A STUDY OF HETEROSIS IN INTERSPECIFIC CROSSES OF BOTHRIOCHLOA

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Bachelor of Science
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1961

Submitted to the Faculty of the Graduate School of
The Oklahoma State University
in Partial fulfillment of the requirements
for the degree of
DOCTOR OF PHILOSOPHY
May, 1965

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A STUDY OF HETEROSIS IN INTERSPECIFIC
CROSSES OF BOTHRIOCHLOA

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ACKNOWLEDGEMENTS

The author would like to take this opportunity to express his appreciation for the valuable advice, guidance, and encouragement throughout the course of this study by his major advisor, and chairman of his graduate committee, Dr. J. R. Harlan. The author would also like to thank the other members of his advisory committee: Dr. A. M. Schlehuber, Dr. J. M. J. deWet, Dr. L. W. Reed, and Dr. L. H. Bruneau for their valuable advice and assistance in writing this dissertation.

Gratitude is expressed to Dr. R. M. Morrison, Bob Walls, Robert Ahring, and Bill Richardson for their able assistance in this study.

Appreciation is also expressed to the United States Department of Health, Education, and Welfare for the National Defense Graduate Fellowship, the National Science Foundation and Oklahoma State University Department of Agronomy for providing assistantship funds and facilities for conducting the study.

The author is also grateful to his wife, Jean, for typing the manuscript and for her patience and encouragement.

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INTRODUCTION

Heterosis is a phenomenon that is at once intriguing and economically important. It is manifested in different groups of organisms, being by no means confined to plants. Heterosis in various groups of organisms is not everywhere the same phenomenon, but these various manifestations probably have much in common and a satisfactory explanation of one will aid considerably in understanding others.

In recent years there has been an increased interest in heterosis resulting from population crosses of various species. The interest in heterosis stems partly from the agricultural superiority of the hybrids over their open-pollinated or pure line parents and partly from the fact that such hybrids presumably represent good experimental material for the study of certain gene actions. There is a need for more information relative to the characterization and magnitude of hybrid vigor to provide a basis for more efficient breeding procedures. Our limited understanding of the cause of heterosis does not provide a basis for predicting the relative amount of heterosis expected in crosses of parents with varying degrees of genetic diversity, but experiments indicate that crosses of unrelated inbred lines of corn show greater heterosis than crosses of related lines. The genetic differences between varieties have probably arisen through isolation accompanied by a combination of mutation, genetic drift, and selection in different environments. Therefore, the degree of geographical separation and the degree of ancestral relationship can be used as an indication of genetic divergence.

The superiority of artificially produced hybrids over their open-pollinated or pure line varieties has been shown in corn, sorghum, cotton, and many other crops. These hybrid populations have produced higher yields, phenotypically more uniform populations, improved quality of the product, and are buffered against environmental variations. The manifestations of heterosis have already increased the value of our corn and sorghum crops by millions of dollars annually and its potential for other crops is being realized and exploited. With the ever growing need to increase production to meet the demands of the rapidly increasing population, the effects of heterosis will need to be exploited on a very large scale.

The objective of this investigation was to compare certain interspecific F_1 hybrids of *Bothriochloa* with their respective parents to determine if heterosis exists and to measure its magnitude, if present. To make this comparison, both green and dry weight yields were determined along with plant height, leaf height, crown width, percent seed set, inflorescence characteristics, and winter hardiness.

In *Bothriochloa*, apomixis can be used to fix F_1 hybrids, but little is known of heterosis in this genus.

REVIEW OF LITERATURE

A. Explanations of Heterosis: Dr. J. G. Koelreuter (1776) was one of the first modern hybridizers of plants and he noted some impressive examples of greater luxuriance in his *Nicotiana* hybrids. Koelreuter had no suggestions as to why the hybrids should exceed their parents in general vigor, and consequently had no concept of heterosis. Probably every hybridizer since the time of Koelreuter has noticed the greater vigor of some hybrids over their parents. Knight (1799) noted the superiority of hybrids over pure types in many plants and concluded that "nature intended that a sexual intercourse should take place between neighboring plants of the same species." Although he advanced a theory concerning physiological vigor and its decline, he did not recognize the heterosis concept.

Darwin (1868) crossed and selfed plants from the same stock and raised plants from each of two types of seed from *Zea mays*. He noted that in many plants that cross-fertilization resulted in increased size, vigor, and productiveness, and that inbreeding usually caused deleterious effects on the plant population. Darwin also demonstrated that an increase in vigor was not a direct result of crossing, since crosses involving different flowers on the same plant and closely related flowers did not cause an increase in vigor. He concluded that the benefit of crossing was only important if the plants which were crossed differed in some characteristic.

Shull (1905) first recognized a case of hybrid vigor in the result of a cross between a so-called Russian sunflower and the wild Helianthus annuus. Both parent types were approximately six feet in height and the tallest of the F_1 hybrids was 14.25 feet in height. Shull concluded that the hybrid vigor resulting from crosses was due to the unlikeness in the constitution of the uniting gametes.

The concept of East and Shull was that both heterosis and the decrease in vigor due to inbreeding naturally cross-fertilized species were manifestations of one phenomenon and that this was closely tied to amount of heterozygosity. Crossing produces heterozygosity in all characters by which the parents differ and inbreeding tends to produce homozygosis automatically. Shull 1914 stated:

> My investigations on the effects of cross and self fertilization in maize has led me as early as 1907 to the conclusion that hybridity itself, the union of unlike elements, the state of being heterozygous, has a stimulating effect upon the physiological activities of the organisms, which effect disappears as rapidly as continuous inbreeding reduces the progenies to homozygous types. There is some danger of misconception due to the fact that all discussions of the stimulus of hybridity have taken place as their starting point for the sake of simplicity, the typical Mendelian distribution of germinal substances. The essential feature of the hypothesis may be stated in more general terms as follows: The physiological vigor of an organism as manifest in its rapidity of growth, its height and general robustness, is possibly correlated with the degree of dissimilarity in the gametes by whose union the organism was formed. The more numerous the differences between the uniting gametes, at least within certain limits, the greater on the whole is the amount of stimulation. These differences need not be Mendelian in their inheritance. To avoid the implication that all the geotypic differences which stimulate cell division, growth and other physiological activities of an organism are Mendeliau in their inheritance and also to gain brevity

> of expression, I suggest that instead of the phrases, stimulus of heterozygosity; heterozygotic stimulation; the word heterosis be adopted.

Bruce (1910) explained heterosis as the combined action of favorable dominant or partially dominant factors, based on mathematical expectations. Bruce demonstrated algebraically that the total number of dominant factors was greater in a hybrid population than in either of the parental populations. He then proposed the dominant factor hypothesis since there was a correlation between the number of dominant factors and heterosis.

Keeble and Pellew (1910) used a similiar hypothesis on a dihybrid basis to explain hybrid vigor in peas. They assumed that two factors were involved and that both showed dominance over the allelomorphic condition, hence the F_1 was taller than either parent because both factors were present together.

Jones (1917) restated Bruce's theory and added the concept of linkage. Jones pointed out that, with linkage the consequences of the dominance hypothesis were much closer to those postulating superior heterozygotes. If a detrimental recessive was linked with a favorable dominant, the heterozygous chromosome would be superior to both homozygotes, and the linked combination might not break up readily.

Ashby (1936) concluded that if dominance of linked factors is invoked to explain the larger primordial size in the embryo, it cannot explain how the metabolic rates in the hybrid (assimilation, respiration, growth rates) remain no greater than the parental rates. He therefore pointed out that the final size of a plant is the result of the initial size of its primordia and the relative growth rate. Since the relative growth rate of the hybrid has no advantage over its parents, size-heterosis must have been due to an initial advantage in embryo size. This was later disproved by East.

East (1936) gave the best idea of the way in which heterosis is expressed when he said, "that invariably it is something that effects the organism as a whole. Its effect is comparable to the effect on a plant of the addition of a balanced fertilizer to the soil. In plants the root system is increased, the branching is more profuse, the leaves are larger and more abundant, growth takes place faster, at least in the early stages and often retains its place longer before showing the characteristic sigmoid curve that indicates approaching maturity." His idea may be stated briefly as follows: size traits are controlled by a large number of genes in various linkage groups; among these genes dominance is virtually non-existent, but there are numerous multiple allelic series; if in a given series each member effects a different physiological condition, then the heterozygous condition may be expected to produce cumulative results; that is if A_1 affects a somewhat different process than its allele A_2, A_1A_2 may have a greater effect than A_1A_1 or A_2A_2. This hypothesis implies some sort of complimentary action between alleles as A_1 supplies what is lacking in A_2, or <u>vice versa</u>.

The idea of superior heterozygotes has been upheld by Hull (1945) who suggested the word overdominance. He noted that in some cases the hybrid between two inbred maize lines had a greater yield than the sum of the two parents. This could not be explained by completely additive dominant gene unless it were assumed that a plant with no favorable dominants had a negative yield. He suggested that overdominance would explain heterosis as the genes would be physiologically stimulated at a locus by the presence of two different alleles.

Dobzhansky (1941) and his co-workers have recorded that in most species there has been, in the course of evolution, accumulations of deleterious recessive characters, which when homozygous reduce the efficency of the organism, but which in the heterozygous condition are without efficiency-reducing effects. The beneficial action of many of the dominant alleles probably is not the result either of directional mutation producing more favorable dominants or of selection tending to eliminate the unfavorable dominants. Instead, it may be due to the accumulation in the population of deleterious recessive mutations. These, if their effects are not too deleterious can often be piled up in significant numbers.

Castle (1946) emphasized the importance of interallelic action in relation to heterosis. He suggested that the effect of interallelic action of a single pair of genes is similiar to that of the killer mutation of Sonneborn, except that the action induced in the dominant gene by its sensitized recessive is beneficial.

Quinby and Karper (1946) reported on the case of a single locus heterosis involving alleles that were free from deleterious effects, but when in certain heterozygous combinations produced hybrid vigor. The conclusion was that heterosis in sorghum is a stimulation of tillering and cell divisionand that the stimulus to greater meristematic growth is enhanced by the heterozygous condition of the Mama gene.

Crow (1948) reported that the dominance hypothesis assumes that an individual with maximum vigor would be one in which all gene loci contain at least one dominant factor. The difference in vigor between any individual and its theoretical maximum would be determined by the number of homozygous recessive loci. The maximum vigor after hybridization would occur if each parent could supply all the dominant alleles lacking in the other, the hybrid thus receiving, at least one dominant gene at each locus. Assuming that all beneficial genes are completely dominant and all deleterious factors are recessive, the average decrease in selective value due to homozygous recessives is equal to the product of the number of gene loci and the average mutation rate. This is true of any population as long as it is at equilibrium regardless of the breeding structure or the amount of selective disadvantage of the individual recessive factors. Prevailing estimates of gene number and mutation rate make it appear unlikely that the product of gene loci and mutation rate is larger than .05. If one assumes that vigor is measurable in terms of selective value, this would be the maximum possible increase in vigor under the dominance hypothesis. Hence, any hybrids between natural populations that have larger increases in vigor must be explained by another hypothesis.

Dobzhansky (1949) reported on inversion heterozygotes in _Drosophila pseudoobscura_ which carry two chromosomes derived from the same population and are superior in adaptive value to the homozygotes. In _D. psedoobscura_ two different kinds of heterosis are well known. The first kind arises from the presence in the population of deleterious recessive mutant genes sheltered by their normal dominant alleles. Accumulation of these deleterious genes is a by-product of the mutation process. The second kind of heterosis is due to complexes of linked polygenes which give specific heterotic interaction effects in the heterozygote. This kind of heterosis is engendered by natural selection as a form of adaptation of the species to its environment. The balanced polymorphism enables an outbreeding species to obtain high mean fitness, and at the same time to preserve great evolutionary plasticity.

Hayman (1957) reported on a survey of different crops and showed that only in maize is yield heterosis directly related to epistasis. In other species and characters, heterosis seems to be a composite phenomenon in which the possible causes of heterosis are epistasis, overdominance, and the accumulation of favorable dominants in the heterozygotes.

Robinson and Cockerham (1961) reported on experimental results on yield and ear height from two open-pollinated parental varieties of corn and found that the relationship between performance and heterozygosity was linear for both yield and ear height. The genetic model of additive and dominant gene effects fits the results satisfactorily.

Penny, Russell, and Spraque (1962) employed the procedure of recurrent selection to obtain information on the types of gene action in yield heterosis in maize. When all the data were considered, the predominant type of selection appeared to have been for genes exhibiting complete or partial dominance or largely additive effects.

The evidence relating to heterosis suggests that the phenomenon is to be explained genetically in terms of various recombination effects. In some cases dominance is the important consideration, while in other cases heterozygosity or overdominance must be considered. In any event, it is the resulting specific gene action which lies at the basis of the physiological advantage or advantages which give rise to heterosis.

B. <u>The Measurement of Heterosis</u>: Hybrid vigor in cotton has been measured in various ways such as: plant height, total length of limbs, fertility of anthers, flower shedding, boll size, bolls per plant, yield of seed cotton, ginning percentage, staple length, seed weight, and node number. Kime and Tilley (1947) found a significant heterosis for yield of seed cotton, yield of lint, rate of blooming, earliness to opening and higher lint indices in Upland cotton. Jones and Loden (1951) reported increases in yield of F_1's over their most productive parent ranging from 0.8 to 47 percent with an average increase of 29.1 percent. This F_1 generation also had an average of 71 percent of its total yield harvested at first picking as compared to an average of 61 percent for the parent generation. Turner (1953) reported that boll number was more important than boll size in determining final yield with the hybrids tested. Hybrids that had higher lint yields, higher lint percent, larger bolls, longer and stronger lint, and that were earlier than the average of the parental lines were reported by Marani (1963). He concluded that the magnitude of average heterotic effects was greatest for yield, medium for boll weight and earliness, and relatively small for the remaining traits.

Hybrid vigor in corn and sorghum is measured in practically the same way: grain yields, stover yields, percentage of lodging, plant height, number of leaves on main stalk, weight of 100 kernels, node number, date of heading, and size of heads cr ears. Quinby (1963) reported on a hybrid, RS630, that was 5% earlier in blooming, 19% taller, produced 21% more tillers, and 11% wider, 2% longer, and 15% larger leaves, was 4% larger in stalk diameter, produced 97% more seed, had seeds 3% larger, threshed 7% higher, and had higher yields of stover by 44%, of heads 96%, grain by 106%, and forage by 71% than the average of its parents.

Webber (1900) crossed a Preuvian corn, Cuzco, with a native variety, Hickory King. The average height of the parental stock was eight feet three inches, while the cross averaged twelve feet four inches, an increase of four feet one inch. In a study of twelve open-pollinated varieties and their intercrosses, Lonnoquist and Gardner (1961) reported that the average yield of the parents ranged from 54.9 to 96.6 bushels per acre, whereas the F_1 yields ranged from 81.8 to 106.9 bushels per acre. The average heterosis relative to the mid-parent was 108.5% and relative to the high parent 102.8%. Ashby (1936) concluded that hybrid vigor in corn was only the result of an increased percentage of germination of hybrid seed and a greater initial weight of the embryo.

In studying the growth and development of two inbred lines of tomatoes and their hybrid, Whaley (1952) noted that the hybrid had a larger number of leaves, a larger leaf area, larger fruit size, and a greater yield than either parent. The hybrid also had a greater activity of the shoot apical meristem and appeared to have a higher catalase activity in the stem tips.

Coffman (1933) crossed Richland X Fulghum oats and the F_1 plants averaged 13.2% taller, bore 17.5% more culms per plant, weighed 48% more, and yielded 35.2% more grain and 51.3% more straw on the average than the larger parent. Coffman and Wiebe (1930) reported on oat crosses in which the height of the hybrids was 4.9% over the mean of their respective parents and the mean length of the panicle was 1.53% longer in the hybrid plants.

In interspecific Andropogon hybrids, Newell and Peters (1961) reported that the hybrid clones exceeded the average of the parent types by 20% in height of leaves, 9% in total height of plants, and 59% in total plant yields. The basal spread of the hybrids was intermediate between the two parents.

These examples are ample to show that heterosis may be measured in a great variety of ways. There are two ways of expressing heterosis a) in terms of increase of the hybrid over the average of the two parents and b) in terms of increase of the hybrid over the best parent. Heterosis would seem to be of little practical value unless the hybrid was demonstrably better than the best parent.

C. Some Examples in Different Crops:

Author	Year	Crop	Heterosis Expressed
Darwin	1876	Corn	Hybrid showed an eight percent increase in height over the best parent.
Richey	1922	Corn	82.4% of hybrids exceeded mid-parent and 55.7 exceeded high parent in yield.
Jones	1945	Corn	Hybrid showed 3 to 104% increase in yield and 0 to 9% increase in height over best parent.
Lonnoquist & Gardner	1961	Corn	Hybrid showed an average of 108.5% in yield relative to the mid-parent.
Moll, Salhuana, & Robinson	1962	Corn	124% of mid-parent value was found in between region crosses.
Paterniani & Lonnoquist	1963	Corn	Hybrid showed a range of -11% to 101% in yield for individual crosses relative to the mid-parent values.
Conner & Karper	1927	Sorghum	Hybrid showed an average increase of 66% in height over tallest parent.
Karper & Quinby	1937	Sorghum	Hybrid was twice as tall and produced three times as much forage as the best parent.
Bartel	1949	Sorghum	Hybrid showed from 6.2 to 113% increase in height over mid-parent.
Stephens & Quinby	1952	Sorghum	Hybrid exceeded the highest yielding variety by 10 to 20%.
Sambandam	1962	Egg Plant	Hybrid yield ranged from 11 to 153% over the mid-parent.
Whaley	1939	Tomato	Hybrid yield was 60% better than best hybrid in fresh weight.
Hatcher	1939	Tomato	Hybrid seed number was lower but seed weight was higher than the selfed parents.

C. Some Examples in Different Crops: (Continued)

Author	Year	Crop	Heterosis Expressed
Whaley	1952	Tomato	The hybrid was seven days earlier and had a larger number of leaves than the best parent.
Sikka et al.	1959	Wheat	Heterosis ranged from 16.4 to 131.4% more than mid-parent.
Gandhi, et al.	1961	Wheat	Hybrid produced 3 to 35% more fodder and 1.6 to 55.6% more tillers than better parent.
Lupton	1961	Wheat	Some hybrids yielded 44% more grain than the best parent.
Schmidt	1962	Wheat	Hybrids yielded from 3% below to 31% above the best parent.
Grafius	1959	Barley	Hybrids showed up to 123.6% increase in yield over mid-parent.
Coffman & Wiebe	1930	Oats	Hybrids were 4.9% taller and yielded 35.2 more grain than parental strains.
Coffman	1933	Oats	Hybrids averaged 13.2% taller and yielded 35.2 more grain than the better parent.
Kime and Tilley	1947	Cotton	Heterosis was expressed in yield, earliness, and quality.
Simpson	1948	Cotton	Naturally crossed plants produced 5.7 to 24.0% greater yield than inbred plants.
Jones & Loden	1951	Cotton	Hybrids averaged from 0.8 to 57% more than average of parents.
Turner	1953	Cotton	The best hybrid averaged 22.5 and 31.8% increase in yield over the check variety.
Turner	1953	Cotton	The hybrid showed a range from 46 to 82% increase in yield over the mid-parent.

C. Some Examples in Different Crops: (Continued)

Author	Year	Crop	Heterosis Expressed
Christidis	1955	Cotton	The hybrid showed a range of 3.0 to 9.5% increase in yield over the best parent.
Fryxell, Staten & Porter	1958	Cotton	A clear heterotic expression found only in fiber length.
Stroman	1961	Cotton	The best hybrid produced 299 pounds of lint more than its nearest strain competitor.
Miller & Marani	1963	Cotton	The hybrid produced 27.5% more lint than mid-parent.
White & Richmond	1963	Cotton	The hybrids exceeded the better parent by 3 to 30% in yield.
Marani	1964	Cotton	The hybrid was earlier, taller, and had greater percent boll retention than mid-parent.
Miller and Lee	1964	Cotton	Yields of top crosses ranged from 100 to 128% of tester parent.
Pate, Joyner & Seale	1960	Sansevieria	Hybrid was superior to best parent in green yields, fiber yields, and percent of fiber leaves.
Burton	1944	Millet	The hybrids produced about twice as much dry matter as the Napiergrass parent.
Burton	1943	Paspalum	The hybrids produced twice as much dry matter as the parental species.
Carnahan	1947	Flax	The hybrids yielded 40% more than average of parents.
Peters & Newell	1961	Bluestem	The hybrid exceeded the average of parents by 59% in yield.

MATERIALS AND METHODS

Accessions: Twelve parental accessions having a tetraploid chromosome complement were used in comparison with their hybrid combinations. The hybrids were the result of crosses made by Richardson using the technique described by him in 1958. All of the hybrids except 56x511-1 were produced by Mr. Richardson in 1958 and were identified as hybrids in 1959. Since these plants reproduce apomictically, seeds for the present study were harvested from increase rows established in a nursery and represent, in effect, clonal increases of the original F_1 plants. The cross 56x511-1 was made by Mr. Richardson in 1956 and is rather sexual. In this case the material in this study was, in part at least, an F_2 population. The parents comprised two botanical varieties of Bothriochloa intermedia, one variety of B. ischaemum, and three hybrids. The B. intermedia var. grahamii included accessions 2655, 5450, 5168, 5404, 5400, 4393, and 4630. The accessions 5400, 4393, and 4630 were used in various combinations of the above to produce the three hybrids used as parents in this study. The B. intermedia var. grahamii is the common Bothriochloa of the Gangetic-Punjabi plains of India and Pakistan, and is now rather wide spread in various tropical countries to which it was probably introduced. This variety was used extensively as a female parent because it is more sexual than other varieties. The B. intermedia var. montana

THE ORIGIN OF PARENTS AND HYBRIDS USED

B. intermedia var. _grahamii_	X _B. ischaemum_ var. _ischaemum_	Hybrid Designation
2655 British Guiana	X 7162 Tashkent, U.S.S.R.	58x503a-2
5450 Delhi, India	X 5704 Peking, China	56x511-1
5168 Pretoria, South Africa	X 7162 Tashkent, U.S.S.R.	58x685a-1
5404 Delhi, India	X 7162 Tashkent, U.S.S.R.	58x733b-1
56x750 = 4630b Source Unknown x 5450 Delhi, India	X Afghanistan	58x323
56x750 = 4630b Source Unknown x 5450 Delhi, India	X 7498 Mardin, Turkey	58x348
56x482 = 5400 Hempur, India x 5168 South Africa	X 6583 Afghanistan	58x70-a&b
56x428 = 4393 Dehra Dun, India x 4630 Source Unknown	X 7498 Mardin, Turkey	58x12B

B. intermedia var. _grahamii_	X _B. intermedia_ var. _montana_	
2655 British Guian	X 5297 Lonavala, India	58x694a-2
5450 Delhi, India	X 5297 Lonavala, India	58x697b-3

B. intermedia var. _montana_	X _B. ischaemum_ var. _ischaemum_	
5410 Matiana, India	X 7162 Tashkent, U.S.S.R.	58x768-1

accessions, 5410 and 5297, comprise part of a robust race found abundantly in the foothills of the Himalaya from Kashmir eastward. The B. ischaemum var. ischaemum is widespread in temperate Eurasia and includes the accessions 5704, 6583, 7162, and 7498. The hybrid 56 x 750 is a highly self sterile and sexual plant obtained from a cross between two facultative apomictic accessions of B. intermedia var. grahamii. This variety seems to be an introgression product between B. intermedia and Dicanthium annulatum and the montana variety is believed to be an introgression product of B. intermedia and B. ischaemum (Harlan, et.al. 1961).

Most of the F_1's studied originated as hybrids between B. intermedia var. grahamii and B. ischaemum, and resembled B. intermedia var. indica in morphological traits.

Cultural Methods: With the exception of the maternal parents 5450 and 56x428, the parent and hybrid cross populations were evaluated both during 1963 and 1964. The maternal parent of the hybrid designated as 58x12B was missing during both years of study. Seeds of A-5450 were available in 1963, but were found to be contaminated with other strains. Measurements taken on A-2655 were substituted for this parent because the two accessions are essentially identical in every known respect.

Seeds of each hybrid and hybrid parent were harvested and processed by hand prior to study. The germination of the seeds was conducted under controlled laboratory conditions. Seedlings were allowed to grow in vermiculite, moistened every other day with a 1:1:1 nutrient solution in the green house until they attained a height of three inches. The seedlings were then transfered by hand to plant vita-bands filled with soil, and remained under green house conditions until transplanted to the field.

Field planting was made at the Agronomy Research Station, Perkins, Oklahoma on a Vanoss sandy loam soil during both years of study. Ten replications of ten plants per replicate of each parent and hybrid combination were planted in a randomized block design in 1963. Six replications of the parents and hybrid combinations were planted in 1964. Each replicate consisted of one row 30 feet long with the plants spaced at three foot intervals. After transplanting, plots were checked at frequent intervals and weak or dead seedlings replanted.

The study area was sprayed after transplanting with Simazine at the rate of two pounds active ingredient per acre for weed control. Various other cultural practices were performed as needed to control weeds and weedy grasses. Supplemental irrigation was not required in 1963, but four inches was applied August 6, 1964 due to very dry soil conditions. The experimental plot was fertilized with ammonium nitrate at the rate of 60 pounds of actual nitrogen per acre.

Data Collection: Data were collected at plant maturity on an individual plant basis for: plant height, height of leaves, crown width, green weight, dry weight, percent seed set, and inflorescence characters. Winter hardiness was evaluated the following spring. Plant height and height of leaves were measured after the plants were gathered up and drawn to an upright position by tying the top and bottom of the plants with binder twine. Plants height and height of leaves were reported in inches.

Crown width was measured after the plants were harvested for forage yields. The average of two width measurements of each plant crown, was recorded in inches for the crown width measurements.

The green weight yields were determined by cutting the individually bundled plants and weighing each on a gram scale. These bundles were then allowed to air dry for approximately six weeks and then the individual dry weights were recorded in grams. The plants are air dried instead of being oven dried due to the large amount of space that would be required to oven dry this large number of plants. The length of time required for these plants to air dry depended on the prevailing climatic conditions.

Percent seed set as reported actually constitutes percent by weight and not by numbers. Hand stripped seed from each parent and hybrid were harvested and the caryopes extracted on a rub-board from two five gram samples and the percent seed set determined on a weight basis. Ahring (1963) reported that any parent or hybrid having 20 percent or more could be considered as having good seed set.

The length of upper and lower racemes shown were obtained by taking the average of the longest two upper and lower racemes on three heads of each plant and reporting the measurements in inches. The axis length was obtained by measuring the distance between the first node and the last branching node of the inflorescence.

Analysis of Data: A randomized block design with approximately ten plants per plot was used in this study. The analysis was done by the IBM 1410 on unweighted plot means to obtain the mean of each character for each population.

The F-test was made and if found to be significant, the Least Significance Difference (L.S.D.) and the Duncan's Multiple Range Test was used to test mean differences. The mid-parent and high parent means were used to evaluate heterosis.

RESULTS AND DISCUSSIONS

The mean, coefficient of variation, and L.S.D. are tabulated in Appendix Tables XV through XIX for plant height, height of leaves, crown width, green weight, and dry weight. The coefficient of variation for each hybrid and parent is tabulated in Appendix Table XXII, for the above characters. A Duncan's Multiple Range Test is presented in Appendix Table XX and XXI for the inflorescence characters and percent seed set. The means of hybrids after being separated into different groups on the basis of a common parent are presented in Appendix Table XXIII.

Results

Plant Height: The heights of all hybrids plants (Table I and II) with the exception of hybrid 58x685a-1 were significantly greater than their mid-parent values in both years of study. An increase in height over that of the taller parent was expressed in 1963 by hybrids 58x503a-2, 58x694a-2, 58x697b-3, 58x768-1, and 58x70-a&b (Table I). The same hybrids, with one exception, exhibited an increase in height over their taller parent in 1964. The height attained by hybrid 58x768-1 (Table II) was slightly greater than its taller parent, but not statistically different in 1964. The hybrid designated as 58x697b-3 was not available for study in 1964.

TABLE I

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR PLANT HEIGHT IN *BOTHRIOCHLOA* IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	28.58**	8.57**
58x694a-2	18.76**	14.69**
56x511-1	29.31**	-1.96
58x697b-3	18.62**	14.56**
58x685a-1	8.90**	-5.32
58x768-1	20.68**	6.39**
58x733b-1	15.77**	-3.64
58x70-a&b	61.10**	33.16**
58x323	21.61**	-1.17
58x348	10.59**	-14.62

** Significantly higher at the 0.01 level.

TABLE II

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND THE MID-PARENT MEANS FOR PLANT HEIGHT IN *BOTHRIOCHLOA* IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	21.80**	3.17*
58x694a-2	12.88**	12.82**
56x511-1	22.98**	-0.46
58x685a-1	3.20	-9.46
58x768-1	19.68**	2.03
58x733b-1	14.64**	-2.54
58x70-a&b	42.84**	21.97**
58x323	25.70**	-3.13
58x348	10.73**	-11.32

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

The hybrids in which heterosis was not expressed relative to the best parent exhibited negative deviations ranging from 14.62% for 58x348 in 1963 to 0.46% for 56x511-1 in 1964.

Height of Leaves: All hybrids in 1963 showed a significant increase in height of leaves over the mid-parent values of their respective parents (Table IV). In 1963, the only hybrids showing a negative deviation from its mid-parent was 58x768-1. The other hybrids exhibited a significant increase over their mid-parent with the exception of hybrid 58x685a-1 (Table III). An increase in height of leaves over that of the best parent was expressed by hybrids 58x70-a&b, 58x503a-2, and 58x733b-1, during both years of study. This increase was significant only for hybrid 58x70-a&b. Three other hybrids exhibited positive deviations from the mean of their best parent, but were not statistically significant (Table III and Iv).

The negative deviations of the remaining hybrids from their best parent was rather low, with a range from 0.59% in 56x511-1 to 9.96% in 58x348. Hybrid 58x348 was the only one to show a negative deviation from its best parent during both years of study.

Crown Width: The crown width of all hybrid plants, with the exception of hybrids 58x694a-2 and 58x768-1 was significantly greater than their mid-parent value in both years of study (Table V and VI). These two hybrids exhibited negative deviations of less than three percent both years. The hybrids 56x511-1 and 58x70-a&b were the only ones to show an increase in crown width over their best parent during both years of study; however, only in 58x70-a&b was the increase significant. Hybrid 58x697b-3 in 1963 and 58x348 in 1964 were the

TABLE III

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND THE MID-PARENT MEANS FOR HEIGHT OF LEAVES IN *BOTHRIOCHLOA* IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	5.52**	3.02
58x694a-2	1.20	-6.05
56x511-1	35.35**	-0.59
58x697b-3	5.97**	-1.62
58x685a-1	0.81	-0.04
58x768-1	-4.04	-11.43
58x733b-1	4.09*	0.15
58x70-a&b	62.07**	25.25**
58x323	38.80**	0.06
58x348	18.64**	-9.94

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

TABLE IV

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND THE MID-PARENT MEANS FOR HEIGHT OF LEAVES IN *BOTHRIOCHLOA* IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	19.50**	2.01
58x694a-2	10.74**	8.17**
56x511-1	26.14**	-0.76
58x685a-1	28.69**	1.99
58x768-1	29.76**	1.36
58x733b-1	29.03**	1.44
58x70-a&b	37.00**	16.67**
58x323	14.86**	-9.87
58x348	14.28**	-9.96

** Significantly higher at the 0.01 level.

TABLE V

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR CROWN WIDTH IN *BOTHRIOCHLOA* IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	4.69*	-0.85
58x694-2	-0.82	-3.97
54x511-1	12.05**	0.42
58x697b-3	10.86**	7.34**
58x685a-1	6.97**	-1.01
58x768-1[a]	-8.00	-13.57
58x733b-1	9.13**	0.60
58x70-a&b	9.56**	5.25**
58x323	15.73**	-2.05
58x348	12.29**	-2.67

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

TABLE VI

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR CROWN WIDTH IN BOTHRIOCHLOA IN 1964

Hybrid	Mid-Parent	High Parent
58x503-2	18.53**	0.88
58x694a-2	-2.70	-9.10
56x511-1	16.79**	2.41
58x685a-1	18.39**	0[a/]
58x768-1	1.21	-17.92
58x733b-1	17.21**	-2.53
58x70-a&b	29.73**	17.38**
58x323	14.97**	1.11
58x348	24.42**	9.15**

** Significantly higher at the 0.01 level.

[a/] 58x685a-1 had the same crown width as its best parent only other hybrids to show a significant increase over their best parent (Table V). Two other hybrids exhibited small increases over their best parent that were non-significant. Negative deviations of the remaining hybrids ranged from 0.85 to 13.57% in 1963 (Table V) and from 2.53 to 17.92% in 1964 (Table VI). The crown width of 58x768-1 in 1963 was smaller than either parent.

Green Weight: The green weight of all hybrids was significantly greater than their mid-parent value in 1964 (Table VIII). In 1963, only 58x768-1 and 58x694a-2 produced less than their mid-parent value. The remaining hybrids expressed a significant increase over their mid-parent with the exception of hybrid 58x685a-1. A significant increase in green weight production over the best parent was exhibited only in hybrids 58x70-a&b and 56x511-1 during both years of study (Table VIII and IX). Two hybrids in 1963 (Table VIII) and three hybrids in 1964 (Table IX), exhibited increases up to 15% over their best parent that were non-significant. Four hybrids exhibited negative deviations from their best parent ranging from 6.01 to 38.93%.

Dry Weight: The dry weight of all hybrid plants, (Table X), with the exception of hybrid 58x783b-1 was significantly greater than their mid-parent value in 1964. In 1963, only three hybrids; 58x694a-2, 58x685a-1, and 58x768-1, failed to show a significant increase in dry weight over their mid-parent (Table IX). The hybrid 58x70-a&b produced over two and one-half times more than its mid-parent and over twice as much as its best parent during both years. An increase over their best parent was exhibited by hybrids 58x70-a&b, 56-511-1, and 58x503a-2 during both years of study. The increase exhibited by hybrid 58x503a-2

TABLE VII

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR GREEN WEIGHT IN *BOTHRIOCHLOA* IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	24.87**	8.31
48x694a-2	-24.96	-32.01
56x511-1	98.27**	22.69**
58x697b-3	11.30**	0.83
58x685a-1	5.38	-6.01
58x768-1	-30.39	-38.93
58x733b-1	24.24**	0.94
58x70-a&b	154.16**	66.42**
58x343	53.15**	-10.41
58x348	17.51**	-27.69

** Significantly higher at the 0.01 level.

TABLE VIII

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR GREEN WEIGHT IN *BOTHRIOCHLOA* IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	58.42**	15.12
58x694a-2	37.32**	11.12**
56x511-1	112.51**	49.84**
58x685a-1	61.05**	13.68
58x768-1	22.34**	-19.73
58x733b-1	16.14*	-24.80
58x70-a&b	163.05**	95.50**
58x323	35.80**	-12.95
58x348	47.08**	-10.97

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

TABLE IX

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR DRY WEIGHT IN BOTHRIOCHLOA IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	11.11**	10.51
58x694a-2	-20.63	-31.90
56x511-1	115.65**	33.25**
58x697b-3	16.78**	2.00
58x685a-1	-1.15	-1.19
58x768-1	-21.63	-28.08
58x733b-1	30.49**	16.08*
58x70-a&b	216.16**	103.88**
58x323	49.27**	-13.79
58x348	39.76**	-15.57

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

TABLE X

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR DRY WEIGHT IN *BOTHRIOCHLOA* IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	49.62**	14.91
58x694a-2	35.02**	7.15
56x511-1	103.53**	59.00**
58x685a-1	51.27**	11.73**
58x768-1	39.96**	-7.18
58x733b-1	13.14	-23.17
58x70-a&b	163.22**	107.42**
58x323	83.97	3.96
58x348	60.52**	5.32

** Significantly higher at the 0.01 level.

was not statistically different from its best parent (Table IX and X). The hybrid designated as 58x733b-1 was the only other case of a hybrid exhibiting a significant increase over its best parent during either year.

Five hybrids in 1963 and two in 1964 showed negative deviations from their best parent ranging from 1.19 to 31.90%. Hybrid 58x768-1 exhibited a negative deviation from its best parent during both years.

Axis Length: Axis length was studied only in 1964. Most of the hybrids were intermediate between the mid-parent and the high parent. Only two hybrids, 58x768-1 and 58x348 failed to show a significant increase in axis length over the average of their parents. These hybrids exhibited negative deviation from their mid-parent of 34.52 and 34.48% respectively (Table XI). The other hybrids showed positive deviations from the average of their mid-parent ranging from 8.42 to 49.79%. The only hybrids to exhibit an increase in axis length over their best parent were 58x694a-2 and 58x685a-1, but these increases were not statistically significant (Table XI). The remaining hybrids expressed negative deviations from their best parent ranging from 10.18% in 58x70-a&b to 57.90% in 58x768-1.

Length of Upper Racemes: Length of the upper racemes was studied only in 1964. A significant increase over the mid-parent was exhibited in hybrids 58x694a-2, 58x768-1, and 58x733b-1. The hybrid designated as 56x511-1 expressed a 2.58% increase over its mid-parent, but this was not statistically significant. The other hybrids exhibited negative deviations from the average of their parents ranging from 2.76

TABLE XI

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS
FROM THE HIGH PARENT AND THE MID-PARENT FOR
AXIS LENGTH IN BOTHRIOCHLOA IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	16.88**	-20.02
58x694a-2	8.42**	3.58
56x511-1	29.39**	-20.76
58x685a-1	49.79**	2.85
58x768-1	-34.52	-57.90
58x733b-1	15.57**	-13.06
58x323	9.68**	-29.06
58x348	-34.48	-61.11
58x70-a&b	23.92**	-10.18

** Significantly higher than the high parent at 0.01 level.

TABLE XII

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND THE MID-PARENT FOR LENGTH OF UPPER RACEME OF BOTHRIOCHLOA IN 1964

Hybrid	Mid-Parent	High Parent
58x503a-2	-2.76	-16.10
58x694a-2	15.32**	9.25*
56x511-1	2.58	-6.51
58x685a-1	-21.63	-30.48
58x768-1	10.80**	3.41
58x733b-1	25.35**	21.95*
58x323	-14.99	-26.36
58x348	-18.50	-29.31
58x70a&b	-6.73	-10.08

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

to 21.6% (Table XII). An increase in upper raceme length over the best parent was expressed in hybrids 58x733b-1, 58x694a-2, and 58x768-1, but the increase was not significant for hybrid 58x768-1. Five hybrids exhibited negative deviations from the mean of their mid-parent and high parent during both years (Table XII).

Length of Lower Racemes: This character was studied in the parents and hybrids in 1964. The only hybrids that failed to show an increase in lower raceme length over the average of their parents were 58x685a-1, 58x323, and 58x348 (Table XIII). The other hybrids exhibited significant increases ranging from 5.17 to 32.78%. An increase in lower raceme length over the best parent was expressed by hybrids 56x511-1 and 58x733b-1, but only in 56x511-1 was the increase significant. The hybrids in which heterosis was not expressed relative to the best parent exhibited negative deviations ranging from 2.51% in 58x694a-2, to 39.70% in 58x323 (Table XIII).

Percent Seed Set: Percent seed set of the parents and hybrids was studied in 1963. A significant increase over the average of their parents was exhibited by hybrids 58x503a-2, 58x323, 58x348, and 58x70-a&b (Table XIV). Negative deviations of the hybrids not expressing heterosis relative to the mid-parent ranged from 8.03 to 62.7%, with three hybrids exhibiting a percent seed set that was lower than either of their parents. A significant increase in seed set over the best parent was expressed by 58x503a-2 and 58x70-a&b. The remaining hybrids exhibited negative deviations from their high parent ranging from 9.87 to 70.50%, with most of the deviations falling between 17 and 36% (Table XIV).

Winter Hardiness: The hybrids and parents were evaluated in the spring of 1964 to determine which plants of the 1963 planting survived the winter. The only plants to recover were the four *Bothriochloa ischaemum* accessions which were used as male parents. There were no hybrids that survived the winter indicating that there was not a transfer of the winter hardiness character from *B. ischaemum* to the hybrid plants. The twenty chromosomes of hardy *B. ischaemum* may not be sufficient to produce winter hardy hybrids, unless a specific combination is used.

TABLE XIII

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT FOR LENGTH OF LOWER RACEME OF BOTHRIOCHLOA IN 1964

Hybird	Mid-Parent	High Parent
58x503a-2	7.76**	-10.41
58x694a-2	6.91**	-2.51
56x511-1	32.78**	20.45*
58x685a-1	-7.82	-16.12
58x768-1	5.95*	-5.70
58x733b-1	15.97**	7.63*
58x323	-22.87	-39.07
58x348	-10.87	-32.24
58x70-a&b	5.17*	-6.18

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

TABLE XIV

THE DEVIATION, IN PERCENT, OF THE HYBRID GENERATION MEANS FROM THE HIGH PARENT AND MID-PARENT MEANS FOR PERCENT SEED SET OF *BOTHRIOCHLOA* IN 1963

Hybrid	Mid-Parent	High Parent
58x503a-2	47.40**	42.64**
58x694a-2	-13.30	-31.30
58x697b-3	-62.78	-70.50
58x685a-1[a]	-8.03	-9.87
58x768-1[a]	-36.27	-51.68
58x733b-1[a]	-22.06	-28.29
58x323	28.42**	-18.69
58x348	20.29**	-17.03
58x70-a&b	51.03**	10.03*

* Significantly higher at the 0.05 level.
** Significantly higher at the 0.01 level.

[a] Percent seed set was lower than either parent.

Discussion

Heterosis as used in this study is defined as 1) a significant increase in the hybrid population over the mid-parent and 2) a significant increase over the best parent, for the character under consideration. Each character studied exhibited heterosis relative to the mid-parent in at least one cross. This was due in most part to the inferior quality and size of the male parents for most characters. The B. ischaemum var. ischaemum plants are low in yield, the plants mature early and are stemmy. With one exception, each character exhibited heterosis in at least one cross with respect to the best parent. This exception was for the character of axis length which was intermediate between the two parents in most cases, although two hybrids gave small positive deviations from the mean of their best parents. The intermediacy of the hybrids for inflorescence characters as found in this study is comparable to results obtained by Chheda and Harlan (1962), who found that hybrids between Bothriochloa intermedia X-750 and Dicanthium fecundum 6525 were intermediate in most characters. Their results showed of the seven hybrids studied, all were intermediate between their parents for axis length and five were intermediate for length of longest raceme. Two of these hybrids exhibited a raceme length longer than that of the longest parent raceme. Harlan (1963) reported that the introgression products between B. intermedia and

B. ischaemum were intermediate between the parents with respect to raceme length and axis length. It should also be noted that the hybrid designated as 58x694a-2 in the present study was a hexaploid that resulted from the fertilization of an unreduced egg. This could possibly explain the increase in axis length and upper raceme length over the best parent, since this hybrid would tend to show more maternal characters. The ranking of this hybrid near the top for most characters chould possibly be explained on this basis, however, both parents of this hybrid were superior to the other parents used. The hybrids 56x511-1 and 58x768-1 were the only other hybrids that were known to be hexaploids. The hybrid 56x511-1 gave consistent increases over the best parent indicating that maternal inheritance may be important, however, 58x768 very rarely gave a significant increase over its best parent.

The increase in percent seed set of some plants could have been due to a specific pollen parent. Celarier and Harlan (1957) reported that most of these materials are pseudogamous and that pollen of a certain kind is required to stimulate seed production. Dewald and Harlan (1961) reported that when B. intermedia 2655 was used as a female, Dicanthium annulatum pollen proved to be much more effective in stimulating seed formation than the plant's own pollen. The foreign pollen not only stimulated more seed, but it was more rapid in its effects. Harlan et al. (1961) reported on the influence of various pollen sources on seed set of X-750. The results showed that when plants of B. intermedia var. grahamii were used as males about twelve seeds were set per inflorescence. When D. annulatum sources were used, the seed set was about 33 per inflorescence. The crossability between X-750 and most accessions of *B. intermedia* was poor, with only 6.6 seed set per inflorescence. Since the material used to determine percent seed set was collected without control of the pollen parent, the source of pollen could have come from a wide variety of plants.

The consistent heterosis for plant height found in this study in comparable to the results of Marani (1961), who found a large degree of heterosis for plant height in interspecific hybrids of cotton. The increase in height of the hybrids in this case was undesirable from an agronomic point of view because of the difficulties in harvesting, cultivation, irrigation, and other cultural practices. The data of the present study indicate that plant height, height of leaves, crown width and yield characters will be most likely to give consistent increases over the mid-parent. These results are comparable to those of Newell and Peters (1961), who reported that interspecific *Andropogon* hybrids exceeded the average of the parent types by 20% in height of leaves, 9% in total height of plants, and 59% in total plant yields. The basal spread of the hybrids was intermediate between the two parents.

The results of hybridization indicate that the expression of heterosis depends on a specific combination of genes, since hybrids having practically the same parents show varying degrees of heterosis and that the mating of diverse types does not necessarily produce heterosis in the hybrids. The desirability of a specific combination depends upon the particular character of interest, since heterosis for one character does not necessarily mean that hybrid vigor will be exhibited for all characters.

In twenty out of thirty-six cases the crosses involving the *Bothriochloa ischaemum* 6583 as the male parent exhibited the greatest heterosis for a particular character over the mid-parent or high parent. A hybrid superior to all others was found in this group for dry weight production. Crosses involving the *B. ischaemum* 7162 as the male parent exhibited greatest vigor in only one out of seven cases relative to the best parent and four out of thirty-nine cases relative to the mid-parent. This parent produced a higher percentage increase in vigor for hybrids having *B. intermedia* var. *grahamii* as the other parent than those having *B. intermedia* var. *montana*. The hybrid 58x733b-1 of this group gave the largest green weight yield of all hybrids in 1963. Since the female parent of hybrid 58x12B was not available for study, the only hybrid having *B. ischaemum* 7498 as its male parent was 58x348. Maximum heterosis was not expressed by this hybrid for any character; however, the crown width of this hybrid was superior to all other hybrids in 1964.

The crosses involving *B. intermedia* var. *montana* accession 5297, as the female parent expressed heterosis in thirteen cases relative to the mid-parent and in seven cases relative to the best parent. There were only two cases in which greatest vigor for a particular character was expressed, but at the same time these hybrids were superior to all others for three characters in 1963 and six characters in 1964. The possible explanation for the lack of heterosis in these hybrids is the fact that the *B. intermedia* var. *grahamii* and *B. intermedia* var. *montana* accessions used in these crosses are hybrids themselves.

These vigorous parents probably arose as a product of introgressive hybridization between two different species and may have built in heterosis as a result of their polyploid condition. The hybrids may, therefore, be very vigorous, but would not necessarily express heterosis relative to their parents. The two crosses involving the self-sterile parent 56x750 as their female parent exhibited heterosis relative to the mid-parent for most characters, but heterosis relative to the best parent was expressed in only one character. This indicates that the specific combination of genes necessary for the expression of maximum vigor did not occur in these hybrids.

The only hybrid expressing heterosis in practically all characters with respect to both the mid-parent and high parent was 58x70-a&b. This hybrid expressed the highest percentage increase in hybrid vigor for six characters; however, only in dry weight production was it superior to other hybrids. This can possibly be explained by the fact that both parents of this hybrid were inferior plants and possibly because one parent was a hybrid itself. These results again indicate the need for specific combinations for heterosis to be expressed, since three other hybrids having practically the same parents expressed varying degrees of heterosis or none at all.

From the present data, it appears that plant height, height of leaves, crown width, and yield characters will be most likely to give consistent increases over the mid-parent as a result of hybridization, since these characters exhibited a hybrid mean greater than the mid-parent more frequently for all crosses. Plant height appears to be the character most frequently expressing heterosis relative to the high parent. The inflorescence characters showed a greater tendency to be intermediate between the parents, with very few instances of a hybrid giving a significant increase over its best parent for inflorescence characters.

The influence of environment was very important. The fact that one hybrid may rank near the top for a character one year and close to the bottom the next indicates that some genotypes express heterosis in one environment, but not in others.

It should be emphasized that this study deals, for the most part, with true interspecific hybrids and that the parents must be genetically quite different from each other. The F_1 plants should, therefore, be highly heterozygous yet they do not necessarily show heterosis. Consistent heterotic expressions are found only in certain individual specific combinations such as in hybrid 58x70-a&b. Other plants derived from almost identical crosses do not show consistent heterosis. Consistent heterotic expressions are found only in certain individual specific combinations such as in hybrid 58x70-a&b. Other plants derived from almost identical crosses do not show consistent heterosis. It may well be that the relatively poor performance of some specific combinations is due to physiological and/or genetic imbalance resulting from the very fact that these are interspecific hybrids and that only occasional specific genetic combinations are able to avoid this kind of imbalance and give a favorable response. In any case, the results would suggest that a relatively few major genes are responsible for heterosis or lack of it in these materials. If a large number of genes were involved, we would expect similar crosses to give similar results and sister plants of a given cross to be more or less alike.

It should also be emphasized that the F_1 plants studied reproduced apomictically with the exception of 56x511-1 which is rather sexual. In studying a given hybrid, therefore, we were not dealing with a population of F_1 plants but with replications of a single clone.

SUMMARY AND CONCLUSIONS

Heterosis was found in at least one cross for all characters studied relative to the mid-parent. Axis length was the only character in which a hybrid mean was not significantly different from the high parent in any cross.

The evidence presented indicates that hybrid vigor is expressed more frequently for plant height, height of leaves, crown width, green weight and dry weight in all crosses relative to the mid-parent. It appears that plant height will give more consistent increases over the high parent as a result of hybridization, since this character exhibited a hybrid mean greater than the high parent mean for all crosses more frequently than any other character. A positive deviation from the mean of the best parent was exhibited in several hybrids for height of leaves, but significance was rarely indicated. A significant expression of heterosis for green and dry weight over the high parent was limited in most cases to two hybrids. The inflorescence characters showed a greater tendency to be intermediate between the parents and there were very few instances of a hybrid exhibiting a significant increase over its best parent for these characters. Heterosis for percent seed set was expressed by four hybrids relative to the mid-parent and two hybrids relative to the best parent. Three hybrids exhibited a percent seed set that was lower than either parent. The winterhardiness of the *B. ischaemum* parents was not found in any hybrid.

Since the crosses between *Bothriochloa intermedia* var. *grahamii* and *B. intermedia* var. *montana* exhibited less heterosis than the other crosses, it seems to indicate that these parents have built-in heterosis due to their origin by introgressive hybridization. The results also indicate that heterosis is probably due to specific combinations of genes rather than to heterozygosity obtained by mating diverse types, since individual combinations may be outstanding, while sister plants may be useless. Some individual clones may make excellent parents even though they may give a poor performance by themselves. The influence of maternal inheritance may also be important in the hexaploid hybrids for some characters.

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APPENDIX

TABLE XV

PLANT HEIGHT, IN INCHES, OF THE PARENTS AND HYBRIDS IN BOTHRIOCHLOA IN 1963 and 1964

Accession		1964	Accession	1963
58x694a-2		60.71	58x694a-2	69.94
56x750		58.95	58x697b-3	69.86
58x323		57.11	58x12B	67.85
58x12B		56.87	56x750	67.48
58x503a-2		55.52	58x323	66.33
58x70-a&b		55.01	58x503a-2	66.21
58x768-1		54.05	58x70a&b	64.41
2655		53.81	5404	63.20
5297		53.74	2655	60.98
5404		53.33	58x733b-1	60.90
5410		52.96	58x511-1	59.79
58x348		52.28	58x768-1	58.57
58x733b-1		51.98	58x348	57.62
5450		50.26	5168	56.84
58x511-1		50.03	5297	56.80
5168		49.48	5410	55.05
56x482		45.10	58x685a-1	53.82
58x685a-1		44.80	56x482	48.37
7162		37.35	7162	42.01
7498		35.48	7498	36.45
6583		31.92	5704	31.63
5704		31.11	6583	31.60
L.S.D.	0.05	0.8276		0.8428
L.S.D.	0.01	1.094		1.107
C.V.		4.61		5.36

TABLE XVI

HEIGHT OF LEAVES, IN INCHES, OF THE PARENTS AND HYBRIDS IN *BOTHRIOCHLOA* IN 1963 AND 1964

Accession		1963	Accession	1964
5297		35.90	58x694a-2	32.15
58x697b-3		35.32	56x750	31.63
5410		35.65	58x12B	30.81
58x694a-2		33.73	58x70-a&b	29.88
58x70-a&b		33.68	5297	29.72
58x12B		33.32	58x768-1	29.25
58x323		33.23	5410	29.21
56x750		33.21	58x503a-2	28.92
58x733b-1		31.76	58x323	28.51
5404		31.71	58x348	28.48
58x503a-2		31.70	2655	28.35
2655		30.77	58x733b-1	28.13
58x768-1		30.69	5404	27.73
56x511-1		30.59	58x685a-1	27.67
58x348		29.91	5450	27.66
5168		29.82	56x511-1	27.45
58x685a-1		29.81	5168	27.13
7162		29.32	56x482	25.61
56x482		26.89	7162	20.05
7498		17.22	7498	18.22
6583		14.67	6583	18.02
5704		14.43	5704	15.87
L.S.D.	0.05	0.518		0.597
L.S.D.	0.01	0.680		0.790
C.V.		6.31		6.16

TABLE XVII

CROWN WIDTH, IN INCHES, OF THE PARENTS AND HYBRIDS IN *BOTHRIOCHLOA* IN 1963 AND 1964

Accession		1963	Accession	1964
58x697b-3		5.41	5297	5.17
58x12B		5.05	5410	5.08
5297		5.04	58x70-a&b	4.93
58x733b-1		5.02	58x348	4.89
5404		4.99	5404	4.75
5168		4.96	58x694a-2	4.70
58x685a-1		4.91	56x511-1	4.66
56x750		4.88	58x12B	4.63
58x694a-2		4.84	58x733b-1	4.63
58x70-a&b		4.81	5168	4.57
5410		4.79	58x685a-1	4.57
58x323		4.78	5450	4.55
58x348		4.75	58x503a-2	4.54
56x511-1		4.74	58x323	4.53
2655		4.72	2655	4.50
58x503a-2		4.68	56x750	4.48
56x482		4.57	56x482	4.20
7162		4.22	58x768-1	4.17
58x768-1		4.14	5704	3.43
5704		3.74	6583	3.40
7498		3.58	7498	3.39
6583		3.38	7162	3.16
L.S.D.	0.05	0.1344		0.0992
L.S.D.	0.01	0.1749		0.1304
C.V.		7.67		8.98

TABLE XVIII

DRY WEIGHT, IN GRAMS, OF THE PARENTS AND HYBRIDS
IN *BOTHRIOCHLOA* IN 1963 AND 1964

Accession	1963	Accession	1964
58x70-a&b	967.99	58x70-a&b	546.75
58x733b-1	912.71	58x694a-2	528.83
56x750	886.99	5297	493.54
58x697b-3	848.06	5410	436.83
5297	846.36	56x511-1	435.16
56x511-1	807.54	58x12B	434.00
58x12B	798.70	5404	433.48
5404	786.26	58x348	419.41
58x323	764.71	58x323	413.98
58x348	748.95	58x768-1	405.50
5410	733.38	56x750	398.20
58x503a-2	677.02	58x685a-1	363.60
5168	613.10	58x733b-1	333.78
7162	612.60	58x503a-2	332.98
2655	606.00	5168	325.41
58x685a-1	605.81	2655	289.77
58x694a-2	576.42	5450	273.67
58x768-1	527.45	56x482	263.59
56x482	474.77	7162	155.31
7498	184.74	5704	153.93
5704	142.93	6583	151.84
6583	137.58	7498	124.36
L.S.D. 0.05	32.47		22.15
L.S.D. 0.01	42.92		29.18
C.V.	17.82		18.62

TABLE XIX

GREEN WEIGHT, IN GRAMS, OF THE PARENTS AND HYBRIDS IN *BOTHRIOCHLOA* IN 1963 AND 1964

Accession	1963	Accession	1964
56x750	1615.39	58x694a-2	1082.46
58x733b-1	1595.54	58x70-a&b	1040.08
5404	1580.68	5297	973.29
58x697b-3	1500.55	5404	926.65
5297	1488.07	56x750	906.23
56x511-1	1482.51	5410	876.07
58x70-a&b	1476.27	58x12B	871.10
58x323	1447.28	56x511-1	862.20
58x12B	1334.17	58x348	806.86
58x503a-2	1308.75	58x323	788.95
5410	1308.62	58x685a-1	755.05
2655	1208.30	58x768-1	703.23
58x348	1168.17	58x733b-1	696.93
58x685a-1	1064.65	58x503a-2	694.44
5168	1132.65	5168	664.15
58x694a-2	1011.74	2655	603.21
7162	987.80	5450	575.38
56x482	887.07	56x482	535.10
58x768-1	799.28	7162	273.47
7498	372.67	6583	255.67
5704	287.14	5704	236.06
6583	274.60	7498	190.92
L.S.D. 0.05	58.42		46.41
L.S.D. 0.01	77.69		61.34
C.V.	17.93		18.43

TABLE XX

AXIS LENGTH AND LENGTH, IN INCHES, OF UPPER AND LOWER RACEMES OF PARENTS AND HYBRIDS IN BOTHRIOCHLOA IN 1964.

DUNCAN'S MULTIPLE RANGE TEST

Accession	Axis Length		Upper Raceme Length		Lower Raceme Length	
5410	3.700	a[1]	2.082	efgh	2.775	def
58x694a-2	3.268	b	2.716	a	3.186	b
5297	3.155	b	2.224	def	2.692	def
56x750	3.098	bc	2.580	ab	3.837	a
58x685a-1	2.918	cd	1.620	k	2.212	hi
2653	2.873	d	2.486	bc	3.268	b
5168	2.837	de	2.330	cd	2.637	ef
5450	2.650	e	2.292	cde	2.552	fg
58x503a-2	2.298	f	2.086	defgh	2.928	cd
58x323	2.198	fg	1.900	hij	2.338	gh
58x511-1	2.100	fg	2.143	defg	3.074	bc
5404	2.099	fg	1.707	jk	2.529	fg
56x482	2.024	g	2.035	fghi	2.836	cde
58x733b-1	1.825	h	2.200	def	2.722	def
58x70-a&b	1.818	h	1.830	ijk	2.661	ef
58x768-1	1.558	i	2.153	defg	2.617	ef
58x128	1.499	i	1.937	ghij	2.920	cd
58x348	1.205	j	1.824	ijk	2.600	ef
7162	1.059	jk	1.804	ijk	2.166	hi
6583	.910	jk	1.890	hij	2.225	hi
5704	.597	l	1.887	hij	2.079	i
7498	.580	l	1.896	hij	1.997	i

[1] Numbers followed by the same letter are not significantly different at the 0.05 level of probability.

TABLE XXI

PERCENT SEED SET OF THE PARENTS AND HYBRIDS IN *BOTHRIOCHLOA* IN 1963

DUNCAN'S MULTIPLE RANGE TEST

Accession	Percent Seed Set	
5410	28.08	a[1]
5297	26.47	a
58x503a-2	22.11	b
58x694a-2	18.19	c
56x750	17.50	c
5404	17.25	c
2655	15.50	cd
5450	15.50	cd
58x348	14.25	d
7162	14.50	d
58x323	14.23	d
5168	13.93	de
58x768-1	13.57	de
58x733b-1	13.07	de
58x685a-1	12.37	de
58x70-a&b	11.18	e
58x12B	8.41	f
58x697b-3	7.81	f
56x482	7.45	f
6583	6.66	fg
7498	4.65	g
5704	4.37	g

[1] Numbers followed by the same letter are not significantly different at the 0.05 level of probability.

TABLE XXII

THE COEFFICIENT OF VARIATION OF THE PARENTS AND HYBRIDS IN BOTHRIOCHLOA FOR PLANT HEIGHT, HEIGHT OF LEAVES, CROWN WIDTH, GREEN WEIGHT AND DRY WEIGHT IN 1963 AND 1964

	Plant Height		Height of Leaves		Crown Width		Green Weight		Dry Weight
Hybrid	1963	1964	1963	1964	1963	1964	1963	1964	1964
58x503a-2	3.78	5.63	5.16	7.72	14.54	11.84	19.15	39.10	45.21
58x694a-2	3.88	5.21	5.36	6.06	12.68	12.91	19.67	31.88	32.11
56x511-1	7.66	11.60	8.33	11.43	13.51	9.44	23.35	34.04	37.17
58x685a-1	5.38	7.90	5.31	9.12	11.80	13.04	20.54	33.32	33.19
58x768-1	6.39	5.79	7.01	7.41	16.31	9.64	22.85	33.23	35.22
58x733b-1	5.38	4.54	11.21	4.89	12.44	12.06	20.90	31.34	33.27
58x70-a&b	3.92	5.63	5.54	10.36	9.93	12.06	19.64	25.36	27.45
58x323	4.78	4.25	6.79	7.09	11.48	10.89	25.17	32.46	34.20
58x348	2.68	4.76	4.22	7.92	13.50	11.10	17.40	24.29	25.89
58x697b-3	4.67	----	6.02	----	13.38	----	23.43	----	----
58x12B	3.48	4.08	5.44	6.57	14.07	12.22	23.30	31.85	34.12
56x750	3.77	4.42	4.85	6.31	13.75	12.69	19.51	33.63	33.52
56x482	14.26	17.38	10.46	16.86	18.43	16.73	35.46	65.28	67.19
5297	4.34	9.48	5.13	10.61	17.68	12.11	27.12	34.31	37.11
5410	5.26	8.64	5.23	8.94	17.43	15.91	28.16	38.72	40.16
5404	3.46	4.31	4.23	7.21	11.71	9.96	15.44	24.19	25.77
2655	4.14	5.99	5.23	7.46	13.08	13.79	25.12	36.60	36.47
5168	4.16	7.56	6.44	8.07	14.35	12.32	19.04	35.59	35.95
5450	----	7.93	----	8.71	-----	10.02	-----	36.88	38.57
7162	5.73	6.56	8.56	10.81	9.78	13.20	13.32	39.25	39.07
7498	5.69	3.69	7.99	8.44	21.37	14.61	30.70	39.47	-----
6583	12.31	8.11	11.17	10.51	20.03	14.82	27.62	52.71	52.17
5704	9.81	7.06	11.41	8.49	13.27	12.18	25.44	43.15	45.99

TABLE XXIII

MEANS OF THE HYBRID PLANTS FOR PLANT HEIGHT HEIGHT OF LEAVES, CROWN WIDTH, GREEN WEIGHT, AND DRY WEIGHT WITH THE HYBRIDS GROUPED ON THE BASIS OF A COMMON PARENT

Hybrid	Plant Height Inches		Height of Leaves Inches		Crown Width Inches		Green Weight Inches		Dry Weight Inches	
	1963	1964	1963	1964	1963	1964	1963	1964	1963	1964
5404x7162 = 58x733b-1	50.90	51.98	31.76	28.13	5.02	4.63	1595.54*	696.93	912.71	333.08
2655x7162 = 58x503a-2	66.21	55.52	31.70	28.92	4.68	4.54	1308.75	694.44	577.02	332.98
5168x7162 = 58x685a-1	53.82	44.80	29.81	27.67	4.91	4.57	1064.65	755.05	605.81	363.60
5410x7162 = 58x768-1	58.57	54.05	30.69	29.25	4.14	4.17	703.23	799.28	527.45	405.50
56x750x6583 = 58x323	66.33	57.11	33.23	28.51	4.78	4.53	1447.28	788.95	764.71	413.98
56x750x7498 = 58x348	57.62	52.28	29.91	28.48	4.75	4.89	1168.17	806.86	748.95	419.41
56x482x6583 = 58x70-a&b	64.41	55.01	33.68	29.88	4.93	4.81	1476.67	1040.08	967.99*	546.75*
56x750x6583 = 58x323	66.33	57.11	33.23	28.51	4.78	4.53	1168.17	788.95	764.71	413.98
56x428x7498 = 58x12B	67.85	56.87	33.23	30.81	5.05	4.63	1334.17	871.10	798.70	434.00
56x750x7498 = 58x328	57.62	52.28	29.91	28.48	4.75	4.89*	1168.17	806.86	748.95	419.41
5450x5297 = 58x697b-3	59.86	--	35.32*	--	5.41*	--	1500.05	--	848.06	--
2655x5297 = 58x694a-2	69.94*	60.71*	33.73	32.15*	4.84	4.70	1011.74	1082.46*	576.42	528.83

* The best hybrid for that character in all groups.

VITA

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