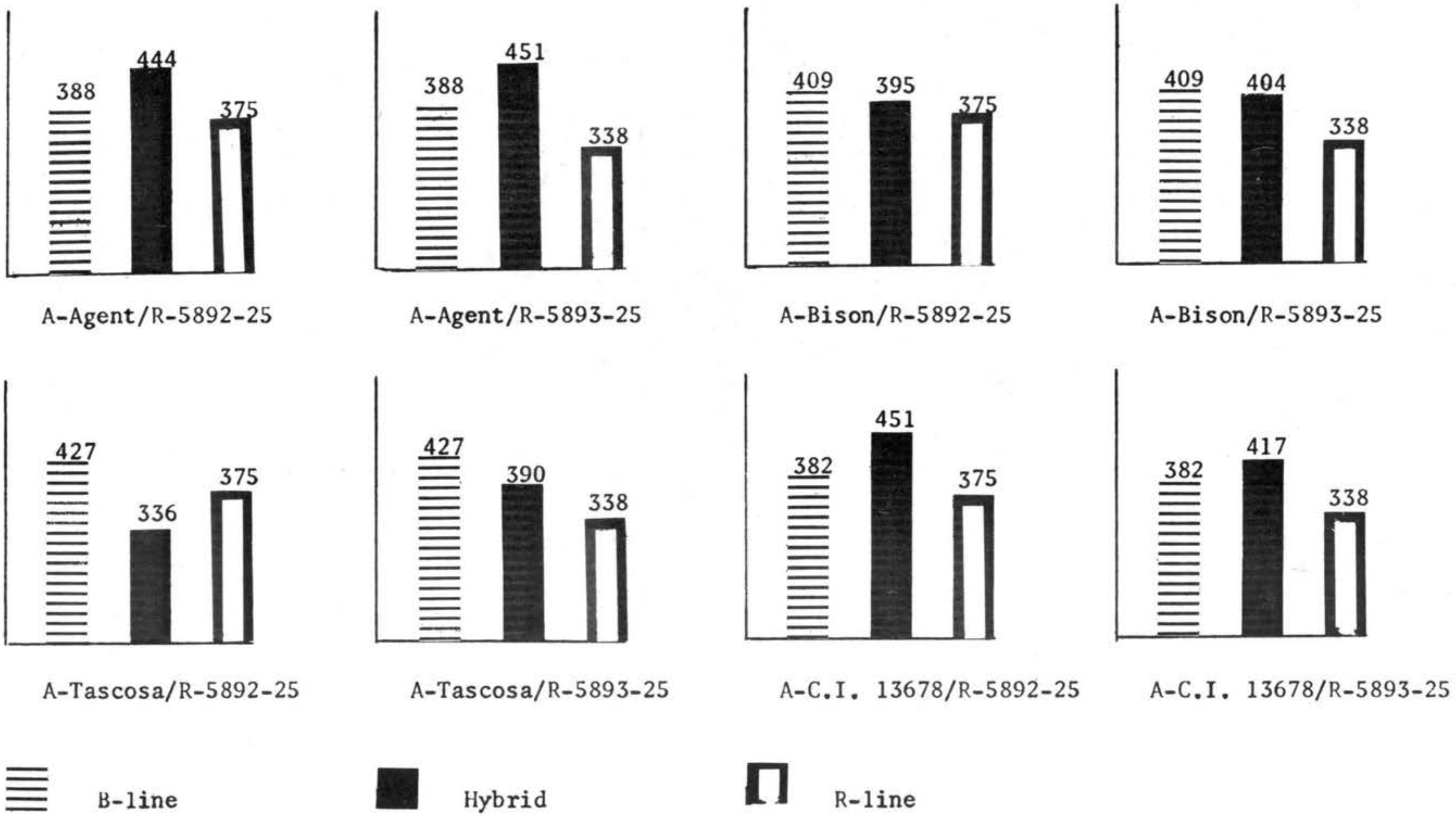

Figure 1. Yield comparison, measured in gms/plot, of hybrids and their respective parents - mean of three tests.

in the study. In most cases they were slightly better than the high-yielding check variety. The yields of the hybrids expressed as the percent of the highest-yielding check variety are presented in Appendix Table XXVI.

Evaluation of the number of tillers on the hybrids provided surprising results as shown in Appendix Table XXV. There were significantly fewer tillers on seven hybrids in comparison to their respective mid-parent values. Figure 2 presents graphic comparisons of the hybrids and their parents. These data show a significant reduction in tillering, but the reason for this reduction is not known. Regardless of the reason for fewer tillers, these data indicate that tiller number is not of major importance in the expression of heterosis for yield exhibited by the four hybrids in this study. This disagrees with the findings of Johnson et al. (19) who suggests that tiller number is of major importance.

The most striking heterotic effect observed in this study was for kernel weight. All eight hybrids exhibited significant high-parent heterosis for this character (Appendix Table XXV). Kernel weight comparisons of the hybrids and their parents are illustrated in Figure 3. When compared to the best check variety, which was also the highest yielding variety, all hybrids, with the exception of A-Tascosa/R-5893-25, had kernel weights similar to this check variety. Kernel weights expressed as percent of the best check variety are presented for all hybrids in Appendix Table XXVII. These results agree with those reported by Briggle (7), Johnson et al. (19), and McIlrath (33), which indicated that kernel weight is of major importance in the expression of heterosis for yield.

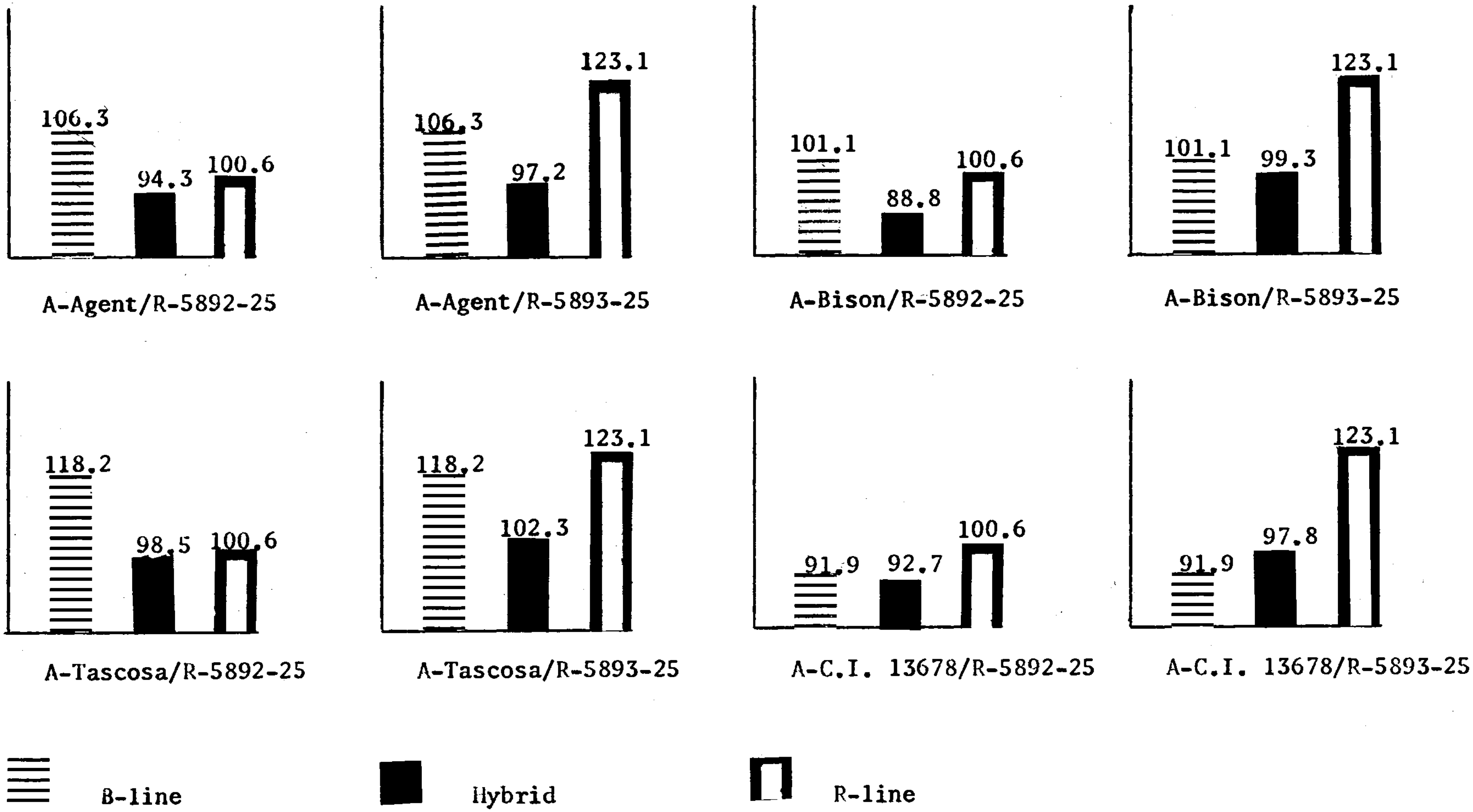

Figure 2. Tiller number comparison of hybrids and their respective parents - mean of three tests.

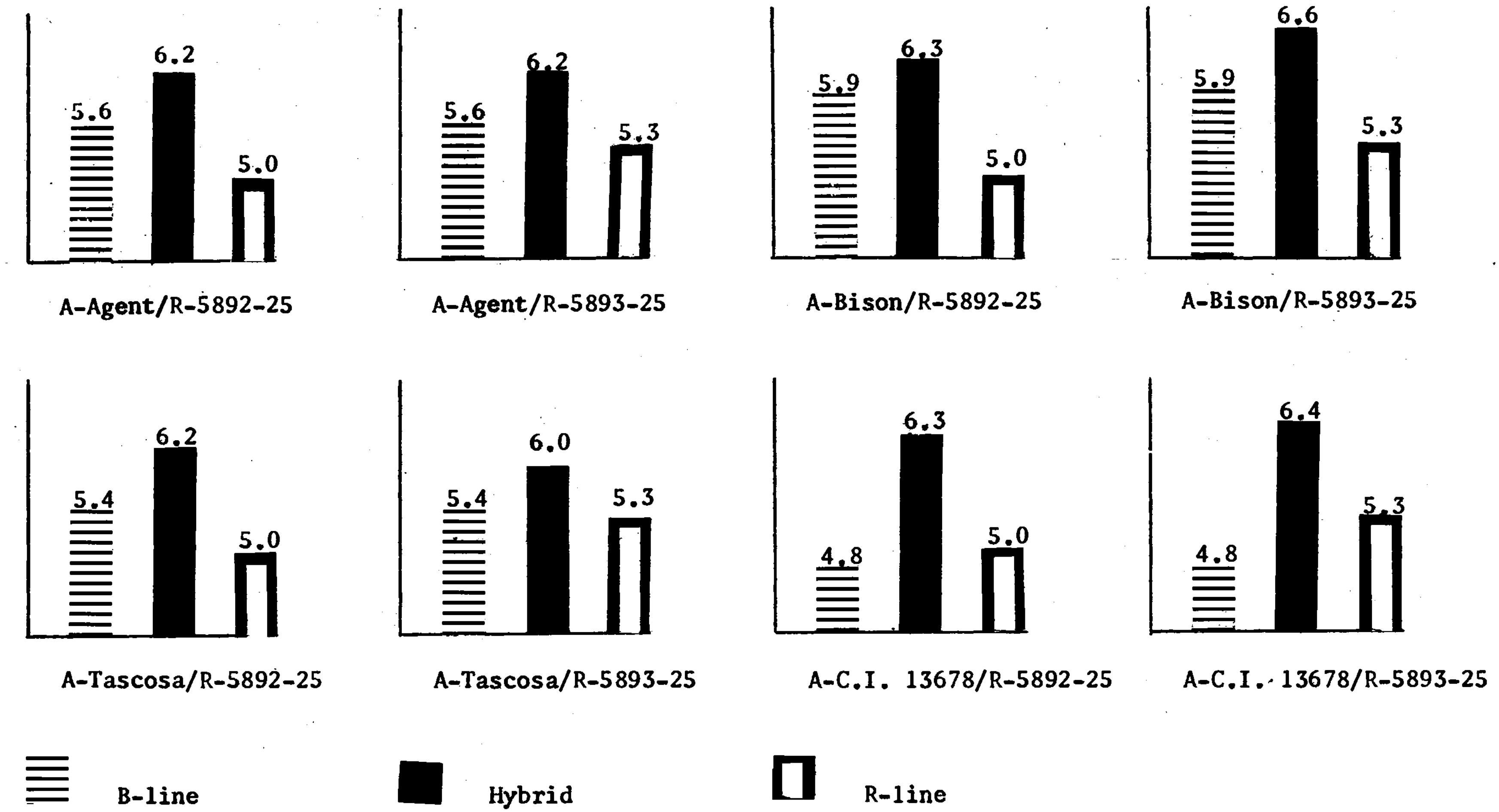

Figure 3. Kernel weight comparison in gms/200 kernels of hybrids and their respective parents - mean of three tests.

All hybrids except A-C.I. 13678/R-5892-25 were similar to their respective mid-parent values for kernels/spike. This hybrid, one of the four top-yielding hybrids, had significantly fewer kernels than its mid-parent (Appendix Table XXV). These data imply that kernels/spike play a minor role in the expression of heterosis for yield expressed by hybrids in this test. Figure 4 presents the comparisons of kernels/spike of the hybrids and their parents. These results do not completely agree with those reported by Merkle et al. (35) and McIlrath (33) who suggest that kernels/spike are of major importance in the expression of heterotic yields. Combining ability analysis, which will be discussed later, implies that kernels/spike may be more important than indicated by these heterosis data obtained in this study.

All eight hybrids in the study exhibited significant mid-parent heterosis for test weights as presented in Appendix Table XXV. Four hybrids had significantly higher test weights than their high-parent. It was interesting to note that the same four hybrids which exhibited heterosis for yield were the same four exhibiting heterosis for test weight. Figure 5 presents graphic comparisons of the test weights of the hybrids and their parents. When the four hybrids exhibiting high-parent heterosis for test weight were compared to the high-check variety, they had significantly lower test weights than the check as shown by Appendix Table XXII.

There were no differences between the hybrids and their respective mid-parent values with respect to heading date (Appendix Table XXV); all eight hybrids being similar to their respective mid-parent values. The data compiled on heading date indicated no heterotic responses were obtained with this group of materials. Appendix Table XXIII presents com-

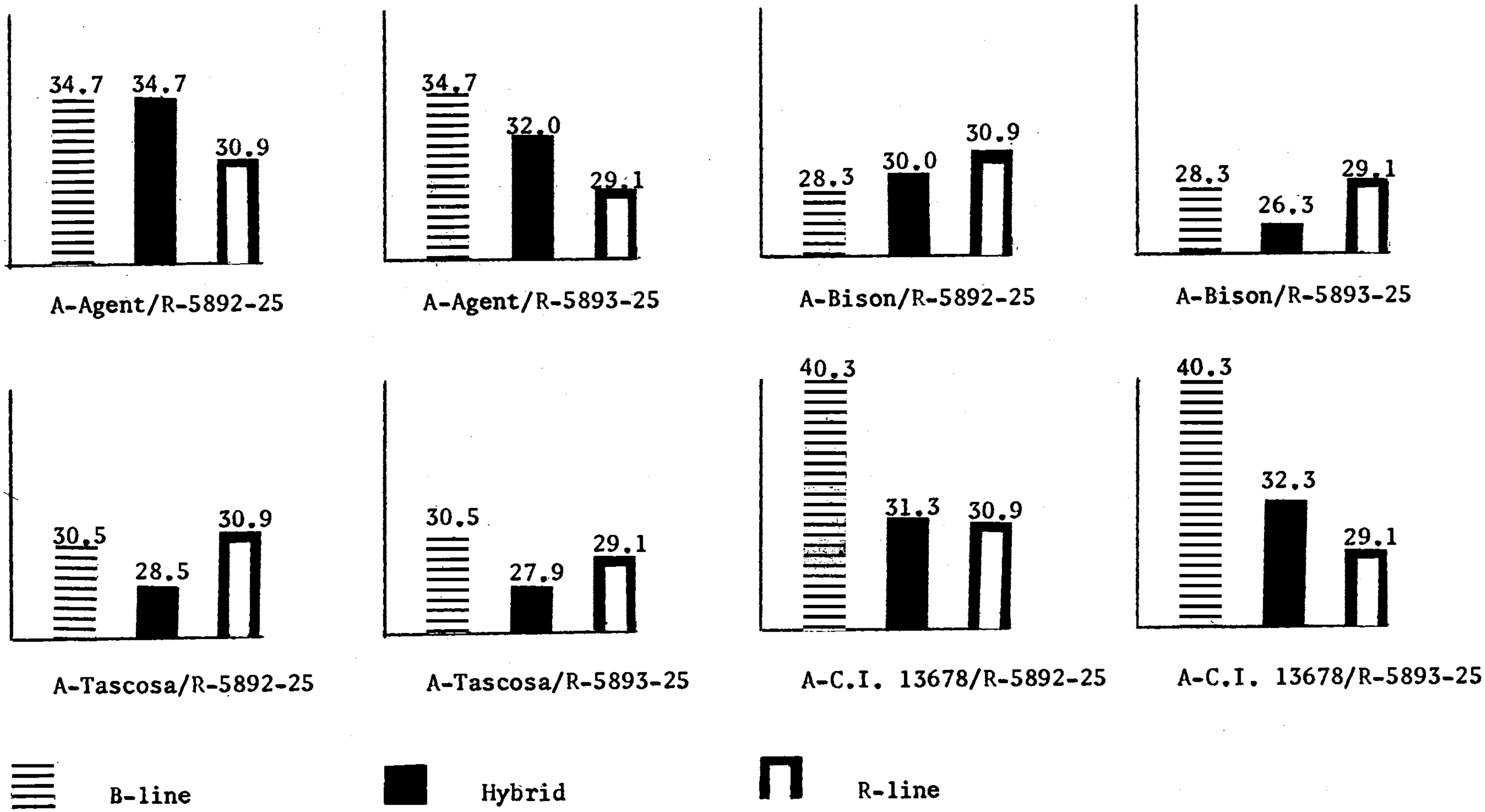

Figure 4. Kernels/spike comparison of hybrids and their respective parents; average number of kernels/spike - mean of three tests.

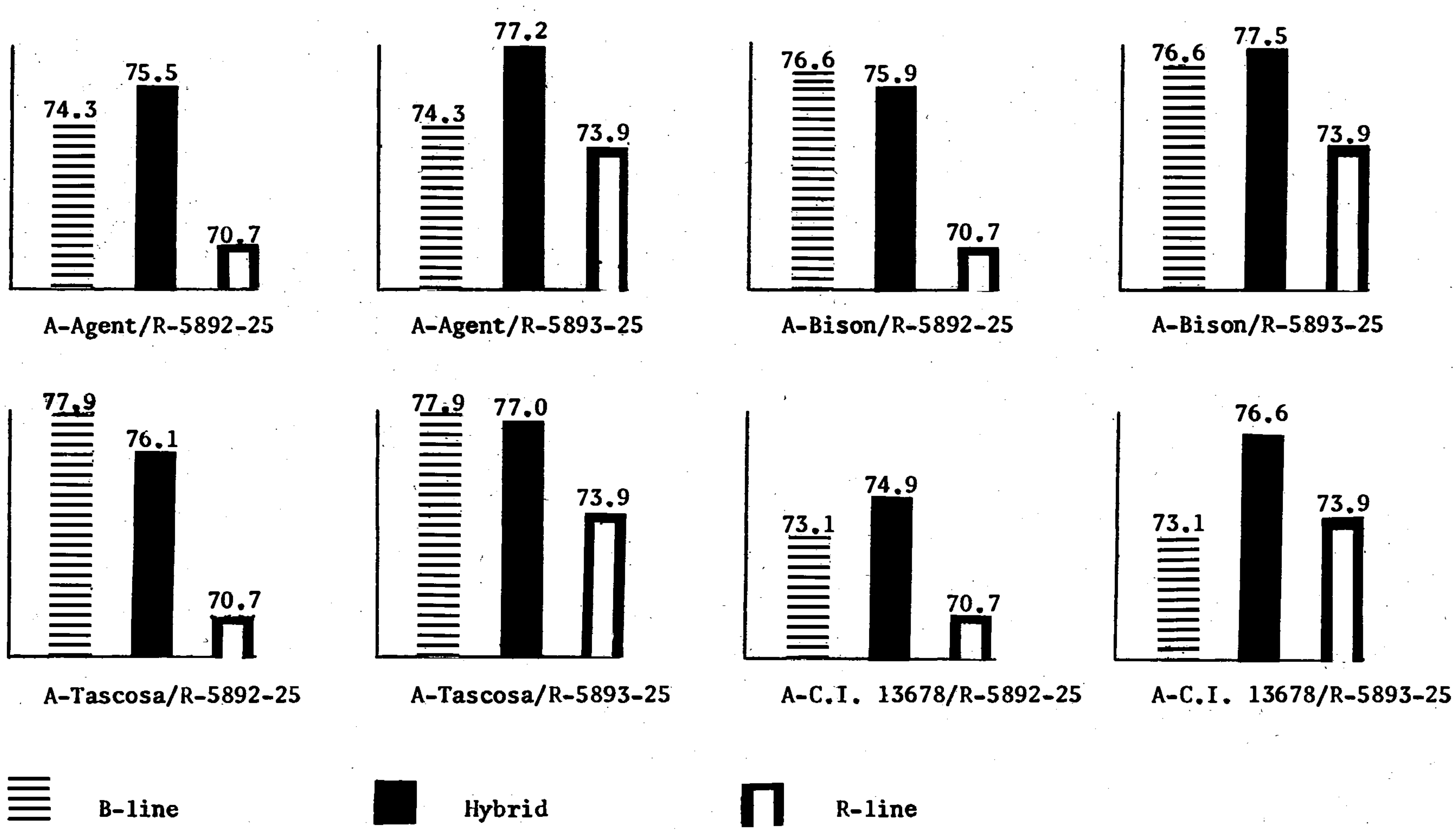

Figure 5. Test weight comparison of hybrids and their respective parents in kg/hl - mean of three tests.

parisons of the hybrids, their parents, and check varieties in this study. As can be seen from this table, hybrids of C.I. 13678 were much earlier than those involving any other male sterile line.

Three hybrids were significantly taller than their respective mid-parent values. Two of these, A-Agent/R-5893-25 and A-Bison/R-5892-25, had rather tall female parents. The third, A-C.I. 13678/R-5893-25, had for its female parent the semi-dwarf line C.I. 13678. Although it was not significant, this hybrid was taller than its tall parent. No hybrid in the study exhibited significant high parent heterosis for plant height.

Combining ability

The method outlined by Kambal and Webster (21) for the evaluation of general and specific combining ability for A x R sorghum hybrids was followed in this study. Analysis of variance was conducted on the hybrids alone for yield, tiller number, kernel weight, kernels/spike, test weight, heading date, and plant height. The sources of variation and the mean squares for all characters are presented in Table V. All characters except tiller number exhibited significant variation for either A-lines, R-lines, A-line x R-line interaction, or a combination of these sources of variation.

Combining ability estimates, both general and specific, were computed for the seven characters studied and are presented in Table VI. The estimates of the components of variances for combining ability and standard errors obtained from the analysis of variance for the seven traits of the eight hybrids are presented in Table VII. These estimates of variance for combining ability were used in obtaining the information

TABLE V

MEAN SQUARES FROM COMBINED ANALYSES OF VARIANCE OF DATA FROM HYBRIDS GROWN IN THREE ENVIRONMENTS

Source of Variation	d.f.	Yield	Tiller Number	Kernel Weight	Kernels per spike	Test Weight	Heading Date	Plant Height
Environments	2	3129.70**	1698**	.69**	3180.36**	41.10**	155.17**	787.18**
Reps in Environments	6	187.31**	567	.57**	34.08**	.34	14.48**	21.90**
A-Lines	3	254.56**	141	.62**	122.33**	2.05**	58.42**	43.24**
A-Lines x Environments	6	90.95**	213	.27*	21.01*	2.03**	10.85**	3.95
R-Lines	1	15.58	561	.08	40.50*	23.34**	4.02	66.12**
R-Lines x Environments	2	48.71*	534	.95**	3.04	1.48*	.21	4.54
A-Lines x R-Lines	3	58.62**	53	.14	19.50	.46	.23	4.20
A-Lines x R-Lines x Environments	6	20.56	128	.03	6.32	.98	.83	2.17
Error	42	13.04	204	.08	8.52	.42	1.81	2.53

on general and specific combining ability.

TABLE VI

GENERAL AND SPECIFIC COMBINING ABILITY ESTIMATES FROM COMBINED ANALYSES OF VARIANCE OF DATA FROM HYBRIDS GROWN IN THREE ENVIRONMENTS

Character	Gca (A-line)	Gca (R-line)	Sca
Yield	6.97**	0.00	4.22**
Tiller Number	0.00	0.27	0.00
Kernel Weight	0.20**	0.00	0.01
Kernels/Spike	4.89**	0.64	1.46
Test Weight	0.09	0.60**	0.00
Heading Date	2.64**	0.10	0.00
Plant Height	2.07**	1.65**	0.22

Analysis of variance of yield data indicated that highly significant variation was present among A-lines (Table V). Highly significant variances were also obtained from A-line x R-line interactions. No significant variation was observed among R-lines. Estimation of combining ability values by means of variance components provided significant general combining ability estimates for A-lines, but these estimates were not significant for R-lines (Tables VI and VII). Estimates of specific combining ability were significant for yield, but were not

TABLE VII

COMBINING ABILITY VARIANCE COMPONENTS AND THE STANDARD ERROR FOR SEVEN TRAITS ON HYBRIDS GROWN IN THREE ENVIRONMENTS

Character	Components of Variance[1]	Estimates of Variance Components
Yield	σ^2_A	6.97±2.29**
	σ^2_R	0.00
	σ^2_{AR}	4.22±3.24**
Tiller Numbers	σ^2_A	0.00
	σ^2_R	0.27±0.54
	σ^2_{AR}	0.00
Kernel Weight	σ^2_A	0.20±0.13*
	σ^2_R	0.00
	σ^2_{AR}	0.01±0.18
Kernels/Spike	σ^2_A	4.89±1.86**
	σ^2_R	0.64±0.99
	σ^2_{AR}	1.46±1.92
Test Weight	σ^2_A	0.09±0.30
	σ^2_R	0.60±0.27**
	σ^2_{AR}	0.00
Heading Date	σ^2_A	2.64±0.86**
	σ^2_R	0.10±0.46
	σ^2_{AR}	0.00
Plant Height	σ^2_A	2.07±1.03**
	σ^2_R	1.65±0.73**
	σ^2_{AR}	0.22±1.07

[1]σ^2_A = variance component for Gca for A-lines, σ^2_R = Gca for R-lines, and σ^2_{AR} = Sca.

significant for any other character. The relative magnitude of general to specific combining ability for yield was 7:4, indicating that general combining ability was approximately twice as important for this trait as specific combining ability.

Comparisons of the mean yield of the hybrids from the three tests grouped by A-line are presented in Table VIII. The best combiner among the A-lines was Agent; however, it was not significantly better than C.I. 13678. Both of these A-lines were significantly better combiners than Bison, which was significantly better than Tascosa. Three hybrids yielded significantly higher than the mean yield of all the hybrids while only one yielded significantly lower. The three high yielding hybrids were A-Agent/R-5893-25, A-Agent/R-5892-25, and A-C.I. 13678/R-5893-25. A-Tascosa/R-5892-25 yielded significantly below the mean of the hybrids.

Analysis of variance for yield indicated that significant genetic variation was present among the hybrids. Combining ability estimates confirm the presence of both general and specific combining ability, implying the importance of both additive and non-additive genetic variance for this trait. The relative magnitude of general to specific combining ability shows additive genetic effects to be more important than non-additive. The general combining ability estimates indicated that the majority of variation for yield was due to differences among A-lines rather than R-lines.

No significant variation was observed among A-lines, R-lines or from A-line x R-line interactions for tiller number (Table V). Also the combining ability estimates for tiller number were not significant as can be seen in Tables VI and VII. Based on these data, it appeared there was no significant variation among hybrids for tillering. Heterosis data indicated that tillering in all hybrids was reduced in comparison to the mid-parent value.

TABLE VIII

MEAN YIELD OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. Yield of Hybrids (gm/plot)
A-Agent	447 a[1]
A-C.I. 13678	434 a
A-Bison	400 b
A-Tascosa	363 c

[1]Means followed by the same letter are not significantly different at the .05 level.

Comparisons of the mean kernel weight of the hybrids grouped by A-lines are presented in Table IX. Highly significant variation among A-lines was indicated by analysis of variance for kernel weight as shown in Table V. There was no significant variation among R-lines, nor was there any significant interactions between A-lines and R-lines. Two A-lines, Bison and C.I. 13678, produced hybrids with significantly higher kernel weights than the other two A-lines, Agent and Tascosa. There was no difference between mean kernel weights of hybrids involving

Bison and C.I. 13678. There was no differences in kernel weights of the hybrids of Agent and Tascosa.

TABLE IX

MEAN KERNEL WEIGHT OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. Kernel Weight of Hybrids (gms/200 kernels)
A-Bison	6.48 a
A-C.I. 13678	6.39 a
A-Agent	6.16 b
A-Tascosa	6.08 b

General combining ability was significant for A-lines but not for R-lines as presented in Table VI. Specific combining ability estimates were not significant for kernel weight. The ratio of general to specific combining ability of 20:1 for kernel weight indicated that the genetic variability was predominately additive. As can be seen from Tables VI and VII, much more variability was present among A-lines than among R-lines. It was noted that heterosis data indicated that kernel weight was of major importance in the expression of heterosis for yield, however, the better combining A-lines for kernel weight were not the same lines which produced the better yielding hybrids.

Analysis of variance for kernels/spike indicated that significant variation occurred among R-lines and highly significant variation was present among A-lines (Table V). Comparisons of the hybrids grouped by R-line and by A-line are presented in Tables X and XI, respectively. These data indicate that hybrids involving the R-line R-5892-25 had significantly more kernels/spike than did those involving R-5893-25. Hybrids involving the A-lines Agent and C.I. 13678 had significantly more kernels/spike than did those involving Bison and Tascosa. It was noted in the heterosis data that hybrids involving the A-lines Agent and C.I. 13678 were the only hybrids exhibiting heterosis for yield. Although this association between yield and kernels/spike was not observed in the heterosis data, it appears that heterosis for yield may be largely affected by the number of kernels/spike.

TABLE X

MEAN KERNELS/SPIKE OF HYBRIDS GROUPED BY R-LINE

R-Line	Ave. Kernels/Spike of Hybrids (No.)
R-5892-25	31.1 a[1]
R-5893-25	29.6 b

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XI

MEAN KERNELS/SPIKE OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. Kernels/Spike of Hybrids (No.)
A-Agent	33.3 a[1]
A-C.I. 13678	31.8 a
A-Bison	28.2 b
A-Tascosa	28.2 b

[1]Means followed by the same letter are not significantly different at the .05 level.

Significant general combining ability variance for kernels/spike was detected for A-lines, however, no specific combining ability variance was observed (Tables VI and VII). General combining ability variance for R-lines was not significant despite the significant difference in the mean number of kernels/spike from hybrids derived from the two R-lines. Combining ability estimates indicate that the predominant gene action involved with kernels/spike is additive, and that considerably more variation in kernels/spike was present among A-lines than among R-lines.

Highly significant variation among A-lines and R-lines was indicated by analysis of variance for test weight (Table V). The variation among A-lines appeared to be due to the differences between Bison and C.I. 13678. Hybrids involving the A-lines Agent and Tascosa were not significantly different from those involving either Bison or C.I. 13678 as indicated in Table XII. Comparison of the mean test weight of hybrids grouped by R-line is presented in Table XIII. Hybrids involving the R-line, R-5893-25, had a significantly higher mean test weight than those involving R-5892-25. The difference in mean test weights of the hybrids grouped by R-line was greater than the difference in mean test weights of the highest and lowest A-lines.

TABLE XII

MEAN TEST WEIGHT OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. T. W. of Hybrids (kg/hl)
A-Bison	76.7 a[1]
A-Tascosa	76.4 ab
A-Agent	76.4 ab
A-C.I. 13678	75.7 b

[1]Means followed by the same letter are not significantly different at the .05 level.

Combining ability estimates were significant only for general combining ability variance among R-lines (Tables VI and VII). Estimates of general combining ability variance among A-lines was not significant, although significant variation was observed among A-lines. The comparisons presented in Table XII indicate that variation was present only between the A-lines with the highest and lowest mean test weights, each of which was similar to the mean test weights of the hybrids involving the other two A-lines. The relative magnitude of the general combining ability estimates for A-lines and R-lines was 1:6, indicating that much more variability for test weight was present in the male parent. These data indicate that additive genetic variance among R-lines was the predominant type of genetic variance.

TABLE XIII

MEAN TEST WEIGHT OF HYBRIDS GROUPED BY R-LINE

R-Line	Ave. T. W. of Hybrids (kg/hl)
R-5893-25	76.7 a[1]
R-5892-25	75.7 b

[1]Means followed by the same letter are not significantly different at the .05 level.

Variability among A-lines was highly significant for heading date as indicated in Table V. Significant variability was not observed among R-lines or for A-line x R-line interactions. One A-line, C.I. 13678, produced hybrids which were significantly earlier in heading date than hybrids derived from any other A-line. Tascosa produced hybrids significantly earlier in heading date than those produced by either Agent or Bison. No difference in heading date was observed between Agent and Bison hybrids. Mean heading dates for hybrids grouped by A-line are compared in Table XIV.

TABLE XIV

MEAN HEADING DATE OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. Heading Date of Hybrids (days from April 30)
A-C.I. 13678	7.8 a[1]
A-Tascosa	10.2 b
A-Bison	11.4 c
A-Agent	11.8 c

[1]Means followed by the same letter are not significantly different at the .05 level.

With regard to heading date, the general combining ability variance, estimate for A-lines was the only combining ability variance estimate to show significance. This is apparent from the data presented in Tables VI and VII. These data indicate that the genetic variance present for heading date is predominately additive and is considerably larger among the A-lines than the R-lines.

Considerable variability was observed among the hybrids for plant height. As can be seen from the data presented in Table V, significant variation was due to both A-lines and R-lines. No A-line x R-line interactions were observed. Although many hybrids were quite tall, lodging was not a major factor during this study. Some lodging was present at Stillwater in 1969, however, the hybrids were not affected more adversely than the parental lines.

Significant variability was observed among the A-lines as shown in Table V, and those hybrids involving Tascosa were significantly shorter than hybrids derived from any other A-line. Comparison of the mean plant height of the hybrids grouped by A-line is presented in Table XV. Although C.I. 13678 is a semi-dwarf line, the hybrids involving C.I. 13678 were significantly taller than the Tascosa hybrids. This is not unusual since the semi-dwarf character is recessive and C.I. 13678 was not significantly shorter than Tascosa. The hybrids grouped by R-line are compared for mean plant height in Table XVI. Hybrids involving the R-line, R-5892-25, were significantly shorter than those involving R-5893-25. The mean height of hybrids involving R-5892-25 were similar to those involving the A-line, A-C.I. 13678.

Combining ability estimates for plant height are presented in Tables VI and VII. General combining ability estimates were significant for both A-lines and R-lines; however, specific combining ability estimates were not significant. The ratio of general to specific combining ability variances was approximately 19:1, indicating a predominance of additive genetic variance. The relative magnitude of general combining ability variances of A-lines and R-lines was approximately 1:1, indicating that variability among A-lines equal to that among R-lines.

TABLE XV

MEAN PLANT HEIGHT OF HYBRIDS GROUPED BY A-LINE

A-Line	Ave. Ht. of Hybrids (cm.)
A-Agent	97.5 a[1]
A-Bison	97.5 a
A-C.I. 13678	93.0 b
A-Tascosa	89.7 c

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XVI

MEAN PLANT HEIGHT OF HYBRIDS GROUPED BY R-LINE

R-Line	Ave. Ht. of Hybrids (cm.)
R-5893-25	96.8 a[1]
R-5892-25	91.9 b

[1]Means followed by the same letter are not significantly different at the .05 level.

Quality

Complete milling and baking analyses were conducted on the hybrids, their parents, and check varieties to determine the effect of the incorporation of exotic T. *timopheevi* cytoplasm into common bread wheats. Quality characters involved in the analysis included the wheat protein, flour protein, flour yield, corrected absorption, average mixing time, loaf volume, corrected loaf volume at 13% protein, grain and texture, and the external loaf score. The results of the quality analyses are presented in Appendix Table XXIX. The B-line counterparts of the A-lines involved in the hybrids were representative of the female parents.

Analyses of variance were not conducted on quality characteristics as seed from the Stillwater and Goodwell nurseries were composited in 1968 in order to provide sufficient seed for the quality analyses. There was sufficient seed in 1969 from the Stillwater nursery to allow complete milling and baking analyses. The mean value of the hybrids and the parental lines are presented for each of the nine quality characters in Table XVII. Hybrids appeared to be equal to or slightly better than the mean parental value for all quality traits. These results agree with those obtained by McNeal et al. (34) and Rooney et al. (46). Dr. D. C. Abbott[1] classified all hybrids as acceptable for milling and baking properties.

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[1]Dr. D. C. Abbott, Biochemistry Department, Oklahoma State University, Stillwater, Oklahoma.

TABLE XVII

MEAN VALUES OF HYBRIDS AND PARENTAL LINES FOR NINE QUALITY CHARACTERS - THREE ENVIRONMENTS[1]

Character	Mean Value			
	Hybrids	R-lines	B-lines	Parental
% Wheat Protein	15.0	15.4	14.6	14.9
% Flour Protein	13.0	13.4	12.5	12.8
% Flour Yield	66.2	66.1	64.3	64.9
Corrected Absorption	61.6	62.8	60.5	61.3
Average Mixing Time (min)	3:33	4:42	3:18	3:47
Loaf Volume (cc)	919	897	880	885
Loaf Volume (corrected for 13% protein)	918	877	903	894
Grain and Texture (15 max)	12+	11	12	12
External Loaf Score (5 max)	4	3+	3+	3

[1]Mean of two analyses, one conducted on a composite of Stillwater and Goodwell nurseries in 1968 and the other from the Stillwater nursery in 1969.

CHAPTER V

SUMMARY AND CONCLUSIONS

Heterosis and combining ability for seven agronomic traits were studied on eight wheat hybrids developed by crossing each of four male sterile lines with two restorer lines. The hybrids were evaluated in nursery plots under three different environments in replicated tests at solid seeding rates. Characters for which analyses were conducted included yield, tiller number, kernel weight, kernels/spike, test weight, heading date, and plant height. Also, seed set percentages were calculated to evaluate the fertility restoration expressed in the hybrids. Complete milling and baking quality was evaluated, but was not statistically analyzed.

High-parent and mid-parent heterosis was measured for each of the seven agronomic traits studied. Estimates of general combining ability for both A-lines and R-lines and specific combining ability were calculated by the method used by Kambal and Webster involving A x R hybrids in sorghum. The combining ability estimates were used to determine the relative additive and non-additive effects of genes influencing the various agronomic traits studied. Seed set percentages were used as an evaluation of the fertility restoring ability exhibited by the two R-line selections and the ease of restoring fertility to the A-lines. Seed set percentages were also used to determine if the level of restoration would affect heterosis and combining ability estimates. Milling and baking analyses were conducted to evaluate the effect of the exotic T. timopheevi cytoplasm on the quality of bread wheats and to give quality information on the hybrids in relation to their parents.

Fertility restoration of the hybrids was good. Seed set on the hybrids averaged 90% of that of the normal varieties. Hybrids involving the R-line, R-5892-25, appeared to be slightly better restored than those with R-5893-25 as the restorer parent. There were significant differences observed in the ease with which the A-lines were restored. Based on the seed set data, fertility was somewhat more easily restored to the Agent and Bison A-lines than to Tascosa or C.I. 13678 A-lines. It was interesting to note that although fertility restoration was not as good in C.I. 13678, hybrids involving this A-line expressed heterosis for yield. It was concluded from these data that the fertility restoration was sufficient to eliminate bias from estimates of heterosis and combining ability.

Based on the combined analysis of three tests, significant mid-parent heterosis was observed in four hybrids for yield, three of which also exhibited significant high-parent heterosis of 16-18%. No hybrid yielded significantly higher than the highest yielding check variety, although all four hybrids exhibiting mid-parent heterosis were similar in yield to the highest yielding check variety. All hybrids had significantly fewer tillers than their respective mid-parent values. It was concluded from these results that tillering apparently was not a major contributor to heterosis for yield exhibited in this study. All eight hybrids exhibited significant high-parent heterosis for kernel weight. Only one hybrid had a lower kernel weight than the high-check variety. Results obtained on kernel weight agree with that of other workers (7, 19, 33) and it was concluded that this trait was important in contributing to the yield of heterotic hybrids. Seven hybrids were equal to their respective mid-parent values for kernels/spike indicating that this trait has a minor role in the expression of heterotic yields obtained in this study. Four hybrids exhibited high-parent heterosis for test weight. These four hybrids were the same four hybrids which exhibited mid-parent heterosis for yield. These results imply that test weight is closely associated with heterotic yields. No heterosis, either positive or negative, was observed regarding heading date. Three hybrids possessed significant mid-parent heterosis for plant height.

Combining ability estimates, both general and specific, were calculated for the seven agronomic characters studied. All characters except tiller number expressed significant general combining ability. The only trait that exhibited significant specific combining ability estimates was yield. Differences were noted to occur between the A-lines and R-lines for general combining ability. There was more variability among A-lines than among R-lines for yield, kernel weight, kernels/spike, heading date, and plant height. More variability was found among the R-lines for test weight than among A-lines. These data indicate that all traits were predominately controlled by additive genetic effects and, with the exception of yield, are not greatly influenced by non-additive effects. The relative magnitude of general to specific combining ability for yield was 7:4, indicating that additive effects were approximately twice as important as the non-additive effects. The prevalence of the additive genetic variance present for all traits involved in this study indicates that selection procedures designed to isolate superior homozygous lines could be effective in a breeding program to increase wheat yields. However, significant heterosis for yield and the evidence of non-additive genetic effects implies that hybridization would also be effective using certain male sterile and restorer lines.

Examination of the milling and baking data indicated that A x R wheat hybrids exhibited quality traits equal to the mid-parent values. There were no detrimental effects observed on the hybrids, indicating that the exotic T. timopheevi cytoplasm created no adverse quality characteristics. All hybrids were considered by the cereal chemist to have acceptable milling and baking quality. It was concluded that if the quality of the parents is satisfactory, the quality of the hybrid will be also. It is possible that the parents could be matched up in such a way as to compliment one another for quality characters when the intermediate is desired.

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APPENDIX

TABLE XVIII

COMPARISON OF MEANS FOR YIELD OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Yield (gms/plot)
A-Agent/R-5893-25	451 a[1]
A-C.I. 13678/R-5892-25	451 a
A-Agent/R-5892-25	444 a
Triumph 64 (check)	437 ab
Tascosa	427 abc
A-C.I. 13678/R-5893-25	417 abcd
Bison	409 abcd
A-Bison/R-5893-25	404 bcd
A-Bison/R-5892-25	395 bcd
A-Tascosa/R-5893-25	390 cde
Agent	388 cde
C.I. 13678	382 cdef
R-5892-25	375 def
KAW 61 (check)	344 ef
R-5893-25	338 f
A-Tascosa/R-5892-25	336 f

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XIX

COMPARISON OF MEANS FOR TILLER NUMBER OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Tiller Number (Tillers/50cm^2)
R-5893-25	123.1 a[1]
Tascosa	118.2 a
Kaw 61 (check)	106.4 b
Agent	106.3 b
Triumph 64 (check)	104.3 bc
A-Tascosa/R-5893-25	102.3 bcd
Bison	101.1 bcd
R-5892-25	100.6 bcde
A-Bison/R-5893-25	99.3 cde
A-Tascosa/R-5892-25	98.5 cdef
A-C.I. 13678/R-5893-25	97.8 defg
A-Agent/R-5893-25	97.2 defg
A-Agent/R-5892-25	94.3 efgh
A-C.I. 13678/R-5892-25	92.7 fgh
C.I. 13678	91.9 gh
A-Bison/R-5892-25	88.8 h

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XX

COMPARISON OF MEANS FOR KERNEL WEIGHT OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Kernel Weight (gms/200 kernels)
A-Bison/R-5893-25	6.6 a[1]
Triumph 64 (check)	6.5 a
A-C.I. 13678/R-5893-25	6.4 ab
A-C.I. 13678/R-5892-25	6.3 abc
A-Bison/R-5892-25	6.3 abc
A-Agent/R-5892-25	6.2 abc
A-Agent/R-5893-25	6.2 abc
A-Tascosa/R-5892-25	6.2 abc
A-Tascosa/R-5893-25	6.0 bcd
Bison	5.9 cd
Kaw 61 (check)	5.9 cd
Agent	5.6 de
Tascosa	5.4 ef
R-5893-25	5.3 ef
R-5892-25	5.0 fg
C.I. 13678	4.8 g

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXI

COMPARISON OF MEANS FOR KERNELS/SPIKE OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Kernels/spike
C.I. 13678	40.3 a[1]
Agent	34.7 b
A-Agent/R-5892-25	34.7 b
A-C.I. 13678/R-5893-25	32.3 bc
A-Agent/R-5893-25	32.0 bc
A-C.I. 13678/R-5892-25	31.3 cd
R-5892-25	30.9 cde
Tascosa	30.5 cdef
A-Bison/R-5892-25	30.0 cdef
R-5893-25	29.1 defg
A-Tascosa/R-5892-25	28.5 efgh
Bison	28.3 efgh
A-Tascosa/R-5893-25	27.9 fgh
Kaw 61 (check)	27.2 gh
Triumph 64 (check)	26.9 gh
A-Bison/R-5893-25	26.3 h

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXII

COMPARISON OF MEANS FOR TEST WEIGHT OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Test Weight (kg/hl)
Kaw 61 (check)	78.8 a[1]
Tascosa	77.9 ab
A-Bison/R-5893-25	77.5 bc
A-Agent/R-5893-25	77.2 bc
Triumph 64 (check)	77.1 bcd
A-Tascosa/R-5893-25	77.0 bcde
A-C.I. 13678/R-5893-25	76.6 cde
Bison	76.6 cde
A-Tascosa/R-5892-25	76.1 de
A-Bison/R-5892-25	75.9 ef
A-Agent/R-5892-25	75.5 ef
A-C.I. 13678/R-5892-25	74.9 fg
Agent	74.3 g
R-5893-25	73.9 gh
C.I. 13678	73.1 h
R-5892-25	70.7 i

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXIII

COMPARISON OF MEANS FOR HEADING DATE OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Heading Date (days from April 30)
Triumph 64 (check)	2.9 a[1]
C.I. 13678	5.5 b
Kaw 61 (check)	6.7 bc
A-C.I. 13678/R-5893-25	7.4 c
A-C.I. 13678/R-5892-25	8.1 cd
Tascosa	8.9 de
A-Tascosa/R-5893-25	9.9 ef
A-Tascosa/R-5892-25	10.5 fg
Agent	11.2 fgh
A-Bison/R-5893-25	11.2 fgh
A-Bison/R-5892-25	11.5 gh
A-Agent/R-5893-25	11.7 gh
A-Agent/R-5892-25	11.9 h
R-5892-25	11.9 h
R-5893-25	12.0 h
Bison	12.2 h

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXIV

COMPARISON OF MEANS FOR PLANT HEIGHT OF HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS

Hybrid, Parent or Check	Mean Plant Height (cm)
C.I. 13678	85.8 a[1]
R-5892-25	86.6 a
Tascosa	87.1 a
Triumph 64 (check)	87.4 ab
A-Tascosa/R-5892-25	87.6 abc
A-C.I. 13678/R-5892-25	88.9 abc
Kaw 61 (check)	91.2 bcd
A-Tascosa/R-5893-25	91.4 cd
R-5893-25	93.7 de
A-Agent/R-5892-25	94.7 def
A-Bison/R-5892-25	96.5 efg
A-C.I. 13678/R-5893-25	96.8 efg
Bison	97.1 efg
Agent	98.6 fg
A-Bison/R-5893-25	98.9 g
A-Agent/R-5893-25	100.3 g

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXV

PERFORMANCE OF HYBRIDS EXPRESSED AS PERCENT OF MID-PARENT AND HIGH PARENT - BASED ON MEANS OF THREE TESTS

Hybrid	Yield		Tillers		Kernel Weight		Kernels/Spike		Test Weight		Heading Date		Plant Height	
	%MP	%HP	%MP	%HP	%MP	%HP	%MP	%HP	%MP	%HP	%MP	%HP	%MP	%HP
A-Agent/R-5892-25	116.2*	114.4*	91.1*	88.7*	117.0*	110.7*	105.8	100.0	104.3*	101.7*	109.1	100.0	102.5	96.1
A-Agent/R-5893-25	118.1*	116.2*	84.7*	79.0*	112.7*	110.7*	100.3	92.2	104.2*	104.0*	109.1	100.0	104.5*	101.8
A-Bison/R-5892-25	100.8	96.6	88.1*	87.8*	114.5*	106.8*	101.3	97.1	103.1*	99.2	100.0	100.0	105.0*	99.5
A-Bison/R-5893-25	108.0	98.8	88.6*	80.7*	117.8*	111.9*	91.6	90.4*	103.1*	101.2	91.7	91.7	103.4	101.8
A-Tascosa/R-5892-25	83.8	78.7	90.0*	83.3*	119.2*	114.8*	92.8	92.2	102.4*	97.7	100.0	83.3*	100.9	100.6
A-Tascosa/R-5893-25	101.8	91.3	84.8*	83.1*	111.1*	111.1*	93.6	91.5	101.4*	98.8	100.0	83.3*	101.1	97.6
A-C.I. 13678/R-5892-25	119.0*	118.1*	96.4	92.1*	128.6*	126.0*	87.9*	77.7*	104.3*	102.5*	100.0	66.7*	102.9	102.6
A-C.I. 13678/R-5893-25	115.8*	109.2	91.0*	79.4*	125.5*	120.8*	93.1	80.1*	104.2*	103.6*	100.0	66.7*	107.6*	103.2

TABLE XXVI

YIELD OF HYBRIDS EXPRESSED AS PERCENT OF THE BEST CHECK VARIETY - MEANS OF THREE TESTS

Hybrid	% of Best Check
A-Agent/R-5893-25	103.2
A-C.I. 13678/R-5892-25	103.2
A-Agent/R-5892-25	101.6
A-C.I. 13678/R-5893-25	95.4
A-Bison/R-5893-25	92.4
A-Bison/R-5892-25	90.3
A-Tascosa/R-5893-25	89.2
A-Tascosa/R-5892-25	76.8

TABLE XXVII

KERNEL WEIGHT OF HYBRIDS EXPRESSED AS PERCENT OF BEST CHECK VARIETY - MEANS OF THREE TESTS

Hybrid	% of Best Check
A-Bison/R-5893-25	101.5
A-C.I. 13678/R-5893-25	98.4
A-C.I. 13678/R-5892-25	96.9
A-Bison/R-5892-25	96.9
A-Agent/R-5892-25	95.3
A-Agent/R-5893-25	95.3
A-Tascosa/R-5892-25	95.3
A-Tascosa/R-5893-25	92.3

TABLE XXVIII

SEED SET PERCENT OF HYBRIDS, PARENTS, AND CHECK VARIETIES - MEANS OF THREE TESTS

Hybrid, Parent or Check	Mean Seed Set (%)
Bison	91.2 a[1]
Agent	90.7 ab
C.I. 13678	89.5 abc
R-5892-25	88.7 abcd
R-5893-25	86.8 abcd
A-Bison/R-5892-25	86.6 bcd
Triumph 64	85.6 cde
A-Agent/R-5892-25	84.7 de
Tascosa	84.4 de
Kaw 61	84.2 de
A-Agent/R-5893-25	82.0 ef
A-Bison/R-5893-25	79.2 fg
A-Tascosa/R-5892-25	76.5 g
A-C.I. 13678/R-5893-25	76.4 g
A-Tascosa/R-5893-25	76.2 g
A-C.I. 13678/R-5892-25	75.5 g

[1]Means followed by the same letter are not significantly different at the .05 level.

TABLE XXIX

AVERAGE QUALITY DATA FOR HYBRIDS, PARENTS, AND CHECK VARIETIES GROWN IN THREE ENVIRONMENTS[1]

Hybrid, Parent or check	Wheat Protein (%)	Flour Protein (%)	Flour Yield (%)	Corrected Absorption (%)	Average Mix Time (min)	Loaf Volume (cc)	Corrected Loaf Volume (at 13% prot)	G & T (15 max)	Ext. Loaf Score (5 max.)
Agent	15.3	13.5	66.3	59.9	3:39	866	839	12	3
Bison	15.1	13.1	66.3	61.0	3:17	959	954	13	3+
Kaw 61	12.8	11.4	67.6	60.6	5:10	810	891	10+	2+
Tascosa	14.7	12.6	67.3	62.6	3:33	856	874	11+	3
Triumph 64	14.3	12.6	68.7	61.1	3:00	875	897	12	3+
C.I. 13678	13.4	10.9	57.2	58.8	2:46	839	946	12	3
R-5892-25	16.2	14.2	64.9	63.6	4:09	973	913	12	4+
R-5893-25	14.6	12.6	67.3	62.0	5:15	820	840	10	3
A-Agent/R-5892-25	15.8	14.0	66.7	61.4	3:32	944	894	12+	4+
A-Agent/R-5893-25	15.2	13.5	68.4	61.1	3:31	861	836	12	3
A-Bison/R-5892-25	15.1	13.3	67.9	62.1	3:25	960	945	13	4+
A-Bison/R-5893-25	14.8	13.0	69.3	62.2	4:02	961	964	13	4
A-Tascosa/ R-5892-25	15.7	13.4	64.2	62.6	3:40	930	913	12+	4
A-Tascosa/ R-5893-25	15.0	12.8	66.0	61.6	4:18	908	918	12	4+
A-C.I. 13678/ R-5892-25	14.8	12.7	63.1	61.2	2:45	918	933	13	4
A-C.I. 13678/ R-5893-25	13.7	11.5	64.3	60.3	3:11	869	946	12	3+

[1]Average of two analyses. One analyses conducted on composite of Stillwater and Goodwell nursery in 1968; the other conducted on Stillwater nursery in 1969.

VITA

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