

INHERITANCE OF PROTEIN CONTENT IN GRAIN  
SORGHUM, SORGHUM BICOLOR (L.) MOENCH

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## CHAPTER I

### INTRODUCTION

The domesticated forms of the genus Sorghum are among the most widely cultivated crops of the world, surpassed only by rice, wheat, and maize in terms of total world acreage (15). All cultivated sorghums as well as a group of semi-wild weed sorghums are included in the complex species Sorghum bicolor (L.) Moench.

The available evidence overwhelmingly favors an African origin of sorghum domestication which probably began about 3,000 B.C. (14,15). Repeated independent domestication, isolated selection for different uses, and introgressive hybridization with wild types has produced tremendous morphological diversity among domesticated sorghums. Much of this genetic diversity has been accumulated and preserved in the world collection of sorghums, which now includes almost 15,000 entries. This huge germ plasm bank has already made a significant contribution to sorghum improvement but its potential is enormous.

However, to most efficiently utilize genetic variability from any source, the plant breeder needs at least a working knowledge of the inheritance of agronomically important traits. Information on the genetics of sorghum has been accumulating for many years, but is not nearly as extensive as that found for some other cereal crops. This is especially true of traits controlling nutritional quality, such as protein content. Protein improvement has not been a major consideration in

most grain sorghum breeding programs; and as a result, very little is known about the nature of the genetic system controlling protein production.

Recognition of a potential world protein crisis has recently placed a new emphasis on nutritional quality in general and protein improvement in particular. This study was initiated in order to investigate the nature of protein inheritance in grain sorghum and evaluate the potential for incorporating better nutritional quality into high yielding hybrid varieties.

## CHAPTER II

### LITERATURE REVIEW

Grain sorghum, Sorghum bicolor (L.) Moench, is the third largest U.S. grain crop and is the most important food item in parts of Africa, India, and China (33,51). Grain sorghum was introduced into the United States with the slave trade from West Africa during the past century. Since its introduction, major changes have occurred in grain sorghum enabling it to become a major world crop.

The selection of mutant height and maturity genes transformed sorghum culture from limited production of tall tropical types to commercial production of early dwarf varieties adapted to machine harvest and temperate climates. Grain yield of these improved sorghum varieties was gradually increased over the years as a result of systematic breeding procedures and incorporation of disease, insect, and drought resistance. However, it was not until the advent of hybrid varieties in the late 1950's that sorghum yields increased dramatically.

Concurrent with these yield advances, there was a gradual decline in grain protein percentage (41,44,48). The widespread use of hybrid varieties alone has resulted in a 1.5 to 2.0% loss in protein content of sorghum grain (48). This negative relationship between grain yield and protein percentage appears to hold true for all of the cereal grains unless special management practices or selected genotypes are used. Pickett (48) however, reports that certain hybrids made among diverse

inbred lines from the world sorghum collection show considerable heterosis for yield with protein content as high as the parents or only slightly lower. It is also noteworthy that total protein production on a unit area basis almost always increases as a result of hybridization (48). The yield increase due to hybridization more than offsets the reduction in grain protein percentage.

#### Importance of Grain Protein Improvement

Approximately two thirds of the world's population rely directly upon one or more of the cereal grains as the major source of protein nutrition (45). Better nutrition for these people, or even maintenance of present nutritional levels, may depend upon improvement of the inherent nutritional quality of the cereals.

In the more developed nations of the world, animal products provide a major portion of the protein requirement. However, production of animal protein is heavily dependent upon the feeding of cereal grains. The importance of more efficient feed grains is obvious in view of the world protein shortage, the expense of protein supplements, and increasing competition from the human population for high protein supplements such as soybean meal. Totusek (61) notes that it is possible for sorghum grain to contain sufficient protein to meet the protein requirement of certain classes livestock. For example, sorghum grain containing 13% protein, supplemented with minerals, vitamins, and fiber if desired would provide an adequate ration, even without urea, for cattle requiring 12% protein in the ration. If the average protein content of the 30.6 million bushel 1973 Oklahoma grain sorghum crop could have been increased by only 1%, it would have produced an 8,415 ton increase in total protein.

production.

## Progress in Other Grain Crops

### Wheat

Improvement of grain protein content in wheat, Triticum aestivum L., has probably received more attention than any other cereal grain, due to its relationship to milling and baking properties of the flour. As early as 1926, Clark (6) noted the negative correlation between grain protein content and yield. He concluded that inheritance of grain protein was complex and suggested that the best way to increase total protein production was to improve yield, while maintaining a constant protein content.

One of the first serious attempts at genetic improvement of grain protein content in wheat was initiated in the mid 1950's at Nebraska, using the soft winter wheat variety Atlas 66 as the principal source of high protein (30,32). Prior to the discovery of Atlas 66, truly superior genetic sources of high protein were not widely available and wheat breeders had not been successful in utilizing existing variability due to large environmental effects (29).

Today, the polygenic nature of protein production in wheat has been demonstrated by a number of studies and superior protein lines have been developed. Stuber, et al. (59) found that the mean protein content of the  $F_1$  from a cross between high and low protein wheat varieties was near the midparent mean, while the  $F_2$  generation was highly variable with some  $F_2$  plants exceeding the parental means. Broad sense heritability estimates ranging from 0.68 to 0.83 were calculated using parental and  $F_1$  variances. Johnson, et al. (32) also noted transgressive segregation in segregating populations of a cross between two high protein varieties,

Atlas 66 and Nap Hal. They attributed this to different genes controlling protein content in the parents. However, in crosses of high and low protein varieties the high parent mean was outside the range of the segregates and the progeny mean was near the low parent mean, suggesting at least partial dominance of low protein. Partial dominance of low protein was also indicated in a study by Davis, et al. (11), in which they compared the ratio of population means to parental means. They found heritability estimates ranging from 0.54 to 0.69 and concluded that inferences may be drawn for protein percentage of different families over a range of environments from tests conducted at one location and in one year. Haunold, et al. (23), working with two populations involving Atlas 66, obtained heritability estimates ranging as high as 0.56. They found the mean grain protein content of  $F_2$  plants and  $F_3$  lines to be intermediate to the parental means and also suggested multigenic control of protein content.

### Corn

One of the earliest examples of direct selection for improved protein content of a grain crop was in corn, Zea mays L. The now famous Illinois corn study was started by C. G. Hopkins at the Illinois Agricultural Experiment Station in 1896 (35,69). He began selection of both high and low protein strains in the Burr White variety, which had an average protein content of 10.92% in the original seed lot. In 1949, after 50 generations of selection, the average protein content of Illinois High Protein was 19.45%, while that of Illinois Low Protein was 4.91%. Progress toward lower protein content in Illinois Low Protein was very slow during the first 25 generations of selection but became more

rapid and consistent during the second 25 generations. Little progress was made toward higher protein content in Illinois High Protein during the last 15 generations of the study prior to 1949. Grain yield was substantially reduced in both strains but the greatest reduction occurred in Illinois High Protein. However, the grain yields of three-way cross hybrids involving Illinois High Protein were good and the grain protein content was significantly higher than commercial hybrids.

As early as 1920, East and Jones (16) proposed combining inbred corn lines with different genes controlling protein, in order to increase protein content in the hybrid. Frey (19) and Genter, et al. (20) later re-emphasized the concept of specific combining ability for protein percentage and proposed selection and use of high protein inbred lines to improve protein content of hybrid varieties. The apparent dominance of low protein content was noted in each of these studies; however, Genter, et al. (20) felt that the confounding effects of hybrid vigor or environment might mask the true nature of gene action and give the appearance of dominance in direct quantitative parent-progeny comparisons when none actually existed. They found a better correlation between the midparental mean and the  $F_1$  progeny mean than between either parent alone and its progeny mean. They concluded from these results that a high degree of dominance did not exist for either high or low protein content.

#### Environmental Effects on Grain Protein

Grain protein content is known to be influenced by a number of non-genetic factors such as soil type (44,56), fertilization (3,4,31,67), moisture (54,56), planting date and rate (70), and air and soil temperatures (56). Schlehuber and Tucker (54) noted that the grain protein

content of wheat tends to be higher when grown in hot, dry climates than when grown in cool, moist climates. Heller and Sieglinger (26) observed considerable variation in grain composition within grain sorghum varieties grown at Perkins and Woodward, Oklahoma. They attributed this variation largely to temperature and moisture differences. Miller, et al. (44) also reported that location within the state (Kansas) considerably affected protein content of sorghum grain. They also observed significant environmental effects at each location from year to year. DeDatta, et al. (12) reported that the protein content of rice grain grown in the Philippines is lower in the dry season than in the wet season.

The effect of nitrogen fertilization upon grain protein content has been well documented by numerous researchers (3,4,31,39,42,60,67). The first effect of applied nitrogen is to increase grain yield if moisture and other growth factors are adequate. Terman, et al. (60) have stated that only when nitrogen is absorbed by the plant in excess of vegetative needs does an increase in protein content of the forage and grain occur. They concluded that differences in inherent protein content among varieties can be shown more clearly under conditions favorable for expression of both yield and protein potential.

A number of studies have shown rather impressive increases in grain protein content by late season nitrogen applications. Hucklesby, et al. (27) found that spring nitrogen applications significantly increased grain yield and protein percentage of all three winter wheat varieties in their study. The increase in grain protein percentage was a function of both date of application and amount of nitrogen applied. Long and Sherbakoff (39) were able to increase wheat grain protein percentage from 11.0 to 13.9 and 15.3%, respectively, by top-dress applications of 25 and

50 pounds per acre of actual nitrogen ( $\text{NH}_4\text{NO}_3$ ) in May as compared to the same treatments in November and March. The May application was apparently too late for maximum effect on yield, but in time for appreciable uptake and elaboration by the plant.

Finney, et al. (17), Croy (9), Sadaphal and Das (53), and others have shown significant increases in grain yield and protein content with late season foliar sprays of urea. The most dramatic results were achieved by repeated sprayings before, during, and immediately after anthesis (17). In all of these studies, the urea seemed to be most effectively absorbed and translocated during periods of greatest plant activity, such as heading and grain filling.

Campbell and Pickett (4) were also able to significantly increase protein content of sorghum grain by sidedress applications of ammonium nitrate at heading. Burleson, et al. (3) noted that protein content of sorghum grain was increased from 6.58 to 7.92 and 10.39% by applications of 60 and 120 pounds of actual nitrogen per acre, respectively. Similar results were obtained by Waggle, et al. (67) on grain sorghum grown in Kansas.

Planting date and rate, soil and air temperature, and precipitation are other non-genetic factors affecting grain protein content. Worker and Ruckman (70) reported that the average protein content of sorghum grain produced from April plantings was 10.12% as compared with 14.02% from July plantings. High air temperatures during the developmental stage and cooler temperatures after anthesis seemed to be advantageous to protein production. Maximum air temperatures above 32 degrees centigrade before maturity are reported to be detrimental to wheat grain protein content (56). Cooler soil temperatures tend to decrease grain protein

content, probably because of reduced nitrogen uptake.

Genter, et al. (20) observed a negative correlation between protein percentage and planting rate in corn. This relationship can probably be attributed to competition for light and available nitrates. Smika, et al. (56) found a highly significant negative correlation between both precipitation and available soil moisture and grain protein content. Stone and Tucker (58) also reported that independent studies involving wheat and grain sorghum indicated a linear reduction in grain protein as total water available to the crop is increased through rainfall or irrigation. A number of other studies on wheat and grain sorghum grown under semi-arid conditions substantiate these results (44,54). The higher protein levels of grain grown under limited moisture conditions can probably be partially explained by lower grain yields and more efficient nitrogen uptake due to a more extensive root system. However, Stone and Tucker (58) suggested that the dilution effect from increased yields is not sufficient to completely explain the water-grain relationship. They suggest that increased water application may cause nitrate movement below the potentially high nutrient absorption zone and reduced nitrate concentration in the soil solution.

#### Potential for Protein Improvement in Grain Sorghum

The prevailing view today is that the genus Sorghum is composed of a complex grouping of diversified races within one or two large polymorphic species (13,22). There is an almost total absence of genetic barriers to hybridization within the genus; therefore, practically the entire range of genetic diversity found within the genus is available to the plant

breeder. The accumulation of germplasm in the world sorghum collection, together with the sorghum conversion program and various screening and indexing programs, has made this genetic diversity much more accessible and potentially useful to the sorghum breeder.

The world collection of sorghum contains considerable genetic variability for almost all traits of agronomic importance, including protein content. Screening of the world collection for protein quantity and quality began at Purdue University in 1965 with the financial support of a U.S.A.I.D. grant (48). Pickett and Oswalt (49) reported that the protein content of the world collection ranges from six to over twenty percent with most of the relatively economical lines falling in the eight to fifteen percentage range. Singh and Axtell (55) recently reported the discovery of two high lysine lines of Ethiopian origin. These lines, IS 11167 and IS 11758, had protein contents of 15.7 and 17.2%, respectively, and opaque endosperm. The relationship between high lysine and the opaque or floury endosperm, first reported in corn by Mertz, Bates, and Nelson (43), seems to hold for sorghum. The opaque gene, which is inherited as a simple recessive, affects only the amino acid composition of the endosperm with no affect on the embryo (55). Additional high lysine mutants have been chemically induced by treatment with diethyl sulfate (46).

Results of several heritability studies indicate that the available variability can be utilized to improve protein percentage in grain sorghums (7,8,36,38,47,52). Heritability estimates for protein content range in magnitude from medium to very high, and are invariably higher than corresponding estimates for yield. Individual estimates range from a low of 0.43 to a high of 0.78, depending upon the population and method

of calculation. Liang, et al. (38) observed high environmental variances for both grain yield and protein percentage, but concluded that yield was predominantly determined by dominant gene action while protein content was strongly influenced by additive gene action.

Pickett (47) has also stated that gene action for protein percentage was predominantly due to additive genes, but a significant amount of non-additive gene action was apparently caused by epistasis or dominance.

Liang, et al. (38) found protein percentage and kernel weight to be highly heritable while grain yield, head weight, and kernel number, had medium heritability values. Estimates for protein content and kernel weight were more variable and dependent upon choice of parents than was yield and the components of yield. Collins and Pickett (7) concluded, from the ratio of general to specific combining ability mean squares in a nine parent diallel cross, that additive gene action was most important for protein content and of less importance for grain yield and lysine percentage of the protein. Hybrids of higher protein parents generally had higher than average protein levels.

Crook and Casady (8) used variance components and midparent-offspring correlation to calculate heritability estimates for a number of agronomic traits. They obtained high heritability estimates for protein percentage, plant height, and panicles per plant; medium heritabilities for yield and kernel weight; and low heritabilities for days to 50% bloom, panicle exertion, leaf area, and test weight. Again, the significant variation of grain protein due to general and specific combining ability was attributed to additive gene action.

The potential for genetic improvement of grain protein content is also dependent upon its relationship to other important agronomic traits.

The negative correlation between grain yield and protein content is almost universally accepted and often cited, but the magnitude of this correlation varies considerably depending upon the population and the environmental conditions under which the estimate was made. Liang, et al. (36) reported a negative but nonsignificant correlation between protein content and yield in a six parent diallel cross. However, large and highly significant negative correlations were reported by Crook and Casady (8), Malm (41), Collins and Pickett (7), and Liang, et al. (37). Grain yield has been reported to be positively correlated with kernel number per head, kernel weight, days to bloom, and plant height while protein content is usually negatively correlated with all of these traits except kernel weight. Malm (41), Liang, et al. (37) and Worker and Ruckman (70) reported significant positive correlations between grain protein content and kernel weight while Crook and Casady (8) and Chakravorty, as reported by Crook and Casady, found protein content and kernel weight to be uncorrelated. Malm (41) suggests that larger kernels may have relatively larger embryos, thus accounting for the higher protein percentages. This theory is somewhat substantiated by a reported positive correlation between protein content and germination percentage of sorghum grain (38).

Most plant breeders involved in cereal grain quality research agree that the potential exists for significant improvement of grain protein content. The physiologic and genetic basis of protein production is still not fully understood, but there is almost universal agreement that protein production is genetically controlled but heavily influenced by environmental factors (5). Johnson, et al. (30,32) noted that strong environmental influences on protein content did not permit fixed levels

of protein as a breeding goal. Breeding programs must therefore be oriented toward relative levels of protein in comparably produced material. In this respect, breeding for improved protein content is little different from breeding for improved grain yield.

## CHAPTER III

### GENERAL MATERIALS AND METHODS

#### Field Experiments

The sorghum material used in this study was grown on a Vanoss fine sandy loam at the Agronomy Research Station, Perkins, Oklahoma in 1972 and 1973. All entries were planted in rows on 40 inch centers using a two-row cone-type planter. Parents and  $F_1$  hybrids were grown in one-row plots and  $F_2$  populations were grown in two-row plots with all entries of a particular experiment randomized within each block. The number of blocks and the number of plants measured per plot varied depending upon the experiment and type of population. A preplant application of fertilizer was broadcast on all experiments in the study. The type and rate of fertilizer application will be specified for each experiment. All cultural practices such as cultivation, irrigation, and weed control were conducted as required.

The sorghum parental lines used in this study were obtained from the Oklahoma Agricultural Experiment Station sorghum breeding program. Most of the lines were advanced generation experimental breeding lines from the pedigree breeding nursery, with medium to high protein content and acceptable agronomic characteristics. The remaining lines were released Oklahoma varieties. The lines were selected on the basis of a previous preliminary protein screening study.

Random plants from each row were bagged before anthesis to insure

selfing. Care was taken to avoid end plants, out-crosses, or other obviously abnormal plants within the row. All data were collected on a single plant basis from individually harvested bagged heads. Grain yield was determined by threshed grain weight, in grams per plant. A random sample of threshed grain from each plant was cleaned and ground for protein analysis. Protein yield per plant was the product of grain yield per plant and its corresponding protein percentage.

#### Laboratory Procedure

Protein content was determined for all material in this study using the Udy dye-binding procedure. Fraenkel-Conrat and Cooper (18) discovered that the disulfonic acid dye, orange G, combined stoichiometrically with basic protein groups at pH 2.2. These groups are furnished by the basic amino acids lysine, arginine, and histidine (34). Udy (62,63) developed the technique by which the binding quality of these basic groups on certain protein molecules could be used to quantitatively measure protein fractions. The dissociated sulfonic acid groups of the dye reacted with the strongly basic R groups of lysine, arginine, and histidine in the protein molecules to form an insoluble protein-dye complex. The amount of dye bound per gram of sample is used to provide an estimate of total protein content. In practice, the estimate is based on the concentration of unbound dye as measured colorimetrically using a light filter (470 mμ).

The dye-binding method was used largely because of its speed and convenience when handling large numbers of samples. Another important feature of the dye-binding method is its close relationship to lysine, an essential amino acid which is limiting in most plant proteins and cereal

proteins in particular. Since lysine is one of the amino acids on which the dye-binding procedure is based, the use of this method to screen for protein content may have the effect of improving protein quality by increasing lysine content.

Udy (63) and Banasik and Gilles (2) have reported a very close correlation between Kjeldahl nitrogen and the dye-binding properties of the protein in samples of wheat and wheat flour. The dye-binding and Kjeldahl results do not appear to be as closely correlated in sorghum grain as in wheat, but MacKenzie and Perrin (40) and Wilson (68) report good relationships when comparing the two methods. When properly used, the dye-binding method seems to be quite suitable for screening in a protein improvement breeding program.

The dye-binding method used in this study was the standard procedure outlined by Udy (64). A representative grain sample, consisting of five to 10 grams, from each plant was hand cleaned to remove foreign material including badly shrunken and diseased kernels. Each sample was then ground to a particle size of 0.015 mm using a Weber cyclone hammermill equipped with a vacuum collecting device. The ground samples were thoroughly blended and a one gm subsample was taken for protein determination.

Each one gm sample of ground sorghum grain was transferred into a two-ounce reaction bottle and 40 ml of the standard reagent dye, obtained from the Udy Analyzer Company, were added. This mixture was shaken vigorously for two hours on an Eberbach shaker. The shaker will hold 44 samples at once and the samples were prepared and placed on the shaker at one minute intervals, which permitted continuous reaction of a large number of samples while maintaining the optimum reaction time. The

colorimeter was equipped with a flow through cuvette which allowed rapid and continuous operation. After a one to two hour warm up period, the colorimeter was adjusted using a standard reference dye giving 42% light transmission. At the end of the required shaking time, the sample solution was filtered into the cuvette through a funnel equipped with a fiber-glass filter disc. The percent light transmission was read when the colorimeter needle had stabilized after approximately 30 seconds. This transmission reading was converted to percent protein using a previously prepared grain sorghum conversion chart (68).

## CHAPTER IV

### TOP-CROSS PROGENY TEST OF SELECTED PROTEIN LINES AND CHARACTER CORRELATIONS

The diallel procedure described in the next chapter provides a systematic approach for identifying parents and hybrids which are superior for the characters under study. However, from a practical plant breeding standpoint, the procedure is too time consuming and too limited with regard to genotypes to be used on a large scale to screen breeding lines for combining ability. Another method commonly used in the commercial development of hybrid varieties is the top-cross progeny test, in which a large number of promising lines are crossed to a common tester and the progeny evaluated. This method is especially common in hybridization systems which utilize some type of cytoplasmic male sterility. The male sterile female parent is usually the tester line in this case and is most often characterized by good agronomic qualities and good general combining ability for performance traits.

The purpose of this experiment was to evaluate a number of promising lines and their  $F_1$  progeny for possible future use in a high protein breeding program. A number of agronomically important traits were evaluated and the average degree of heterosis was noted for each. Phenotypic and genetic correlation coefficients were also calculated in order to determine the relationship between protein percentage and other important agronomic traits.

## Materials and Methods

### Experimental Materials and Design

The 44 paternal lines used in this experiment consisted of experimental inbred lines from the Oklahoma State University pedigree sorghum breeding nursery. These lines were derived from rather diverse parentage and represented a wide range of variability for such traits as kernel size and color, plant height, panicle type, and maturity. These lines were also characterized by medium to high protein content. The male sterile tester line used in this experiment was AOK 15, an Oklahoma variety with above average protein percentage and good agronomic characteristics.

Each of the 44 paternal lines was crossed onto AOK 15 in the greenhouse during the winter and spring of 1972. The 45 parents and 44  $F_1$ s were grown in the field in 1972. The normal male fertile B-line was used to represent OK 15 in the field planting in order that selfed seed could be obtained. The experiment was planted on June 15 in single row plots 12 feet long and 40 inches apart. Plants within plots were thinned to a uniform spacing of approximately six inches after emergence. Fertilizer, according to soil test, was broadcast preplant at the rate of 225 pounds per acre 45-0-0, 100 pounds per acre 0-46-0, and 50 pounds per acre 0-0-60. A majority of the paternal lines were good restorers, however a few gave B reactions or were poor restorers. If fertility was not restored in the  $F_1$ , then bagged heads were hand pollinated in order to achieve seed set. Five random plants were bagged and harvested from each plot and the following traits were measured from bagged heads:

1. Grain Yield - the total weight of threshed grain in grams per

plant.

2. % Protein - the protein percentage of a random sample of whole ground grain from each plant, measured using the dye-binding method.
3. Protein Yield - the total protein production in grams per plant estimated by multiplying grain yield times % protein and dividing by 100.
4. Kernel Weight - The weight in grams of 100 randomly chosen hand cleaned kernels.
5. Kernel Number - The total number of kernels per head as estimated by dividing grain yield per head by the weight of 100 kernels and multiplying by 100.
6. Panicle Length - The length in centimeters from base to tip of panicle.
7. Plant Height - The total height in centimeters from basal node to tip of panicle.
8. Maturity - The number of days from planting to anthesis.

The parentage, number of generations of self fertilization, and line identification numbers for the 45 parental lines used in this experiment are given in Table I. Since AOK 15 was a common parent for all crosses, hereafter, a hybrid as well as its paternal parent will be referred to by the appropriate line identification number.

### Statistical Procedures

Heterosis was measured for each trait in each  $F_1$  population in terms of  $F_1$  deviations from midparent and high-parent values. Significance of these estimates were determined using adjusted LSD values. Five

TABLE I

PARENTAGE, NUMBER OF GENERATIONS OF SELFING, AND LINE IDENTIFICATION  
NUMBERS FOR THE PARENTS USED IN A TOP-CROSS PROGENY TEST

Line Id. No.	Gen.	Pedigree
1	F <sup>4</sup>	(AOK 8 X Feki Mustachi Sel-ROKY 8)-1-8-1
2	F <sup>4</sup>	(AOK 24 X A S. <u>vulgare</u> -J.G.)-7-2-2
3	F <sup>5</sup>	(A Red-Y8 Sel X Cy 12-Kau-Cy 11-7663)-1-2-1
4	F <sup>5</sup>	(AOK 11 X Msumbiji)-1-1-1
5	F <sup>7</sup>	(Cy 12-Kau-Cy 11-7663 X Wiley)-1-1-1-1-1
6	F <sup>7</sup>	(AOK 24 X Dwf. Hydro-Rice-Do #1-Kau)-2-1-1-1
7	F <sup>7</sup>	(A Red X ROKY 34)-1-2-1-2-1
8	F <sup>7</sup>	(A Red X ROKY 34)-1-3-2-1-1
9	F <sup>8</sup>	(SA 7663 <sup>2</sup> X BC)-1-1-1-1-2-1
10	F <sup>8</sup>	(SA 7663 <sup>2</sup> X BC)-1-1-1-1-2-2
11	F <sup>12</sup>	(A Red-Kau-5-1-2 X Kau)-3-1-1-2-1
12	F <sup>8</sup>	(A Red-Kau X Korgi <sup>2</sup> )-E1-1-1-1-1-1
13	F <sup>5</sup>	(Korgi <sup>3</sup> X BC)-1-1-1
14	F <sup>11</sup>	(Cy 1-Korgi-Kau Y. X Ryer)-1-2-1-1-(2)-2
15	F <sup>11</sup>	(A Red X Calico)-1-4-2-1-1-1-2-1
16	F <sup>12</sup>	(Cy 11-332-Kau-2-2 X TR-WWRK)-1-3-1-3-1-1-1-1
17	F <sup>12</sup>	(A Red-Kau-Eth 21 X ROKY 10)-1-2-2-1-1-1
18	F <sup>11</sup>	(A Wheat-Collubi X ROKY 7)-2-1-2-2-1
19	F <sup>14</sup>	(A Red-Kau-5-5-2 X Dr. Res.)-3-2-3-2-1-1
20	F <sup>9</sup>	(A Wht-Scent X ATR-AR-K-5-1-India-Cy 11-Korgi-4)-1-1-2-1-1-1
21	F <sup>12</sup>	(ATR X AR-K-5-1-India-Cy #11-Korgi-4)-2-1-1-1-1-1
22	F <sup>18</sup>	C.I. 692 X Waxey Sweet
23	F <sup>20</sup>	Y-4 white (thick mesocarp) Tex 63 X Kaura-2-10-2-4
24	F <sup>+</sup>	51 X 5 (chinch bug resistant milo derivative)
25	F <sup>23</sup>	Bonar-Day X #1-7-1-2
26	F <sup>14</sup>	(Y. Darset X Ladore)-2-2-1
27	F <sup>28</sup>	(Kashakashi X 10)-2-2-1
28	F <sup>6</sup>	(OK 8 X WBH)-2-1

TABLE I (Continued)

Line Id. No.	Gen.	Pedigree
29	F	(Def. Endo. X Ryer)-1-4-2-1
30	F <sup>8</sup>	(OK 8 X Wiley)-1-1-1-1-1
31	F <sup>7</sup>	(Bonar-Day-#1-7-1-2 X Tx. 63-Sol K-1-3)-1-1-1-1-1
32	F <sup>16</sup>	Red X Kau-5-1-2
33	F <sup>+</sup>	BTR X <u>S. splendidum</u> -5-1-1-2
34	F <sup>7</sup>	(OK 24 X OK 15)-1-1-1-1-1
35	F <sup>7</sup>	(BOK 8 X OK 24)-1-2-2-1-1-1
36	F <sup>8</sup>	(B Red-Kau-5-1-1 X Dr. Res.)-2-2-2-1-1
37	F <sup>14</sup>	Long Glume X Do #1-1-1-1-1-3-1
38	F <sup>19</sup>	ms <sub>2</sub> (3) X Wx. Dwf. Kafir-6-1
39	F <sup>22</sup>	ms <sub>2</sub> (3) X Wx. Dwf. Kafir-Lowe-3
40	F <sup>18</sup>	Til. K X 44 X Y. Peric.-2
41	F <sup>18</sup>	Tan Redlan
42	F <sup>20</sup>	dd RK Mut.
43	F <sup>+</sup>	BOKY 55 Tall Mut.-1-2-2
44	F <sup>+</sup>	Sumac X Wiley-1-1-2-2-1
	F <sub>7</sub>	
AOK 15	F <sub>+</sub>	C.I. 811 X Redlan-3

\*F<sub>+</sub> indicates advanced generation inbred lines and varieties where the exact number of generations of selfing<sup>+</sup> is unknown.

plants were measured in each entry and separate analyses of variance conducted for each generation, indicated that unequal variances existed in parents and  $F_1$  for some traits. Therefore, standard errors (SE) were calculated as follows:

$$\text{SE for hybrid vs high-parent} = [(\sigma_1^2 + \sigma_2^2)/5]^{1/2},$$

where  $\sigma_1^2$  and  $\sigma_2^2$  are parental and  $F_1$  error variances, respectively, and

$$\text{SE for hybrid vs midparent} = [(\frac{1}{2}\sigma_1^2 + \sigma_2^2)/5]^{1/2}.$$

Mean heterosis for each trait was also determined by pooling midparent and high-parent deviations across all  $F_1$  populations. Midparent and high-parent heterosis estimates, expressed as percent of the appropriate means, were calculated as follows:

$$\text{Midparent heterosis} = (\bar{F}_1 - \bar{MP})/\bar{MP},$$

and

$$\text{High Parent heterosis} = (\bar{F}_1 - \bar{HP})/\bar{HP}.$$

Tests of significance were made on the numerator of these equations using the appropriate LSD values. A significant mean deviation was assumed to indicate significance of the estimate.

Correlation coefficients were estimated for all possible observed character combinations in both parental and  $F_1$  populations. Nested analyses of variance and covariance were conducted for each character within each generation. This analysis provided a total mean square correlation for each trait, containing both environmental and genetic covariances, and an entry variance component correlation, in which the

environmental effects were removed. Total mean square correlations were used as estimates of phenotypic correlations and entry variance component correlations were used as estimates of genetic correlations, with certain restrictions which will be mentioned later.

Variation between plants within entries was used to calculate standard errors for the estimates. The standard probability test (57) was used to test significance of the phenotypic correlation coefficients from zero. Since the genetic correlations are based on variance components which may not be normally distributed, an appropriate error term was not available and tests of significance were not made.

### Results and Discussion

The parental lines used in this experiment had all been selfed for at least four generations and most lines were in the range of  $F_6$  to  $F_{12}$ . The diverse parentage of these lines is apparent from the pedigrees given in Table I. Further evidence of genetic variability in these lines is provided by the data in appendix Table XXI. This table gives the plot mean values of the eight observed characters for each parent and its  $F_1$  hybrid when crossed to AOK 15. Grain yield ranged from 6.6 to 52.7 grams per plant in the parents and 12.0 to 86.7 grams in the hybrids. Protein percentage ranged from 10.8 to 16.3% in the parents and 11.0 to 14.9% in the hybrids. Protein yield ranged from 0.86 to 6.01 grams per plant in the parents and 1.64 to 9.70 grams in the hybrids. Kernel weight ranged from 1.81 to 5.09 grams per 100 seeds in the parents and 1.95 to 3.93 grams in the hybrids. Kernel number ranged from 366 to 2025 kernels per panicle in the parents and 610 to 2965 kernels per panicle in the hybrids. The parents ranged in height from 60 to 205 cm while their hybrids

ranged from 89 to 228 cm. Head length ranged from 16 to 34 cm in the parents and from 17 to 31 cm in the hybrids. The parents were found to range in maturity from 52 to 70 days to bloom while their hybrids ranged from 52 to 75 days.

The environmental variance, as measured by variation between plants within entries, was rather large for grain yield, kernel weight, kernel number, and protein percentage. These traits are all quantitative in nature and are presumed to be controlled by a large number of genes. The polygenic control of these traits may make them somewhat more susceptible to environmental influences, but the higher variances could also be an indication that the inbred lines are not completely homogeneous for these traits. Repeated selfing would insure an approach to homozygosity but advanced generation lines are usually maintained from bulk seed lots and some heterogeneity may be preserved in unselected traits such as protein percentage.

The importance of heterosis in sorghum breeding is well demonstrated in Tables II and III. Table II gives the mean heterosis for each trait, in terms of percent of high-parent and midparent means, while Table III gives the performance of each individual hybrid expressed in terms of mean deviations from its midparent and high-parent. In general, the hybrids were higher yielding, taller, and earlier than their parents. They also had larger heads with more but smaller kernels and lower grain protein percentage. The greatest degree of heterosis was exhibited for kernels per panicle with the hybrids having 52 and 49% more kernels than their average midparent and high-parent, respectively. These results are in general agreement with Quinby (50) who also reported that an increase in kernels per panicle contributes more to the increased yield of hybrids

TABLE II  
AVERAGE PERFORMANCE OF PARENTAL AND F<sub>1</sub> GENERATIONS AND MEAN HETEROSIS  
EXPRESSED AS PERCENT OF HIGH-PARENT AND MIDPARENT MEANS

Trait	Generation Mean		Percent Mean Heterosis		Number of Crosses Showing Significant* Heterosis	
	MP	F <sub>1</sub>	MP	HP	MP	HP
Grain Yield	33.98	49.45	45.5**	24.4**	24 (1) <sup>a</sup>	16 (1)
% Protein	13.39	12.62	-5.73**	-6.1**	4 (21)	0 (12)
Protein Yield	4.51	6.07	34.6**	14.2**	22 (1)	12 (1)
Kernel Weight	2.96	2.86	-3.66**	-14.3**	4 (10)	0 (2)
Kernel Number	1168	1777	52.2**	49.2**	26 (1)	18 (1)
Plant Height	96.6	111.3	15.2**	13.1**	29 <sup>b</sup>	21 <sup>c</sup>
Panicle Length	22.0	24.8	12.5**	4.8**	30	11
Maturity	59	58	0.63**	0.14	29 <sup>d(6)</sup>	19 <sup>e(4)</sup>

\*,\*\*F<sub>1</sub> mean significantly different from its high-parent or midparent mean at the .05 and .01 levels of probability, respectively, based on LSD.

<sup>a</sup>Number in parenthesis indicates heterosis in the negative direction.

<sup>b,c</sup>Taller than midparent and tall parent, respectively.

<sup>d,e</sup>Earlier than midparent and early parent, respectively.

TABLE III

PERFORMANCE OF TOP-CROSS HYBRIDS EXPRESSED AS MEAN DEVIATIONS FROM MIDPARENT  
AND HIGH-PARENT FOR THE EIGHT CHARACTERS UNDER STUDY

Line* Id. No.	Characters															
	Grain Yield		% Protein		Protein Yield		Kernel Weight		Kernel Number		Plant Height		Panicle Length		Maturity	
	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP <sup>a</sup>	HP <sup>b</sup>
1	-26.8	-26.7	1.20	0.44	-3.23	-3.68	0.08	0.02	-832	-833	17.3	8.0	0.0	-3.2	1.4	1.2
2	12.1	7.3	-0.47	-1.01	1.29	0.47	0.10	-0.45	417	349	5.9	6.8	0.3	-1.0	1.1	0.4
3	21.0	15.4	-1.44	-1.67	1.96	1.15	0.43	0.75	1002	938	0.8	-5.6	6.6	4.4	-4.4	-4.8
4	16.0	12.9	-0.18	-1.22	1.82	1.04	0.35	0.98	931	716	4.9	1.6	2.1	-1.0	0.5	-2.0
5	29.5	16.4	-2.28	-3.21	3.03	1.39	-0.08	-0.20	887	475	11.9	10.2	2.7	2.2	2.5	2.0
6	-3.3	-4.4	1.14	-0.15	-0.08	-0.48	0.17	-0.31	-142	-454	3.8	-4.4	1.9	0.2	0.5	-3.0
7	32.1	25.6	-1.06	-2.01	3.20	2.85	-0.10	-0.42	1117	735	4.4	1.6	2.1	-1.8	1.0	1.0
8	15.0	11.5	-1.24	-1.79	1.29	0.98	-0.38	-0.38	710	572	7.4	-7.0	2.5	-0.2	0.0	-1.0
9	26.3	19.9	-2.25	-2.93	2.37	1.69	-0.27	-0.41	893	668	14.0	-3.0	3.1	3.0	1.0	1.0
10	18.3	11.1	-2.14	-2.41	1.38	0.53	-0.24	-0.35	708	519	23.9	12.2	2.5	1.2	-1.0	-1.8
11	28.1	20.1	-1.18	-1.61	2.92	1.72	0.06	-0.06	840	596	29.7	19.2	5.9	2.2	0.1	-2.8
12	29.7	23.0	-3.02	-3.99	2.45	1.77	-0.51	-1.28	894	566	21.5	17.0	3.1	2.4	3.0	3.0
13	47.7	45.6	-2.01	-2.12	4.61	4.26	-0.28	-1.16	1225	976	62.5	37.8	4.6	3.0	3.9	1.0
14	30.2	23.2	-0.92	-1.25	3.25	2.22	-0.69	-0.88	1502	1344	24.0	9.0	3.0	2.0	-15.9	-19.4
15	11.9	10.5	-1.26	-1.44	0.94	0.68	-0.09	-0.60	416	85	13.3	9.8	3.1	-0.4	2.0	1.8
16	17.8	7.7	-0.93	-0.94	1.94	0.59	-0.03	-0.79	724	664	12.8	8.6	2.3	0.6	2.7	0.2
17	23.6	21.6	-1.90	-2.00	1.92	1.61	-0.26	-0.93	1034	717	16.7	13.8	3.5	2.4	-0.9	-4.8
18	13.6	6.5	-0.97	-2.40	1.65	1.05	-0.14	-0.12	391	249	6.6	5.6	2.7	-0.8	2.6	1.8
19	-9.4	-18.3	-0.20	-0.49	-1.25	-2.46	-0.43	0.11	-369	-581	5.4	-0.6	1.2	-3.0	3.0	3.0
20	9.8	3.1	-0.44	-1.11	1.18	0.42	-0.31	-0.20	228	223	13.7	-0.8	-0.4	-3.0	0.1	-3.0
21	-4.0	-16.9	-0.10	-1.56	-0.45	-1.99	-0.30	0.11	-155	-508	10.1	8.2	2.5	1.8	0.3	-1.2
22	32.5	26.4	-0.41	-0.59	3.96	3.09	-0.05	-0.73	1290	1174	13.8	5.4	4.1	3.4	1.5	0.0
23	23.6	21.1	-1.42	-1.50	2.27	1.89	-0.53	-0.75	1152	1142	3.7	-1.8	5.7	1.2	2.5	1.0
24	10.6	-4.5	-1.13	-1.40	1.04	-0.95	-0.53	-0.88	705	297	1.6	-5.6	0.7	-1.2	3.4	3.2
25	28.8	19.3	-1.64	-2.40	3.11	1.99	-0.68	-1.32	1813	1724	10.3	7.0	3.4	2.8	-5.7	-6.6

TABLE III (Continued)

Line* Id. No.	Characters															
	Grain Yield		% Protein		Protein Yield		Kernel Weight		Kernel Number		Plant Height		Panicke Length		Maturity	
	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP	HP	MP <sup>a</sup>	HP <sup>b</sup>
26	-7.3	-9.4	-0.44	-0.03	-0.91	-1.03	-0.14	-0.64	-203	-369	14.7	10.0	3.0	0.6	2.0	2.0
27	12.1	8.3	-0.69	-1.81	1.44	1.28	0.54	-0.02	136	5	28.8	24.0	-1.4	-3.8	1.8	0.0
28	23.2	12.7	-0.98	-1.24	2.64	1.29	-0.10	-0.32	791	519	14.0	13.6	3.0	-1.6	1.0	0.0
29	59.3	46.9	-2.54	-2.71	5.84	4.20	0.14	-0.40	2036	1774	25.4	13.2	5.4	5.2	-18.6	-21.6
30	16.6	8.1	-0.28	-0.57	2.16	1.06	0.35	-0.24	387	338	9.5	6.0	5.1	4.0	-0.4	-2.8
31	-9.7	-22.2	-0.51	-0.49	-1.26	-2.79	-0.47	-1.24	-142	-326	9.2	8.2	1.2	-1.6	2.5	1.0
32	10.6	1.4	-0.05	-0.53	1.24	-0.10	-0.45	-1.05	694	600	-0.7	-6.2	4.7	3.2	2.8	1.8
33	24.8	14.8	-1.47	-1.53	2.46	1.09	-0.32	-0.75	1113	927	8.3	1.8	-0.6	-6.4	0.8	-0.2
34	3.7	0.6	1.05	-0.57	0.92	1.11	0.27	0.03	-5	-215	3.5	1.8	1.2	0.6	0.8	0.8
35	9.9	-3.1	0.53	-0.41	1.18	-0.57	-0.79	-0.99	783	420	5.9	-6.4	4.6	3.6	2.8	1.6
36	10.2	3.5	-0.42	-0.85	1.08	0.29	-0.20	-0.92	592	496	9.5	7.8	2.2	-2.6	1.2	0.4
37	25.3	24.4	-1.90	-0.07	2.08	2.02	0.14	-0.23	722	495	27.4	14.4	2.8	-4.0	2.7	2.0
38	-2.4	-3.7	-0.79	-1.44	-0.62	-1.05	-0.70	-1.38	327	-17	-4.6	-5.4	0.0	-3.0	4.2	2.0
39	11.5	6.8	-0.44	-0.74	1.24	0.52	0.05	-0.51	427	332	0.6	-2.0	2.7	2.4	2.0	2.0
40	2.6	-6.6	-0.31	-0.31	0.12	-1.10	-0.14	-0.84	326	287	11.1	10.6	2.4	0.2	1.0	0.0
41	-2.7	-6.1	1.33	-0.06	-0.03	-0.18	-0.39	-0.86	75	-304	8.6	8.0	1.3	0.0	1.0	1.0
42	20.2	3.6	-0.12	-0.26	2.13	-0.09	0.51	-0.25	627	225	50.5	33.2	4.7	3.4	0.5	-5.0
43	4.5	-4.6	-0.86	-1.17	0.35	-0.83	0.18	-0.57	98	79	6.2	-3.4	4.2	0.2	3.8	0.6
44	33.2	32.6	-0.57	-1.14	4.13	3.88	0.65	-0.01	656	239	77.6	22.4	4.9	4.4	0.1	-4.0
LSD																
.05	12.9	13.9	0.87	0.97	1.54	1.68	0.42	0.46	479	519	7.2	8.0	2.2	2.5	0.63	0.76
.01	17.0	18.3	1.14	1.27	2.03	2.20	0.55	0.60	629	683	9.4	10.6	2.8	3.3	0.83	0.00

\*See Table I for identification of parents.

<sup>a,b</sup> Positive values indicate F<sub>1</sub> earlier than midparent and early parent, respectively.

than any other single trait. Largely as a result of more kernels per head, the hybrids outyielded their mean midparent and high-parent by 46 and 24%, respectively. Highly significant positive midparent and high-parent heterosis was also observed for protein yield, plant height, and panicle length. Highly significant negative heterosis was observed for protein percentage and kernel weight. Maturity was the trait showing the least overall heterosis; however this was largely due to a few specific crosses in which early parents produced very late hybrids. A vast majority of the hybrids were significantly earlier than their parents.

Individual hybrids ranged considerably in their degree of heterosis for most traits. Sixteen hybrids yielded significantly more than their best parent and only one cross yielded less than either of its parents. Hybrid number 29 produced the highest degree of heterosis for grain yield and the highest yield with a 95% superiority over its best parent. However, this cross also produced one of the largest decreases in protein percentage. Only four hybrids had higher protein percentages than their midparent and none were higher than their highest parent. Twelve crosses produced hybrids with significantly lower protein percentage than either parent, with the greatest reduction being 21 and 26% below the midparent and high-parent, respectively, for entry 12. Although protein percentage was significantly reduced in the hybrids, protein production on a per plant basis was greatly increased by hybridization. The hybrids produced 35 and 14% more protein per plant than their average midparent and high-parent, respectively. In view of this relationship, the apparent lack of positive heterosis for protein percentage does not seem too alarming if increased protein production were the only goal. However, from a nutritional standpoint, protein percentage of the grain is the critical factor

and improvement in this area may necessitate development of relatively high protein parental lines which will combine to produce high yielding hybrids with a minimal reduction in protein percentage.

A knowledge of the relationship between traits and especially agronomically important traits is often of vital importance in planning and successfully carrying out a breeding program. Phenotypic correlation coefficients, estimated independently for each generation, are given in Table IV. Yield was positively correlated with all observed traits with the notable exception of protein percentage. As expected, highly significant negative correlations were observed between grain yield and protein percentage ( $-.453$  and  $-.671$  for parents and  $F_1$ , respectively). The higher negative correlation in the hybrids was probably due to the heterotic trends described previously.

Highly significant correlations of  $.846$  and  $.854$  for parents and  $F_1$ , respectively, were noted between grain yield and number of kernels per head, suggesting the importance of kernel number in determining total yield. Plant height, kernel weight, and head length were also correlated with yield while maturity was correlated with yield in the hybrids, but did not significantly influence yield in the parents. The extremely high correlation between grain yield and protein yield again stresses the importance of grain yield in determining total protein production.

Protein percentage was negatively correlated with grain yield, protein yield, kernel number, and head length in both generations. Plant height did not seem to be related to protein percentage and the influence of maturity was not consistent in parents and hybrids. Kernel weight was uncorrelated with protein percentage in the hybrids but these traits demonstrated a small positive correlation in the parents. In general,

TABLE IV  
PHENOTYPIC CORRELATION COEFFICIENTS ESTIMATED FROM PARENTAL<sup>a</sup> AND F<sub>1</sub><sup>b</sup> DATA

	Grain Yield	% Protein	Protein Yield	Kernel Weight	Kernel Number	Plant Height	Panicle Length	Maturity
Grain Yield		-.453**	.967**	.148*	.846**	.339**	.277**	.033
% Protein	-.671**		-.236**	.147*	-.463**	.109	-.152*	.131
Protein Yield	.982**	-.549**		.188**	.804**	.405**	.254**	.091
Kernel Weight	.202**	.009	.226**		-.347**	.288**	-.112	.018
Kernel Number	.854**	-.666**	.827**	-.303**		.215**	.289**	.048
Plant Height	.351**	-.092	.370**	.422**	.099		.159*	.245**
Panicle Length	.171*	-.147*	.147*	-.060	.178**	.067		-.206**
Maturity	.388**	-.237**	.361**	-.059	.416**	.166*	-.067	

<sup>a</sup>Upper right-hand corner.

<sup>b</sup>Lower left-hand corner.

\*,\*\*Significantly different from zero at the .05 and .01 levels of probability, respectively (223 d.f. for parents and 218 d.f. for hybrids).

the traits most positively correlated with yield were most negatively correlated with protein percentage. A notable exception to this inverse relationship seems to be kernel weight. Kernel weight was not as closely correlated with yield as some of the other yield components but it was the only yield component not negatively correlated with protein percentage. Crook and Casady (8) and Chakravorty, as reported by Crook and Casady, found protein content and kernel weight to be uncorrelated, while other workers have reported small but significant positive correlations between protein content and kernel weight (37,41,70). These relationships suggest that it may be possible to maintain or even increase grain yield by selecting for larger seed during a protein improvement breeding program.

Genetic correlations for each trait in parents and in  $F_1$ s are given in Table V. These estimates are true genetic correlations only if the average dominance effects for each trait are zero. Since this assumption is probably not met for most of the traits, these estimates may be invalid to some extent. However, they do provide some insight into the relationship between traits after adjustment for environmental variances and covariances. Only minor differences were noted between genetic and phenotypic correlations. The genetic correlations between grain yield and protein percentage were more strongly negative than the phenotypic correlations, while the genetic correlations between grain yield and plant height were closer than the phenotypic correlations. The high positive correlation between grain yield and kernel number is still evident and apparently plant height, head length, and maturity are genetically more important in determining grain yield of the hybrids than the phenotypic correlations would indicate. The genetic correlation between

TABLE V  
GENETIC CORRELATION COEFFICIENTS ESTIMATED FROM PARENTAL<sup>a</sup> AND F<sub>1</sub><sup>b</sup> DATA

	Grain Yield	% Protein	Protein Yield	Kernel Weight	Kernel Number	Plant Height	Panicle Length	Maturity
Grain Yield		-.521	.960	.104	.835	.417	.272	.048
% Protein	-.777		-.278	.101	-.474	.153	-.142	.149
Protein Yield	.981	-.655		.135	.797	.529	.250	.130
Kernel Weight	.201	-.034	.213		-.425	.315	-.114	.010
Kernel Number	.866	-.739	.844	-.298		.252	.376	.070
Plant Height	.451	-.135	.494	.593	.124		.156	.256
Panicle Length	.247	-.346	.204	-.049	.257	.008		-.219
Maturity	.521	-.329	.505	-.096	.580	.172	-.073	

<sup>a</sup>Upper right-hand corner.

<sup>b</sup>Lower left-hand corner.

kernel weight and protein percentage is very small and perhaps not significant, but does remain positive.

## CHAPTER V

### DIALLEL ANALYSIS OF GRAIN YIELD, PROTEIN

#### CONTENT, AND PROTEIN YIELD

The diallel cross is a rather powerful tool to study the various properties and parameters of the genetic system controlling a quantitative trait. The diallel analysis, as outlined by Jinks and Hayman (24, 25,28), attempts to partition phenotypic variation into genotypic and environmental variation and to further divide the genotypic variation into additive and dominance components. These values can then be used to calculate heritability estimates, draw inferences about the genetic system, and determine the most efficient breeding procedures. The Jinks-Hayman analysis is based on several assumptions with regard to the genetic system. These are as follows (10):

1. diploid segregation,
2. homozygous parents,
3. no reciprocal differences,
4. no genotype-environment interaction within locations, and years,
5. no epistasis,
6. no multiple alleles, and
7. uncorrelated gene distributions.

The failure of one or more of these assumptions may influence and could to some extent invalidate inferences derived from the analysis. Certain tests are available to determine the validity of these assumptions.

The diallel analysis procedure, as described by Griffing (21), is a systematic method of evaluating a population or a select group of inbred lines for combining ability in hybrid combinations. The concept of general and specific combining ability has become increasingly important to plant breeders with the widespread use of hybrid varieties in many crops. Depending upon the inclusion of parental inbreds or reciprocals in the analysis, Griffing lists four possible experimental methods: 1) parents and all  $F_1$ s including reciprocals 2) parents and one set of  $F_1$ s without reciprocals, 3) all  $F_1$ s including reciprocals without the parents, and 4) one set of  $F_1$ s without reciprocals or parents. He also distinguishes between two sampling assumptions: 1) the parents are a selected or fixed set and inferences apply only to those parents, or 2) the parents are a random sample from some population about which inferences are to be made. These two assumptions are designated as models I and II, respectively.

The data in this experiment were analyzed separately using the Jinks-Hayman and Griffing procedures. Each of these methods provides unique information about the nature of the genetic system and together they more clearly resolve the mechanisms of inheritance than either could alone.

## Materials and Methods

### Experimental Materials and Design

The six parental lines used in this experiment consisted of four experimental breeding lines from the Oklahoma State University pedigree breeding nursery and two released Oklahoma varieties which have been widely used as maternal parents for hybrid production. These parents and their general morphological characteristics were as follows:

1. (A Wht-Collubi X ROKY 7)-2-1-2-2-1 - experimental line,  $F_{12}$ , medium large brown kernels, purple plant color, 90-95 cm tall, awnless,
2. (SA 7663<sup>2</sup> X BC)-1-1-1-1-2-1 - experimental line,  $F_9$ , large yellow kernels, tan plant color, 120-130 cm tall, awnless,
3. Bonar-Day X #1-7-1-2 - experimental line,  $F_{24}$ , small brown kernels, purple plant color, 75-85 cm tall, awned,
4. Y-4 white - Texico 63 X Kaura-2-10-2-4 - experimental line,  $F_{21}$ , medium white kernels, purple plant color, 95-105 cm tall, awned,
5. B Wheatland - released variety, medium large red kernels, purple plant color, 80-90 cm tall, awnless, and
6. BOK 8 - released variety, medium small red kernels, red plant color, 80-90 cm tall, awnless.

These parents were chosen to represent the range in protein content normally found in grain sorghum produced in the U.S. and are not necessarily intended to be a random sample of any sorghum population. Hereafter, parents will be identified by their respective numbers and crosses by the appropriate number combinations.

The diallel crosses were made in the greenhouse in the winter and spring of 1973. All possible crosses including reciprocals were made using tweezer emasculation and hand collection and transfer of pollen. The six parents and 30  $F_1$ s were grown in the field at the Perkins Agronomy Research Station in 1973. The experiment was planted on June 23 in a randomized complete block design with four replications. Plots were single rows 12 feet long and 40 inches apart. Plants within plots were thinned to a uniform spacing of approximately one foot with one plant per hill. Fertilizer, according to soil test, was broadcast preplant at the

rate of 265 pounds per acre of 45-0-0 and 170 pounds per acre of 0-60-0. One irrigation, consisting of approximately one inch, was made after planting in order to insure uniform emergence. Two plants were bagged and harvested from each plot and grain yield, protein percentage, and protein yield were determined from bagged heads on an individual plant basis.

### Statistical Procedures

The diallel statistics necessary for the Jinks-Hayman analysis were derived from variances and covariances of elements in the diallel tables of means. Each replication was treated as a single diallel and analyzed separately as outlined by Verhalen and Murray (65,66). An analysis of variance indicated no reciprocal differences for the observed traits and reciprocal crosses were pooled, providing four observations per block for each hybrid. A diallel table of means was developed for each block by averaging over plants within entries and the following statistics were calculated:

$V_{OLO}$  = variance among parents,

$V_r$  = variance among elements of the  $r^{\text{th}}$  parental array,

$W_r$  = covariance between elements of the  $r^{\text{th}}$  array and the parents,

$W_r'$  = covariance between elements of the  $r^{\text{th}}$  array and the array means,

$V_{1L1}$  = mean variance of the  $r$  arrays,

$V_{OL1}$  = variance of the array means,

$W_{OL01}$  = mean covariance between the arrays and the parents,

$M_{LO}$  = mean of the parents, and

$M_{L1}$  = overall mean of the diallel table.

An array consists of a parent and the five  $F_1$  hybrids derived from it.

An array mean is the average of the six elements composing a particular array.

Environmental variances were estimated from between plant variation within entries and each block was adjusted independently for environmental effects. Tests for homogeneity of variances indicated unequal error variances for parents and  $F_1$ , therefore separate estimates of environmental variance were made for parents and  $F_1$ . After adjustment for environmental variances the diallel statistics become:

$$V_{OL0}' = V_{OL0} - E_0 = D \quad ,$$

$$V_{1L1}' = V_{1L1} - [E_0 + (n - 1)E_1]/n = \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F \quad ,$$

$$V_{OL1}' = V_{OL1} - [E_0 + (n - 2)E_1]/n^2 = \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} H_2 \quad ,$$

and

$$W_{OL01}' = W_{OL01} - (E_0/n) = \frac{1}{2} D - \frac{1}{4} F \quad ,$$

where  $n$  equals the number of parents,  $D$ ,  $F$ ,  $H_1$ , and  $H_2$  are genetic parameters, and  $E_0$  and  $E_1$  are parental and  $F_1$  environmental variances, respectively. These adjusted statistics were then used to calculate least-squares solutions for the genetic parameters by the following equations:

$$D = \text{estimate of additive variance} = V_{OL0}' \quad ,$$

$$H_1 = \text{estimate of dominance variance} = V_{OL0}' - 4W_{OL01}' + 4V_{1L1}' \quad ,$$

$$H_2 = \text{estimate of dominance variance} = 4(V_{1L1}' - V_{OL1}') \quad ,$$

and

F = estimate of the distribution of dominant versus recessive alleles in the parents =  $4W_{OLO1}' - 2V_{OLO}'$ .

Since the analysis was conducted independently for each block, four independent estimates were calculated for each genetic parameter for each trait, and standard errors were calculated from the variance of the individual estimates around the mean estimates.

The diallel data were also subjected to combining ability analysis using model I, method 1 of Griffing, which includes parents and all  $F_1$ s including reciprocals. An analysis of variance on a plot mean basis was used to partition total variance by genotypes, blocks, and genotypes by blocks. The sum of squares due to genotypes was then partitioned into general combining ability, specific combining ability, and reciprocal effects, with  $n-1$  degrees of freedom for g.c.a. and  $n(n-1)/2$  degrees of freedom for s.c.a. and reciprocal effects. Differences within effects were tested by the appropriate F ratios. General combining ability for each parent and specific combining ability for each cross was estimated by weighted deviations of the appropriate means from the overall mean. Appropriate standard errors were also calculated for these effects.

### Results and Discussion

The results of analyses of variance conducted on a plot mean basis for each observed trait in each generation are shown in Tables VI and VII. The presence of highly significant differences among parents and hybrids indicates the presence of genetic variability in this population and suggested that detailed analyses of gene action and combining ability could be conducted. Overall means for each parent and mean performance of its  $F_1$  progeny when crossed to the other five parents are

TABLE VI  
ANALYSIS OF VARIANCE OF DIALLEL CROSS PARENTAL MEANS

Source	d.f.	Mean Squares		
		Grain Yield	% Protein	Protein Yield
Blocks	3	49.168*	0.248	0.457
Parents	5	713.816**	20.108**	8.371**
Error	15	14.977	0.367	0.190

\*,\*\*Significant at the .05 and .01 levels of probability, respectively.

TABLE VII  
ANALYSIS OF VARIANCE OF DIALLEL CROSS  $F_1$  MEANS

Source	d.f.	Mean Squares		
		Grain Yield	% Protein	Protein Yield
Blocks	3	126.356	0.273	1.009
$F_1$ s	14	479.343**	14.000**	6.625**
Error	42	76.318	0.264	0.749

\*,\*\*Significant at the .05 and .01 levels of probability, respectively.

presented in Table VIII. Considerable positive heterosis is apparent for grain yield and protein yield, while negative heterosis is suggested for protein percentage. These trends closely agree with those reported in the previous chapter.

#### Jinks-Hayman Diallel Analysis

The validity of estimates and inferences derived from the Jinks-Hayman analysis is dependent to some extent upon how closely the previously stated assumptions are met (10). In order to determine if the assumptions of the analysis were fulfilled by the traits in this experiment, two broad, general tests were employed as outlined by Verhalen and Murray (65,66) and Baker (1). Table IX gives the analysis of variance of the quantity  $(W_r - V_r)$ . The quantity  $(W_r - V_r)$  was calculated for each of the six parental arrays in each of the four blocks and should be constant over arrays if all of the assumptions are met. The significant array mean squares for protein percentage and protein yield suggest at least partial failure of the assumptions for these traits.

Another general test of the assumptions is given by an analysis of the  $(V_r, W_r)$  regression. The regression coefficients for each trait along with their 95% confidence limits are shown in Table X. In this test, regressions for each trait are expected to be significantly different from zero but not from one if all of the assumptions are met. If the theoretical model perfectly fit the true model then all points would lie on a regression line of unit slope. All three traits partially failed the assumptions in this test, although all regressions were different from zero and the regression for percent protein was very close to one.

TABLE VIII  
PARENTAL AND MEAN  $F_1$  PERFORMANCE FOR GRAIN YIELD,  
PROTEIN PERCENTAGE, AND PROTEIN YIELD

Parent	Grain Yield		% Protein		Protein Yield	
	P	$F_1$	P	$F_1$	P	$F_1$
1	39.2	66.6	13.7	11.6	5.33	7.68
2	38.4	63.8	13.9	11.4	5.26	7.22
3	15.5	54.1	16.5	11.6	2.53	6.25
4	12.9	56.9	15.9	11.2	2.02	6.30
5	44.8	57.0	11.2	11.0	4.99	5.92
6	34.0	49.6	11.2	11.3	3.82	5.54

TABLE IX  
ANALYSIS OF VARIANCE OF ( $W_r - V_r$ ) VALUES

Source	d.f.	Mean Squares		
		Grain Yield	% Protein	Protein Yield
Total	23			
Blocks	3	27953.4	1.042*	2.280
Arrays	5	32192.1	1.079*	4.478*
B X A	15	13676.8	0.309	1.156

\*,\*\*Significant at the .05 and .01 levels of probability, respectively.

TABLE X  
( $V_r$ ,  $W_r$ ) REGRESSION COEFFICIENTS

Trait	Coefficient	95% Confidence Limits
Grain Yield	.424	.120 - .728
% Protein	.830	.673 - .987
Protein Yield	.404	.112 - .698

The only test of a specific assumption was for reciprocal differences. Analyses of variance of reciprocal effects indicated no significant differences, thus satisfying the assumption of no reciprocal differences for the observed traits. The assumption of diploid segregation was not tested but can almost surely be safely assumed. The parents were all advanced generation lines which had been selfed for a number of generations and should be homozygous, even for polygenic traits, but the possibility of residual heterogeneity within a line does exist and may account for some of the noncompliance previously noted. The assumptions of no genotype-environment interaction, no epistasis, and no multiple allelism were not tested and may be invalid for some and perhaps all of the observed traits.

Partial failure of the assumptions probably indicates a more complex genetic system than that described by the theoretical model (24). However, Hayman (24) states that it is still possible to make estimates of the population parameters and genetic components for such traits although it is realized that such estimators are less reliable than they would

have been had all the assumptions been satisfied. Therefore, genetic parameters were estimated and interpreted as if the assumptions had been fulfilled.

Diallel means and statistics for grain yield, protein percentage, and protein yield are shown in appendix Tables XXII, XXIII, and XXIV, respectively. The  $(W_r - V_r)$  quantities given in these tables show rather conclusively that only certain parents are responsible for the significant deviations observed in the  $(W_r - V_r)$  analysis. Parents one and six deviate from the normal pattern in both grain yield and protein yield, while parents two, six, and possibly one show considerable deviations in  $(W_r - V_r)$  quantities for protein percentage. The  $(W_r - V_r)$  values for parents three, four, and five are very consistent in all three traits. Since parent six seems to produce inconsistent results in all three traits, removal of it from the analysis would have probably better satisfied the assumptions, but the decision was made to leave all parents in the analysis.

Estimates of genetic and environmental variance components for each of the three traits are presented in Table XI. Additive genetic variance, as estimated by  $D$ , was found highly significant for protein percentage and significant for grain yield and protein yield. Dominance genetic variance, as estimated by  $H_1$  and  $H_2$ , was significant for all three traits.  $D$ ,  $H_1$ , and  $H_2$ , as variances, are expected to be positive but  $F$ , as an indicator of the relative frequencies of dominant to recessive alleles in the parents, may take sign. Parameter  $F$  was significantly different from zero only for protein percentage and its positive value indicates a preponderance of dominant alleles controlling this trait. However, it should be remembered that the dominant alleles for protein

percentage are apparently operating in the direction of lower protein content. F values near to or equal to zero for grain yield and protein yield indicate a relatively equal distribution of dominant and recessive alleles in the parents as a group. The relatively large values for  $H_1$  as compared to D, suggests that dominant gene action is more important than additive gene action for these traits. This is especially true for grain yield and protein yield.  $E_0$  and  $E_1$  estimate parental and  $F_1$  environmental variances, respectively.

TABLE XI  
ESTIMATES OF GENETIC AND ENVIRONMENTAL VARIANCE COMPONENTS

Parameter	Trait		
	Grain Yield	% Protein	Protein Yield
D	166.8*	4.82**	1.94*
$H_1$	886.8*	7.96*	7.93*
$H_2$	772.1*	6.32*	6.71*
F	110.7	5.37*	0.49
$E_0$	22.9*	0.48	0.30*
$E_1$	39.7**	0.10*	0.46*

\*,\*\*Significantly different from zero at the .05 and .01 levels of probability, respectively.

The genetic parameters D,  $H_1$ ,  $H_2$ , and F were used to calculate various estimator ratios in order to obtain further information about the

genetic systems operating for each trait. These estimators and their standard errors are presented in Table XII. The ratios  $H_1/D$ ,  $(H_1/D)^{1/2}$ , and  $(V_{1L1}-E)/(W_{0L01}-E/n)$  are weighted overall estimates of the average degree of dominance at each locus. Estimates of zero indicate no dominance, between zero and one indicates partial dominance, one indicates complete dominance, and greater than one indicates overdominance. Overdominance is suggested for all three traits in this experiment, but again one should remember that in the case of protein percentage, the direction of overdominance is toward lower protein in the  $F_1$ .

The ratio  $H_2/4H_1$  is an estimate of the average frequency of negative versus positive alleles at each locus in the parents. Only loci which exhibit dominance are included in this estimate. A maximum value of 0.25 is attained when the parents have an equal distribution of alleles. The parents in this experiment do not appear to have equal distribution of alleles for any of the observed traits.

The ratio of total number of dominant to recessive alleles in each parent is estimated by  $(4D H_1)^{1/2} + F/(4D H_1)^{1/2} - F$ . All estimates are greater than zero, implying a preponderance of dominant genes in the parents. This estimate suggests that the unequal distribution of alleles in the parents is due to an excess of dominant genes.

Narrow sense heritability, estimated on a plot mean basis, was calculated using the following equation:

$$h^2 = \frac{1}{4} D / \left( \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F + E \right) .$$

A heritability of 0.56 was calculated for protein percentage as compared to 0.17 for grain yield and 0.19 for protein yield. The heritability estimate obtained for protein percentage is within the range reported in

other studies (8,38) but the estimate obtained for grain yield is somewhat low possibly due to a large environmental variance as a result of measuring yield from individual plants. These results suggest that selection for improved protein content would produce faster and more consistent results than would selection for improved grain yield.

TABLE XII  
MEAN RATIOS ESTIMATING GENETIC CHARACTERISTICS

Estimator	Trait		
	Grain Yield	% Protein	Protein Yield
Average Dominance			
$H_1/D$	$5.83 \pm 2.7$	$1.66 \pm .36$	$4.21 \pm 1.4$
$(H_1/D)^{1/2}$	$2.36 \pm 0.6$	$1.28 \pm .15$	$2.03 \pm 0.3$
$(V_{1L1}-E)/(W_{0L01}-E/n)$	$5.04 \pm 3.0$	$1.81 \pm .48$	$2.80 \pm 0.8$
Distribution of Alleles			
$H_2/4H_1$	$.22 \pm 0.01$	$.20 \pm .01$	$.21 \pm 0.02$
Dominant to Recessive Ratio			
$(4DH_1)^{1/2}+F/(4DH_1)^{1/2}-F$	$1.34 \pm 0.23$	$2.54 \pm .20$	$1.13 \pm 0.19$
Heritability			
$\frac{1}{4} D / (\frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F+E)$	$.17 \pm 0.07$	$.56 \pm .07$	$.19 \pm 0.06$

### Diallel Analysis for Combining Ability

The combining ability analyses of variance for grain yield, protein percentage, and protein yield are given in Table XIII. Highly significant F ratios were observed in all traits for both general and specific combining ability effects. Reciprocal effects were not significant for any trait. A comparison of the relative magnitude of the g.c.a. and s.c.a. variance components indicated that specific combining ability was much more important than general combining ability for grain yield, protein percentage, and protein yield. These results again suggest the importance of dominant gene action in governing these traits.

The significant g.c.a. and s.c.a. effects for each trait indicated that estimates of individual effects for each parent and parental combination could be calculated. The general combining ability effects for the three traits in each of the six parents are given in Table XIV. Parent one gave the highest g.c.a. estimates for grain yield and protein yield while parent three gave the highest estimate for protein percentage. Parent one appears to be the best overall parent in the experiment in terms of general combining ability while parent six is unquestionably the poorest.

The specific combining ability effects for the three traits in each parental combination, are shown in Table XV. Six of the 15 crosses exhibited significant positive s.c.a. effects for grain yield while none exhibited significant negative effects. Parents one by three produced the highest s.c.a. effect for grain yield and parent one was involved in three of the four hybrid combinations with the highest s.c.a. effects. Only parents one by five and five by six produced significant positive s.c.a. effects for protein percentage, while seven crosses exhibited

TABLE XIII

OBSERVED MEAN SQUARES AND VARIANCE COMPONENTS FROM GENERAL AND SPECIFIC COMBINING ABILITY  
ANALYSES FOR GRAIN YIELD, PROTEIN PERCENTAGE, AND PROTEIN YIELD

Source	d.f.	Mean Squares			Components		
		Grain Yield	% Protein	Protein Yield	Grain Yield	% Protein	Protein Yield
General Combining Ability	5	491.162**	3.281**	7.847**	38.404	0.264	0.629
Specific Combining Ability	15	365.904**	3.052**	3.302**	335.595	2.944	3.008
Reciprocals	15	17.023	0.085	0.178			
Error	105	30.309	0.108	0.294			

\*,\*\*Significant at the .05 and .01 levels of probability, respectively.

TABLE XIV  
ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS FOR  
GRAIN YIELD, PROTEIN PERCENTAGE, AND  
PROTEIN YIELD FROM DIALLEL CROSS

Parent	General Combining Ability Effects		
	Grain Yield	% Protein	Protein Yield
1	8.594*	0.225*	1.189*
2	6.095*	0.061	0.796*
3	-5.806*	0.703*	-0.467*
4	-3.923*	0.224*	-0.510*
5	1.535	-0.734*	-0.162
6	-6.496*	-0.480*	-0.847*
SE ( $\hat{g}_i$ )	1.451	0.087	0.143

\*Significantly different from zero at the .05 level of probability.

TABLE XV

ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR GRAIN YIELD, PROTEIN PERCENTAGE, AND PROTEIN YIELD

Parent	Parent					
	1	2	3	4	5	6
1	-31.435 <sup>a</sup>	12.639*	14.703*	11.038*	-5.557	-1.389
	1.500 <sup>b</sup>	-0.120	-0.905*	-0.752*	0.403*	-0.126
	-3.150 <sup>c</sup>	1.506*	1.475*	1.060*	-0.559	-0.332
2	-27.224	1.814	-0.244	11.305*	1.710	
	2.058	-0.723*	-0.202	-0.726*	-0.287	
	-2.426	0.042	0.153	0.735*	-0.011	
3	-26.360	3.888	1.318	4.636		
	3.339	-1.114*	-0.157	-0.440*		
	-2.632	0.354	0.280	0.481		
4	-32.751	10.579*	7.490*			
	3.727	-1.254*	-0.405*			
	-3.059	0.683*	0.809*			
5	-11.691	-5.955				
	0.918	0.816*				
	-0.779	-0.360				
6	6.493					
	-0.442					
	0.588					
Standard Error	Grain Yield		% Protein		Protein Yield	
SE( $\hat{s}_{ii}$ )	4.588		0.274		0.452	
SE( $\hat{s}_{ij}$ )	3.308		0.197		0.326	

\*Significantly different from zero at the .05 level of probability.

<sup>a</sup>Grain yield.<sup>b</sup>Protein percentage.<sup>c</sup>Protein yield.

significant negative effects. Six crosses produced significant positive s.c.a. effects for protein yield with the greatest positive effect occurring with parents one by two. Parent one seems to be superior in terms of specific combining ability as well as general combining ability and parent five, which was relatively poor in terms of g.c.a., produced high s.c.a. effects in certain crosses.

## CHAPTER VI

### PROTEIN INHERITANCE IN SEGREGATING POPULATIONS

The previous experiments have been concerned only with trait relationships in inbred parental lines and their  $F_1$  hybrids. Major emphasis was placed on these relationships because of the importance of hybrid varieties in commercial grain sorghum production. However, development of improved inbred lines for hybridization usually involves selection within and between genetically variable source populations artificially created by crossing diverse germplasm. The purpose of this experiment was to study protein inheritance in segregating populations and evaluate recombinants within those populations for sources of high protein germplasm.

#### Materials and Methods

The  $F_2$  populations examined in this experiment were derived from crosses made in the greenhouse during the winter and spring of 1972. The  $F_1$  progeny from these crosses were grown in the field during the summer of 1972 and individual plants were bagged to obtain selfed seed. The  $F_2$  populations and their parents were planted in the field on June 15, 1973 in a randomized complete block design with three replications.  $F_2$  populations were grown in two-row plots 25 feet long and 40 inches apart and their parents were grown in single row plots of the same dimensions. Plants within rows were thinned to a uniform spacing of approximately six

inches after emergence. Fertilizer, according to soil test, was broadcast preplant at the rate of 265 pounds per acre of 45-0-0 and 170 pounds per acre of 0-60-0. Five plants, covering the observed range of height and maturity, were bagged and harvested from each row in each block for a total of 15 parental plants or 30  $F_2$  plants per entry. Grain yield, protein percentage, and protein yield were determined on an individual plant basis.

The parentage, number of generations of self fertilization, and line identification numbers for the 16 parental lines used in this experiment are given in Table XVI. Hereafter, parents and segregating populations will be referred to by their appropriate line identification number and number combination, respectively. Lines two through 14 are restorer lines while lines one, 15, and 16 are non-restorers. All crosses involving line one were made using male sterile AOK 15 as the maternal parent and thus segregated for sterility in the  $F_2$  generation. Since lines 15 and 16 were non-restorers, they produced male sterile  $F_1$  progeny when crossed to AOK 15. Five plants from each of these male sterile  $F_1$  rows were hand pollinated using lines two, three, four, five, and six as pollen sources. The  $F_2$  hybrids thus produced were grown with the parents and  $F_2$  segregating populations.

### Results and Discussion

The mean grain yield, protein percentage, and protein yield of the inbred lines used as parents in this experiment are given in Table XVII. Protein percentage of these lines ranged from 11.6 to 16.0 percent, while grain yield and protein yield ranged from 13.6 to 56.4 and 2.03 to 6.54 grams per plant, respectively. Parent seven was highest in grain yield

TABLE XVI  
PARENTAGE, NUMBER OF GENERATIONS OF SELFING, AND LINE  
IDENTIFICATION NUMBERS FOR THE PARENTS  
OF F<sub>2</sub> SEGREGATING POPULATIONS

Line Id. No.	Gen.	Pedigree
1	F <sub>+</sub>	BOK 15
2	F <sub>8</sub>	(Cy 12-Kau-Cy 11-7663 X Wiley)-1-1-1-1-1
3	F <sub>9</sub>	(SA 7663 <sup>2</sup> X BC)-1-1-1-1-2-2
4	F <sub>9</sub>	(A Red.-Kau X Korgi <sup>2</sup> )-E1-1-1-1-1-1
5	F <sub>12</sub>	(A Wht-Collubi X ROKY 7)-2-1-2-2-1
6	F <sub>24</sub>	Bonar-Day X #1-7-1-2
7	F <sub>8</sub>	(A Red. X ROKY 34)-1-2-1-2-1
8	F <sub>9</sub>	(SA 7663 <sup>2</sup> X BC)-1-1-1-1-2-1
9	F <sub>6</sub>	(Korgi <sup>2</sup> X BC)-1-1-1
10	F <sub>12</sub>	Cy 1-Korgi-Kau Y. X Ryer
11	F <sub>12</sub>	(A Red. X Calico)-1-4-2-1-1-1-2-1
12	F <sub>21</sub>	Y-4 white
13	F <sub>29</sub>	(Kashakashi X 10)-2-2-1
14	F <sub>20</sub>	(Long Glume X Do #1)-1-1-1-3-1
15	F <sub>7</sub>	(BOK 8 X WBH)-2-1
16	F <sub>15</sub>	(B Red.-Kau-5-1-1 X Dr. Res.)-2-2-2-1-1

TABLE XVII  
 MEAN\* GRAIN YIELD, PROTEIN PERCENTAGE, AND PROTEIN  
 YIELD OF PARENTS OF F<sub>2</sub> POPULATIONS

Line Id. No.	Character		
	Grain Yield	% Protein	Protein Yield
1	41.6	11.6	4.81
2	18.4	14.5	2.63
3	27.4	13.7	3.72
4	26.3	14.0	3.66
5	21.0	15.4	3.18
6	13.6	16.0	2.16
7	56.4	11.6	6.54
8	18.2	14.5	2.58
9	32.9	12.7	4.13
10	17.3	11.9	2.03
11	31.2	13.0	4.04
12	32.9	13.3	4.24
13	23.3	14.7	3.42
14	34.2	12.5	4.26
15	18.9	14.3	2.63
16	23.4	14.6	3.38
LSD .05	4.91	0.54	0.59
LSD .01	6.46	0.71	0.77

\*Mean of 15 observations.

and protein yield but was lowest in protein percentage. Parent six, which had the highest protein percentage, was an extremely poor yielder.

Population means and ranges for each of the observed traits in each of the  $F_2$  populations are shown in Table XVIII. Considerable variation was noted both between and within segregating populations for all traits, indicating significant genetic diversity.

The highest average  $F_2$  grain yield was produced from a cross between parent one and parent seven. Parent seven was apparently able to transmit its superior yielding ability to its  $F_2$  progeny. The highest mean  $F_2$  protein percentage of 13.8% was produced from a cross between parent five and parent two. Parent five had the second highest protein percentage of the 16 parents and parent two ranked in the upper one-third.

In general, the mean grain yield and protein yield of the  $F_2$  populations was greater than their respective parents, while protein percentage of the  $F_2$  was lower than their parents. These general trends agree closely with the relationships noted in Chapters IV and V between parents and  $F_1$  and are probably largely due to dominance and overdominance effects from heterozygous loci still present in the  $F_2$ . Although the  $F_2$  population means were skewed toward the direction of dominance, transgressive segregates were observed in both directions for all traits, suggesting the importance of additive gene combinations in certain recombinants. Those segregates which fell outside the parental range due to additive gene combinations would be especially important in a breeding program concerned with improved protein content. Since dominance and overdominance effects are apparently operating in the direction of lower protein percentage, it would be the recombinants with favorable recessive combinations that would be utilized in a grain protein improvement

TABLE XVIII

MEAN\* AND RANGE FOR GRAIN YIELD, PROTEIN PERCENTAGE, AND PROTEIN YIELD FOR F<sub>2</sub> POPULATIONS

Cross	Character					
	Grain Yield		% Protein		Protein Yield	
	Mean	Range	Mean	Range	Mean	Range
1 X 2	41.2	14.7 - 75.6	11.8	9.5 - 14.1	4.79	2.07 - 9.32
3 X 2	36.6	25.0 - 55.5	12.2	10.2 - 14.1	4.44	3.09 - 6.01
5 X 2	35.9	11.6 - 67.8	13.8	9.5 - 16.3	4.84	1.89 - 8.52
4 X 2	36.6	13.7 - 62.8	12.9	9.8 - 15.7	4.58	1.76 - 7.00
1 X 4	37.9	12.6 - 101.8	12.6	10.4 - 14.4	4.67	1.69 - 11.02
3 X 4	30.1	19.5 - 45.8	13.3	12.2 - 15.3	4.00	2.71 - 6.32
6 X 4	35.5	11.0 - 68.5	12.3	10.0 - 14.9	4.26	1.60 - 8.61
5 X 3	36.7	17.5 - 68.5	13.1	11.0 - 15.8	4.73	2.11 - 8.34
4 X 5	29.6	9.2 - 52.1	12.2	10.4 - 13.9	3.55	1.17 - 6.05
1 X 5	38.5	15.8 - 57.3	12.8	9.4 - 15.1	4.85	2.31 - 7.76
6 X 5	44.0	23.4 - 66.0	12.9	11.2 - 15.2	5.66	3.23 - 8.20
1 X 6	32.5	12.6 - 62.1	12.5	9.3 - 16.5	3.95	1.69 - 7.12
1 X 7	65.2	23.9 - 99.0	10.9	8.6 - 14.1	6.92	3.38 - 9.44
1 X 8	39.8	12.7 - 81.6	12.2	9.0 - 16.0	4.71	2.03 - 10.14
1 X 9	34.7	15.0 - 55.9	12.4	10.3 - 17.0	4.23	2.06 - 6.74
1 X 10	38.5	15.6 - 79.0	11.6	9.6 - 13.7	4.38	1.93 - 8.10
1 X 11	44.4	17.7 - 83.2	12.2	10.1 - 14.9	5.32	2.63 - 8.41
1 X 12	51.6	26.6 - 77.9	11.4	7.5 - 13.7	5.81	2.97 - 8.13
1 X 13	31.5	18.5 - 53.3	13.7	10.6 - 17.8	4.19	2.82 - 6.35
1 X 14	42.7	12.4 - 79.7	11.1	8.2 - 12.4	4.72	1.37 - 7.85
LSD .05	6.71		0.59		0.71	
LSD .01	8.82		0.78		0.93	

\*Mean of 30 observations.

program.

Table XIX gives the performance of  $F_2$  populations expressed as mean deviations from midparent and high-parent. Mean grain yield of the  $F_2$  significantly exceeded their respective midparent yield in 70% of the populations and their high parent yield in 40% of the populations. Only 15% of the populations produced an average yield significantly below their highest yielding parent. Mean protein percentage of the  $F_2$  was significantly below their midparent mean in 75% of the populations and below their high parent in 90% of the populations. None of the  $F_2$  populations had a mean protein percentage significantly greater than their highest parent and only 5% significantly exceeded their midparent mean. Sixty-five percent of the  $F_2$  populations exceeded their midparent mean in protein yield and 30% exceeded their high parent.  $F_2$  heterosis estimates in this experiment may be higher than would normally be expected, since extremely poor agronomic types were avoided when bagging individual  $F_2$  plants. However, it is rather apparent that a great deal of heterosis is still present in the  $F_2$  for all observed traits even though individual  $F_2$  plants were measured which exhibited transgressive segregation away from the direction of dominance for all traits.

Table XX gives the means and ranges of  $F_2$  hybrids produced by crossing restorer lines two through six onto the male sterile  $F_1$  hybrids resulting from crosses of AOK 15 by non-restorer lines 15 and 16. Lines two through six were used as pollinators because of their R reaction and because of their relatively high protein percentage. These crosses produced responses very similar to true  $F_2$  populations for all traits. None of the paternal lines appear to consistently transmit superior grain

TABLE XIX

PERFORMANCE OF F<sub>2</sub> POPULATIONS EXPRESSED AS MEAN DEVIATIONS  
FROM MIDPARENT AND HIGH-PARENT FOR GRAIN YIELD,  
PROTEIN PERCENTAGE, AND PROTEIN YIELD

Cross	Character					
	Grain Yield		% Protein		Protein Yield	
	MP	HP	MP	HP	MP	HP
1 X 2	11.2	-0.4	-1.3	-2.7	1.07	-0.02
3 X 2	13.7	9.2	-1.9	-2.3	1.26	0.72
5 X 2	16.2	14.9	-1.2	-1.6	1.93	1.66
4 X 2	14.2	10.3	-1.4	-1.6	1.43	0.92
1 X 4	3.9	-3.7	-0.2	-1.4	0.43	-0.14
3 X 4	3.2	2.7	-0.6	-0.7	0.31	0.28
6 X 4	15.5	9.2	-2.7	-3.7	1.35	0.60
5 X 3	12.5	9.3	-1.5	-2.3	1.28	1.01
4 X 5	5.9	3.3	-2.5	-3.2	0.13	-0.10
1 X 5	7.2	-3.1	-0.7	-2.6	0.85	0.04
6 X 5	26.7	23.0	-2.8	-3.1	2.99	2.48
1 X 6	4.9	-9.1	-1.3	-3.5	0.46	-0.86
1 X 7	16.2	8.8	-0.7	-0.7	1.24	0.38
1 X 8	9.9	-1.8	-0.9	-2.3	1.01	-0.10
1 X 9	-2.6	-6.9	0.2	-0.3	-0.24	-0.58
1 X 10	8.5	-3.1	-0.2	-0.3	0.96	-0.43
1 X 11	8.0	2.8	-0.1	-0.8	0.89	0.51
1 X 12	14.3	10.0	-1.1	-1.9	1.28	1.00
1 X 13	-1.0	-10.1	0.5	-1.0	0.07	-0.62
1 X 14	4.8	1.1	-1.0	-1.4	0.18	-0.09
LSD .05	5.34	5.88	0.50	0.57	0.58	0.65
LSD .01	7.02	7.73	0.66	0.75	0.76	0.85

TABLE XX

MEAN\* AND RANGE FOR GRAIN YIELD, PROTEIN PERCENTAGE, AND PROTEIN YIELD OF F<sub>2</sub> HYBRIDS

Cross	Character					
	Grain Yield		% Protein		Protein Yield	
	Mean	Range	Mean	Range	Mean	Range
1/15 X 2	52.9	33.4 - 93.7	11.5	10.1 - 12.8	6.01	4.01 - 10.25
1/15 X 3	51.8	30.5 - 84.8	11.1	8.6 - 12.6	5.67	3.60 - 10.42
1/15 X 4	36.5	24.8 - 58.2	11.9	10.4 - 13.8	4.32	3.12 - 6.26
1/15 X 5	41.9	23.0 - 66.6	11.1	10.1 - 12.7	4.62	2.85 - 7.66
1/15 X 6	38.1	14.8 - 59.3	11.8	7.3 - 14.7	4.42	2.18 - 6.59
1/16 X 2	45.9	20.0 - 78.3	11.5	8.4 - 14.6	5.07	2.80 - 7.29
1/16 X 3	47.3	22.0 - 70.3	11.4	9.3 - 13.9	5.33	3.07 - 7.81
1/16 X 4	42.4	26.3 - 91.9	12.2	11.2 - 13.4	5.12	3.12 - 10.57
1/16 X 5	31.8	14.3 - 78.4	13.8	10.3 - 15.7	4.19	2.24 - 8.08
1/16 X 6	34.1	18.4 - 51.4	12.6	9.1 - 14.9	4.22	2.58 - 6.52

\*Mean of 15 observations.

yield or protein percentage, but B-line number 16 does seem to contribute genes for higher protein percentage.

## CHAPTER VII

### SUMMARY AND CONCLUSIONS

The objective of this study was to obtain information about the genetic system controlling protein content in grain sorghum and evaluate the potential for incorporating better nutritional quality into high yielding hybrid varieties. A top-cross progeny test of selected protein lines was conducted to evaluate their performance in hybrid combinations and to study the relationships between important agronomic traits in parental and hybrid generations. Significant positive heterosis was noted for grain yield, protein yield, kernel number per panicle, plant height, panicle length, and maturity while negative heterosis was observed for protein percentage and kernel weight. Protein percentage was found to be negatively correlated with yield and the components of yield with the exception of kernel weight. Kernel weight was uncorrelated with protein percentage but positively correlated with grain yield. Phenotypic and genetic correlations agreed very closely for the traits under study.

A six-parent diallel cross was made and analyzed using the Jinks-Hayman (24,25,28) and Griffing (21) procedures. Additive genetic variance was important for protein percentage as well as for grain yield and protein yield. Dominance genetic variance was also important for all three traits and apparently dominant gene action was more important than additive gene action in governing these traits. Dominant and recessive

alleles did not appear to be equally distributed in this parental set with a majority of dominant genes suggested for all traits. Overdominance was indicated for all traits, but for protein percentage, the direction of overdominance was toward lower protein in the  $F_1$ . A heritability estimate of 0.56 was calculated for protein percentage as compared to estimates of 0.17 for grain yield and 0.19 for protein yield.

The diallel analysis for combining ability indicated highly significant g.c.a. and s.c.a. effects for all three traits. Specific combining ability effects were found more important than general combining effects for all traits, suggesting the importance of dominant gene action. Two of the six parents exhibited positive g.c.a. effects for yield, three for protein percentage, and two for protein yield. Six of the 15 crosses produced significant s.c.a. effects for grain yield while none exhibited significant negative effects. Only two crosses exhibited significant positive s.c.a. effects for protein percentage.

Twenty  $F_2$  populations and their parents were evaluated for grain yield, protein percentage, and protein yield. A comparison of  $F_2$  and parental means indicated a considerable amount of heterosis still present in the  $F_2$  generation. Although the  $F_2$  population distributions were skewed toward the direction of dominance, transgressive segregates were noted for both parental extremes for all traits. A majority of the plants within  $F_2$  populations had protein percentages below their midparent means but most crosses also produced a few recombinants with protein percentages higher than either parent.

The apparent dominance of low protein content in grain sorghum rules out the use of heterosis for improvement of grain protein percentage. However, heritability and additive genetic variance estimates calculated

in this study, along with the presence of  $F_2$  recombinants superior to either parent in protein percentage, indicate that the potential exists for substantial increases in protein percentage of parental lines using available germplasm and established breeding methods. The negative genetic correlations between grain yield and protein percentage observed in this study suggests that extremely high protein levels may not be obtainable without unacceptable yield reduction of inbred lines and hybrid varieties. However, simultaneous selection for grain yield and protein percentage should produce good yielding inbred lines with substantially improved protein content. Greatest progress would be expected by emphasizing selection for increased kernel size to improve or maintain grain yield.

Perhaps the most important consideration in such a breeding program would be retention of improved protein levels in high yielding hybrid varieties. The best approach would probably involve development of improved protein parental lines that maintain high combining ability for yield while minimizing protein reduction in the hybrid. Some form of reciprocal recurrent selection might be utilized to obtain these results.

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## APPENDIXES

TABLE XXI

PARENTAL AND F<sub>1</sub> HYBRID MEANS FOR EIGHT CHARACTERS FROM A TOP-CROSS PROGENY TEST

Line* Id. No.	Character															
	Grain Yield		% Protein		Protein Yield		Kernel Weight		Kernel Number		Panicle Length		Plant Height		Maturity	
	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>
1	37.9	12.0	11.8	13.8	4.43	1.64	3.15	3.32	1190	358	26.8	23.6	113	121	54	55
2	30.1	47.0	12.3	12.3	3.67	5.78	2.24	2.88	1326	1675	23.0	22.0	97	102	56	56
3	28.7	55.2	12.9	11.7	3.70	6.47	2.70	2.58	1066	2130	24.8	29.2	82	89	60	64
4	33.4	52.6	11.3	12.1	3.76	6.36	2.08	2.35	1621	2336	26.6	25.6	88	96	54	56
5	13.4	56.1	15.2	12.0	2.03	6.70	3.57	3.37	366	1666	19.4	22.6	98	108	58	56
6	42.0	37.6	10.8	13.2	4.52	4.84	2.36	3.02	1815	1361	23.8	24.0	78	90	52	55
7	52.7	78.3	11.5	11.3	6.01	8.86	2.70	2.91	1956	2691	28.2	26.4	100	102	59	58
8	48.6	60.1	12.2	11.6	5.94	6.92	3.32	2.95	1468	2040	25.8	25.6	124	117	57	58
9	26.9	59.6	14.7	11.8	3.95	7.00	3.63	3.21	741	1859	20.6	23.6	129	126	59	58
10	25.4	50.8	13.9	11.5	3.61	5.84	3.10	2.98	814	1710	23.0	24.2	118	130	61	61
11	23.5	59.8	12.5	11.7	2.90	7.03	3.34	3.40	703	1786	27.8	30.0	116	135	53	56
12	26.3	62.7	15.3	11.3	3.94	7.08	4.87	3.60	536	1757	21.8	24.2	104	121	59	56
13	35.5	85.3	13.1	11.2	4.62	9.58	5.09	3.93	693	2167	17.2	23.4	144	182	65	58
14	25.8	62.9	12.7	12.1	3.27	7.54	2.96	2.45	875	2535	18.4	22.4	65	104	52	71
15	42.5	53.1	13.7	12.3	5.83	6.51	2.31	2.73	1852	1938	27.4	27.0	102	112	59	57
16	19.6	47.4	13.4	12.4	2.62	5.90	1.82	2.54	1071	1855	23.8	24.4	86	103	64	59
17	35.8	61.4	13.2	11.3	4.70	6.93	1.98	2.40	1825	2542	22.6	25.0	89	109	67	64
18	25.5	46.2	16.2	13.8	4.12	6.37	2.81	3.21	907	1440	27.4	26.6	93	100	62	58
19	21.9	21.5	13.9	13.4	2.89	2.85	2.70	3.44	766	610	28.8	25.8	107	106	59	56
20	26.3	42.8	14.7	13.6	3.81	5.74	2.32	3.13	1182	1414	25.6	22.6	124	123	53	56
21	14.0	22.9	16.3	14.7	2.24	3.33	2.95	3.44	485	683	21.8	23.6	91	103	56	57
22	27.5	66.2	13.0	12.8	3.58	8.41	2.00	2.60	1422	2597	19.0	23.8	78	100	56	56
23	34.8	60.9	13.2	11.8	4.57	7.21	2.88	2.58	1210	2352	29.4	30.6	106	104	56	55
24	9.7	35.3	13.9	12.5	1.35	4.37	2.63	2.45	375	1488	16.6	19.2	80	89	59	56
25	20.6	59.0	14.9	12.5	3.07	7.30	2.06	2.01	1013	2915	21.6	24.4	88	102	57	64
26	35.7	30.4	14.3	14.3	5.06	4.28	2.34	2.69	1522	1154	25.2	25.8	85	105	59	57
27	32.1	48.0	15.6	13.8	5.00	6.60	2.21	3.31	1453	1458	15.6	16.6	104	128	63	59

TABLE XXI (Continued)

Line* Id. No.	Character															
	Grain Yield		% Protein		Protein Yield		Kernel Weight		Kernel Number		Panicle Length		Plant Height		Maturity	
	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>	P	F <sub>1</sub>
28	18.8	52.4	13.9	12.6	2.62	6.61	2.90	3.02	647	1710	29.6	28.0	94	108	57	57
29	15.0	86.7	13.7	11.0	2.03	9.52	2.26	2.94	666	2965	20.0	25.6	70	108	53	75
30	22.9	47.9	13.9	13.3	3.11	6.38	2.14	3.09	1092	1529	18.2	24.4	88	101	54	57
31	14.8	17.5	15.3	14.9	2.26	2.53	1.80	2.09	824	865	26.0	24.4	93	103	56	55
32	21.2	41.1	12.4	12.8	2.63	5.21	2.12	2.28	1003	1791	23.4	26.6	84	89	57	55
33	19.8	54.5	13.2	11.8	2.58	6.41	2.46	2.58	819	2118	32.0	25.6	108	110	57	57
34	45.9	46.5	12.4	13.9	5.70	6.43	2.84	3.36	1609	1395	21.6	22.2	98	100	59	58
35	13.8	36.7	13.1	13.8	1.81	4.74	2.94	2.34	464	1611	18.4	24.0	70	88	61	57
36	26.3	43.2	14.2	13.3	3.75	5.61	1.89	2.41	1384	1880	30.0	27.4	98	106	57	57
37	41.7	66.0	13.0	11.3	5.42	7.45	2.59	3.10	1645	2140	34.0	30.0	121	135	60	57
38	37.2	36.0	12.0	11.9	4.46	4.30	1.98	1.95	1878	1861	26.4	23.4	96	91	63	57
39	30.3	46.6	12.8	12.6	3.88	5.84	2.20	2.82	1381	1713	21.0	23.4	90	93	59	57
40	21.5	33.2	13.3	13.0	2.88	4.22	1.94	2.49	1113	1478	16.0	20.6	96	106	57	57
41	46.5	40.4	10.8	13.4	5.01	5.13	2.38	2.47	1948	1644	23.0	23.0	94	103	59	58
42	6.6	43.3	13.1	13.1	0.86	5.22	1.81	3.08	386	1416	17.8	23.8	60	128	70	64
43	21.7	35.2	14.0	12.8	2.97	4.49	1.85	2.77	1229	1308	28.4	28.6	76	91	53	52
44	40.8	73.4	14.5	13.3	5.82	9.70	2.02	3.32	2025	2264	21.4	25.8	205	228	67	63
B 15	39.8	49.5	13.3	12.6	5.32	6.07	3.33	2.86	1191	1777	20.4	24.8	95	111	59	58
LSD .05	13.9		0.97		1.68		0.45		519		2.48		8.0		0.76	
LSD .01	18.3		1.27		2.20		0.60		683		3.26		10.6		1.00	

\*See Table I for identification of parents.

TABLE XXII  
DIALLEL MEANS\* FOR GRAIN YIELD

Parent	Parent						Array Means	V <sub>r</sub>	W <sub>r</sub>	(W <sub>r</sub> -V <sub>r</sub> )
	1	2	3	4	5	6				
1	39.21	80.79	70.95	69.17	58.03	54.17	62.05	296.51	-73.74	-370.25
2		38.43	55.56	55.39	72.39	54.77	59.55	263.78	59.33	-204.45
3			15.49	47.62	50.51	45.79	47.65	362.77	163.29	-199.48
4				12.86	61.65	50.53	49.54	418.94	216.06	-202.88
5					44.84	42.54	54.99	203.49	-8.07	-211.56
6						33.98	46.96	90.22	0.31	-89.91

\*Averaged over plants and blocks.

TABLE XXIII  
DIALLEL MEANS\* FOR PROTEIN PERCENTAGE

Parent	Parent						Array Means	V <sub>r</sub>	W <sub>r</sub>	(W <sub>r</sub> -V <sub>r</sub> )
	1	2	3	4	5	6				
1	13.70	11.91	11.77	11.44	11.64	11.36	11.97	1.06	0.16	-0.89
2		13.92	11.78	11.83	10.35	11.04	11.81	1.54	1.26	-0.28
3			16.49	11.56	11.56	11.53	12.45	4.11	2.76	-1.35
4				15.92	9.98	11.08	11.97	4.36	3.10	-1.26
5					11.20	11.35	11.01	0.75	-0.48	-1.23
6						11.23	11.26	0.25	0.08	-0.17

\*Averaged over plants and blocks.

TABLE XXIV  
DIALLEL MEANS\* FOR PROTEIN YIELD

Parent	Parent						Array Means	V <sub>r</sub>	W <sub>r</sub>	(W <sub>r</sub> -V <sub>r</sub> )
	1	2	3	4	5	6				
1	5.33	9.59	8.29	7.84	6.56	6.11	7.29	3.35	-0.50	-3.84
2		5.26	6.47	6.54	7.47	6.03	6.89	2.65	0.69	-1.96
3			2.53	5.47	5.75	5.26	5.63	3.82	2.03	-1.79
4				2.02	6.11	5.55	5.59	4.14	2.40	-1.74
5					4.99	4.73	5.93	1.69	0.46	-1.23
6						3.82	5.25	1.04	0.30	-0.75

\*Averaged over plants and blocks.

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