BREEDING SORGHUM FOR IMPROVED DIGESTIBILITY AND FEEDING EFFICIENCY

by

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INTRODUCTION

Grain sorghum (Sorghum bicolor (L.) Moench) is the dominant feedgrain grown in the state of Kansas. Kansas is the leading producer of sorghum in the U. S., and the second largest cattle feeding state, finishing approximately 3 million head of cattle annually in feedlots. Sorghum acreage will likely increase as ground water supplies decrease and irrigation costs increase, and may replace corn, especially in western Kansas, primarily because of its higher yield potential than corn under dryland or limited irrigation conditions.

However, grain sorghum has not been fully utilized as a feedgrain due to its highly variable feeding quality, leading to discrimination by producers (Hibberd, Hintz and Wagner, 1980). Many factors contribute to the digestibility and the quality of grain sorghum. Why sorghum varieties differ so widely in dry matter digestibility, and which components of the grain contribute to these differences are issues that need to be addressed. The inheritance, interrelationships, and the importance of genotype X environment interactions must be better understood before a successful program to genetically improve grain sorghum quality can be developed.

The primary objectives of this study were : 1) to develop and evaluate techniques to screen for sorghum grain digestibility; 2) to determine which seed characteristics have a significant effect on digestibility; and 3) to determine the importance of location on digestibility.

LITERATURE REVIEW

Grain sorghum has not been fully utilized as a feedgrain due to its highly variable feeding quality, which has led to discrimination by producers (Hibberd, Hintz and Wagner, 1980). Some of the factors identified by researchers that affect the feeding quality of sorghum include seed characteristics of the grain, variable response to environmental conditions, and processing methods during feed preparation.

Much research has been conducted on the various seed characteristics that may affect the quality and digestibility of grain sorghum. Some of the characteristics include: endosperm type, endosperm texture, endosperm color, pericarp color, and the presence of a testa layer.

Endosperm type refers to the type of starch present, whether it is waxy or non-waxy. Waxy endosperm is composed of nearly 100% amylopectin and non-waxy endosperm is about 75% amylopectin and 25% amylose (Lichtenwalner, Ellis and Rooney, 1978). Studies by Brethour and Duitsman (1965), McCollough et al. (1972), and Samford et al. (1971) have shown that sorghum grain with the waxy endosperm type was more digestible than the non-waxy endosperm type. Sherrod et al. (1969) reported that feed utilization was more efficient with the waxy

endosperm grain.

Waxy endosperm is the result of a recessive gene, and because endosperm tissue is 3n, with two genes originating from the female parent and one gene from the male parent, three doses of the recessive waxy gene (wxwxwx) are necessary for the endosperm to appear waxy. Studies reported by Lichtenwalner, Ellis and Rooney (1978), and Tovar, Liang and Cunningham (1977) have shown that incremental increases in the waxy gene have increased digestibility over non-waxy types.

Many explanations for the improved digestibility of waxy endosperm sorghums have been proposed. Using microscopy, Sullins and Rooney (1974) reported that waxy endosperm may be more digestible because of the structure of the endosperm. The peripheral endosperm is located just below the aleurone cell layer and is made up of small starch granules well embedded in a dense amorphous proteinaceous matrix (Rooney and Clark, 1968). The waxy endosperm type had a smaller proportion of peripheral endosperm in the kernel than did the non-waxy type as observed by Sullins and Rooney (1974). Also contributing to the increased digestibility of the waxy type was the fact that the protein matrix surrounding the starch granules was more easily solubilized than the proteins in the non-waxy type, thus releasing more of the starch for

utilization (Sullins and Rooney 1974, Walker and Lichtenwalner, 1977, Lichtenwalner, Ellis and Rooney, 1978). A third possible explanation reported by Tovar, Liang and Cunningham (1977), and Sullins and Rooney (1975) was that the waxy starch was more susceptible to enzyme activity than is non-waxy starch.

Endosperm texture is defined as the proportion of floury to corneous endosperm within a sorghum kernel (Rooney and Miller, 1982). Transmission and scanning electron microscopy have been used to determine if there are structural differences between floury and corneous endosperms that may be related to differences in quality and digestibility. Seckinger and Wolf (1973) reported that corneous and floury cells differ in density and protein content. The protein granules in floury endosperm are not as tightly packed (less dense) and are smaller than those found in corneous endosperm. Corneous cells contain about twice as much protein as floury cells, and have fewer soluble proteins and more kafirin proteins than floury endosperm (Cagampang and Kirleis, 1984).

Several experiments have been conducted to assess the effect of endosperm texture on the nutritional quality of sorghum. Samford et al. (1971) reported in their results of cattle feeding trials that floury endosperm grain was significantly more digestible than corneous

endosperm grain. Rate of gain in rats fed a floury endosperm diet was significantly better than for those fed a highly corneous endosperm diet, but differences between intermediate and corneous textures were not significant (Elmalik et al., 1986). Cohen and Tanksley (1973) reported no significant differences in protein or crude fiber digestibilities among floury, intermediate and corneous endosperm textures. These contrasting results indicate the need for more research concerning the role that endosperm texture plays in the nutritional quality of sorghum.

Sorghums with a true yellow endosperm contain high levels of carotenoid pigments and the genes affecting carotenoid content are homozygous. Very few yellow endosperm varieties are grown in the U.S., but it is not uncommon to see heteroyellow endosperm hybrids (Rooney and Miller, 1982). Endosperm color is a factor that has been included in many laboratory and feedlot studies. Hibberd, Schemm and Wagner (1978) compared the in vitro dry matter disappearance (IVDMD) and in vitro gas production of white and heteroyellow endosperm sorghums and concluded that they did not differ significantly in dry matter digestibility. Hibberd, Hintz and Wagner (1980) also reported no significant difference between white, heteroyellow and yellow endosperms when comparing IVDMD.

Conversely, Noland et al. (1976) reported that the protein present in yellow endosperm sorghum was significantly more digestible than white endosperm sorghum. In feedlot trials, McCollough et al. (1972) found that yellow endosperm sorghums tended to have better feed efficiency than white endosperm sorghum. As in the studies on endosperm texture, these contrasting results indicate a need for a further investigation into the role of endosperm color in the overall nutritional quality of sorghum.

Another seed characteristic that may contribute to the variable feeding quality of sorghum is the pericarp color. Two genes are responsible for pericarp color, the R-Y- genes, determining whether the pericarp is genetically red (R-Y-), colorless or white (R-yy, rryy), or lemon yellow (rrY-). There is no association between yellow pericarp color and yellow endosperm (Rooney and Miller, 1982), and they should not be confused. Brown pericarp sorghums are associated with the presence of a testa layer, which is controlled by the complementary B1 and B2 genes. When both are present in the dominant condition, a testa is present, and in combination with the dominant spreader gene S-, impart a brown color to the pericarp.

Noland et al. (1977) fed sorghum cultivars with

yellow and brown pericarps to pigs and reported that those with a yellow pericarp were more digestible than those with a brown pericarp. This difference probably resulted from tannins that are concentrated in the testa layer of brown pericarp sorghums. When McCollough et al. (1972) compared sorghums with the pericarp colors bronze, dark red, red and white, they found that the pericarp color did not influence the nutritive value of the grain.

The testa is a highly pigmented layer that is found just beneath the cross and tube cells in the seed of some sorghum genotypes. The presence or absence is genetically controlled, and is present when the complementary genes, B1 and B2, are both present in the dominant condition (B1-B2-) (Rooney and Miller, 1982). The testa layer is important in determining the nutritional quality of grain sorghum because a large portion of the tannins, polyphenolic compounds, are found in the testa layer (Blakely et al., 1979).

The effects of tannins on the utilization of grain sorghum by monogastric and ruminant animals has been well documented. Schaffert et al. (1974) reported that high tannin was associated with low *in vitro* dry matter disappearance (IVDMD) and low *in vitro* protein disappearance, and suggested that the amount of digestible protein may be a major factor limiting the

utilization of high tannin sorghums. Kofoid et al. (1982) compared two random-mating populations, each with two subpopulations, one with a testa and one without a testa, and reported that the testa subpopulations of both populations had less IVDMD and lower metabolizable energy than the nontesta subpopulations. Schaffert et al. (1974) reported that 62% of the difference in IVDMD between low and high tannin sorghums can be attributed to an undigestible tannin-protein complex. More specifically, Chibber et al. (1978) suggested that tannins associate strongly with the kafirin (particularly the cross-linked kafirins) protein fraction of the seed. Because of the nature of this tannin-kafirin complex, the solubility of the protein is greatly reduced; thus, as the tannin content increases, the percent of soluble protein decreases.

There are some agronomically desirable traits associated with high tannin sorghum, such as bird resistance, the inhibition of preharvest seed germination (Harris and Burns, 1970), and the inhibition of preharvest seed molding (Harris and Burns, 1973). These are valuable characteristics in the southeastern U.S. and other parts of the world, where birds can be a major problem, and where grain maturation occurs during periods of high temperature and humidity, promoting seed germination and

molding. A compromise needs to be reached between an acceptable tannin level, to improve digestibility, and a certain amount of loss of these protective characteristics (Harris and Burns, 1973).

As described by many authors, the variety or genotype of sorghum used in digestibility studies was a primary contributing factor to the variable results obtained; thus, not all varieties of sorghum have equal digestibilities or feed efficiency ratings. Environmental conditions during growth may aggravate or mediate varietal effects (Hibberd et al., 1979). Environmental factors that could affect the feeding quality of grain sorghum relating to the location in which the sorghum is grown may include: moisture conditions, soil type and fertilizer rates (Hibberd, Hintz and Wagner, 1980). Hibberd, Hintz and Wagner (1980) found that the crude protein content was highly influenced by both hybrid and location, indicating a significant hybrid by location interaction. However, the starch content was not significantly affected by hybrid or location. Connor et al. (1976) investigated the effect that different geographical regions in Australia had on the metabolizable energy values of sorghum in poultry diets, and found a significant hybrid by location interaction. They concluded there was a complex of factors such as soil type and climatic conditions that

influenced the metabolizable energy content of sorghum for poultry. Genotype by environment interactions were also important to food quality, affecting the chemical and physical properties of the grain (Rooney and Murty, 1982). Miller et al. (1964) studied the effect of location on the protein content of grain sorhgum samples analyzed from several different counties in Kansas, and reported that protein content varied from location to location. They also studied the effect of the addition of nitrogen fertilizer and reported an increase in the protein content of the grain and an increase in yield.

The environment also has a physical effect upon the grain itself, affecting the preharvest seed germination (sprouting) and preharvest molding. These are problems in the southeastern U.S. and in areas of the world where grain maturation occurs during periods of high temperature and humidity (Harris and Burns, 1973). Genotype also has an influence on the extent of sprouting and molding, and high tannin genotypes have been shown to retard preharvest seed germination and preharvest seed molding (Harris and Burns, 1970, 1973). According to York (1976), sorghums with white and yellow pericarps, coupled with softer starch endosperms, are prone to molding and sprouting. Lichtenwalner et al. (1979) studied the nutritive value of weathered sorghum and concluded that although feed intake

was reduced (related to the dusty nature of the grain), weathered sorghum does not detract from its nutritive value.

Year has also been shown to significantly affect the measurement of certain nutritional traits (Kofoid et al., 1982). A significant year by subpopulation interaction was reported, indicating that the subpopulations did not respond the same from one year to the next. This was probably due to a difference in the two growing seasons, 1976 being favorable for plant growth, and 1977 having unfavorably high temperatures and low rainfall. Connor et al. (1976) also reported a significant year by hybrid interaction.

The third major factor influencing grain sorghum quality is the method by which it is processed before feeding. Hibberd et al. (1983) investigated two different processing methods, dry rolling and reconstitution, and evaluated the effects of variety and processing on the site and extent of starch digestion in steers. They concluded that reconstitution of the sorghum (adding adequate water to raise the moisture level to 30%, storing the grain for 21 days, and then rolling it) increased the ruminal starch disappearance to 91% for the red pericarp sorghum studied, but that the dry rolling process resulted in larger quantities of starch disappearing in the small

and large intestines. Sullins et al. (1971) used microscopic analyses to determine whether the structure of the endosperm in reconstituted grain was modified. They reported that there was indeed a modification in the peripheral endosperm, releasing a larger portion of the starch and protein. Rolling or grinding the reconstituted grain caused more complete breakdown of the endosperm, and these two processes partially explained the increased feed efficiency of reconstituted grain sorghum.

Although many studies have demonstrated the increased efficiency of processed grain sorghum, the fact that the grain must be processed before feeding has been one factor in the discrimination against grain sorghum by livestock producers (Hibberd et al., 1983). Samford et al. (1971) pointed out that processing provided only an immediate solution to the problem of reduced utilization, and that long range improvement will come through the alteration of some physical or chemical characteristic. Therefore, this study was designed to evaluate genetic manipulation to improve digestibility and feed efficiency (as compared to maize), and not processing methods.

Experimental Material

The experimental material in this study consisted of 100 S_1 lines from KP7B, and 10 commercial hybrid checks ("DK 42Y", "Asgrow Topaz", "Cargill 70", "Delange DSA 131", "Funks G-550", "Golden Acres T-E Y-60", "NK 2656", "Paymaster DR 1125", "Warner's W-685 DR", and "Seed Tec/WAC 3502"). The S_1 lines were derived from an elite B population, KP7B, and selected for drought tolerance. The population KP7B was developed by crossing 8 relatively unrelated B lines (Table 1) with sterile plants from the population IAP2Bms$_3$. The lines used in the development of IAP2B are described in Tables 2 and 3. Part of the B lines X IAP2Bms$_3$ F_2's was grown in isolation, and the other part, the F_2 steriles, along with steriles from a YE (yellow endosperm) kafir population were used as females in crosses with 5 B lines from the original 8 B lines and 7 additional B lines (Table 1). The seed harvested from these crosses plus the seed from the F_2's grown in isolation was bulked and grown in isolation and allowed to random mate in 1984 and 1985.

The parents contributed different seed characteristics that have been implicated in differences in the quality of grain sorghum. BTx623, BTx625, and BKS9

TABLE 1

The 15 B lines and their pedigrees used in the development of KP7B

B lines	Pedigree
BOK11	Dwarf Hydro X Rice-1-3-E2
BKS9	Shrock X Ellis
BKS45	Pink Kafir X Day
BKS46	CK-60 X Short Kaura
BKS52	Redlan X Short Kaura
BKS56	CK-60 X (ACK-60) X (H69-2) X Pioneer 846)
BTx623	CK-60 X SC 170
BTx625	CK-60 X SC 170
BKS67	BKS56 X BKS66
BSC599	Rio Derivative - Sudan
B1778	SC 33 / SC 56
B1887	Rio / SC 134
B4R	B Martin / Rio
BSC35-6	Durra - Ethiopia
BTx2803	Bulk of [Tx2754 X (BTx3197 X SC170-6)]

TABLE 2

The 10 B lines and their pedigrees crossed with NP2B to develop IAP2Bms$_3$

B lines	Pedigree
Redbine 58	Martin X Caprock sib
WD4	Dwarf Kafir X Rice Khafir-3-7-13
OKY54	Dwarf Redlan X Double 1-Short Kaura-2-1-E3-2
OKY55	Dwarf Redlan X Double 1-Short Kaura-19-3-1-1
S12	Spur-Western Blackhull X Redbine-60
KS18	White Martin X Short Kaura
KS22	Pink-Kafir-Day X Westland
KS24	Spur-Western Blackhull X Redbine-60
KS56	BCK-60 X (ACK-60 X (H69-2) X Pioneer 846)
KS57	BCK-60 X (ACK-60 X (H69-2) X Pioneer 846)

TABLE 3
Eight Coes sterile lines used to develop NP2B.

Lines	Pedigree
CK-60	DD Tx Blackhull Kafir X DD Khafir selection
Dwarf Redlan	(ms_3 X Tan Waxy Dwarf k-6-1) X Redlan
Martin	Select outcross in Wheatland
Redlan	Kafir X Milo CI 1090
Reliance	Coes sib X Sooner milo
Tx606	Combine Kafir SA 6062-1-20
Westland	Select outcross in Wheatland
Wheatland	Field cross in Blackhull kafir X Dwarf milo

contributed waxy endosperm (Table 1). A number of parents, particularly those with Short kaura in their pedigree - BKS46 and BKS52 of the 8 B lines, and OKY54, OKY55 and KS18 of the 10 B lines making up IAP2B - and YE kafir were sources of yellow endosperm.

Experimental Methods

Environments

The entries were grown in two replications of a blocks-in-reps design in four environments in two locations during the summer of 1986. The environments included irrigated and dryland conditions at the Southwest Branch Experiment Station in Garden City and low nitrogen and high nitrogen conditions at a location 15 miles NE of Manhattan, KS, near Olsburg, KS.

In all environments, the plots consisted of one row 6 m long and 75 cm apart at the rate of 100 seeds per 6-m row resulting in one plant every 6 cm. These were then thinned at the 3-4 leaf stage to approximately 133,333 plants/ha, except in the Garden City dryland environment, where they were thinned to approximately 66,666 plants/ha. In Garden City, the dryland environment was planted on June 12, 1986 in a field where sorghum was grown the previous year. Nitrogen was applied to the dryland experiment at the rate of 275 kg/ha. The irrigated environment was planted on June 13, 1986 in a separate

pre-irrigated field (250 mm applied in April). Nitrogen was applied at the rate of 825 kg/ha. One hundred mm of water was applied by flood irrigation on July 6, July 17, and Sept. 3. Weeds were controlled by a pre-emergence application of 16.5 kg/ha of propachlor (Ramrod) and 5.5 kg/ha of atrazine and hand weeding.

The two environments studied in Olsburg were planted on June 12, 1986 in a field that had been fallowed in 1985 and had been planted to sunflowers in 1984. The nitrogen treatment consisted of an application of approximately 248 kg/ha prior to planting, and then an additional 248 kg/ha of nitrogen was sidedressed on July 30, 1986 by opening a furrow beside each row and distributing 88 g of urea to half of the experiment. Two border rows were planted to separate the low and high nitrogen treatments.

Traits Measured

In the field a number of traits were measured, including days to flowering, which is defined as the number of days after planting when 50% of the plants in a row had 50% of their anthers extruded. The percent effective tillering and percent green leaf retention were measured by counting the number of tillers and the number of green leaves on the plants in a meter section of row during anthesis and again just prior to harvest, and then

expressed as percent of tillers and percent of green leaves at harvest. Plant height was measured by taking the average height of each plot in cm. Heads were harvested from a meter section of row, threshed and dried at 35° C to uniform moisture and then weighed to obtain grain yield in kg/ha. A sample of 300 seeds was counted and weighed and then recalculated as 1000-seed weight in g/1000 seeds. A 50 g sample of seed was cleaned using a seed cleaner and hand picked to remove all chaff and foreign material. This sample was then ground in a Udy Cyclone sample mill (Udy Company, Boulder, CO) using a 1.0 mm screen in preparation for laboratory analyses for crude protein and protein digestibility. A 0.25 g sample of ground material was then analyzed for nitrogen content following the microkjeldahl procedure using a Technicon Autoanalyzer (Technicon, Inc., Terrytown, N.Y.). The percent crude protein was calculated by multiplying nitrogen X 6.25. Percent digestible protein was determined using a modified *in vitro* pepsin protein digestibility assay as reported by Axtell et al. (1981) and Kirleis (personal communication, 1987). The pepsin used was porcine pepsin 1:10,000 (Sigma Chemical Co., St. Louis, MO) with an activity of 1200-2000 units per mg of protein. Following the procedure of Kirleis, 0.25 g of ground sample was incubated in a pepsin solution of 0.5 mg

of pepsin per 1 ml of 0.1 M phosphate buffer (pH 2.0) at 37° C for 2 hours in a shaking water bath. The suspensions were then centrifuged at 4,800 X g and 4° C for 20 minutes. The supernatant was removed and the residue washed with 15 ml of 0.1 M phosphate buffer (pH 7.0) and centrifuged as before. A microkjeldahl digestion was then performed on the undigested pepsin residue. Percent protein digestibility was calculated using the following formula: % protein digestibility =

$$\frac{\text{total sample N} - \text{residue N}}{\text{total sample N}} \times 100$$

Traits Scored

The seed characters scored were : pericarp color, molding, sprouting, endosperm color, endosperm texture, endosperm type, and presence of a testa layer. Procedures used to determine each of these characters are outlined below.

To determine the pericarp color, a rating scale was created using seeds representative of each color present in the population. The rating scale was as follows : 1 = white, 2 = white with red spots, 3 = yellow, 4 = greenish yellow (immature yellow seed), 5 = greenish light red (immature red seed), 6 = light red, 7 = dark red, 8 = brown, 9 = mixed.

Measurements of weathering were taken by creating a

scale to visually rate the amount of molding and sprouting of the seeds. The scale was the same for both traits, and was as follows : 1 = no mold or sprouting, 2 = less than 50% of seeds moldy or sprouted, 3 = more than 50% of seeds moldy or sprouted.

The color of the endosperm was determined by cutting 5 seeds per sample and visually rating them using a sample card with seeds of known endosperm colors, and classifying them according to the following scale : 1 = white, 2 = heteroyellow, 3 = yellow.

A visual rating system described by Maxson et al. (1971) and Rooney and Miller (1982) was used to determine the endosperm texture. The same 5 seeds used in scoring the endosperm color were used for visually scoring each sample for the proportion of floury to corneous endosperm. A 5-point scale was used, with 1 being the most corneous endosperm texture and 5 being the most floury endosperm texture.

An iodine test was used to determine the type of starch present in each sample, whether it was waxy (100% amylopectin) or non-waxy (75% amylopectin and 25% amylose) starch (Whistler and Paschall, 1967). An iodine stock solution was prepared using 0.65 g of I_2 and 1.95 g of KI in 100 ml of distilled water, and then diluted to make a working solution containing 3 ml of

stock solution in 97 ml of distilled water. This working solution was then added to the cut kernels used in the color and texture determinations, mixed and observed after allowing the color to develop. A blue color indicated non-waxy starch and was assigned a 1 in the rating scale, and a red or brown color indicated waxy starch and was assigned a 2 in the rating scale.

A bleach test, as described by Kofoid, Maranville and Ross (1978), was used to determine the presence of a testa layer. The scale, as described and illustrated by Kofoid, Maranville and Ross (1978), was a 9-point scale, 1 indicating no color development of the seed, 7 indicating a black rather than red color development in some of the seeds, and 9 indicating that all the seeds were black.

Statistical Analyses

A blocks-in-reps design was used, with 10 S_1 lines and 1 hybrid check randomly assigned to each of 10 blocks. A blocks-in-reps design is useful for the evaluation of genetic material in that the number of replications and block sizes are relatively unrestricted, and allows for evaluating large numbers of entries without having to use a large number of replicates (Schutz and Cockerham, 1966). This design has been shown to be practical where treatments such as fertilizer and irrigation are most

easily superimposed on whole replications of the experiment (Ross and Gardner, unpublished material). Data were analyzed with the Statistical Analysis Systems procedures (S.A.S. Institute, Inc., Raleigh, NC).

ANALYSIS OF VARIANCE

A combined analysis over environments and separate analyses for each environment were performed for flowering, height, yield, 1000-seed weight, percent protein, and percent digestibility. The entry sums of squares were divided into within S_1 families, within hybrid checks and a comparison of S_1 families vs. hybrid checks. The sources of variation, degrees of freedom and expected mean squares for the combined and separate location analyses are shown in Tables 4 and 5, respectively.

The statistical analyses included an evaluation of the means of the S_1 families, the hybrid checks and the selected families.

PHENOTYPIC CORRELATIONS

Phenotypic correlations were calculated for all of the traits measured and scored and for the 110 entries, 100 S_1 lines and 10 hybrid checks separately and were combined over 4 environments. Pearson's r correlation was used for the traits flowering, height, yield, 1000-seed

TABLE 4

Form of variance analysis and mean square expectations for combined analyses of S_1 lines and check hybrids.

SOURCE	DF*	MEAN SQUARE EXPECTATIONS
Location	l-1	
Rep (Location)	(r-1)l	
Block (Rep)(Loc)	(b-1)rl	
Entry (Block)	(f-1)b	$\sigma^2 e + r\sigma^2_{fl} + rl\sigma^2_f$
S_1 lines	(s-1)b	$\sigma^2 e + r\sigma^2_{sl} + rl\sigma^2_s$
checks	(c-1)	$\sigma^2 e + r\sigma^2_{cl} + rl[k]^2$
S_1 vs checks	(f-1)b-[(s-1)b+(c-1)]	
Location X Entry (Block)	(l-1) (f-1)b	$\sigma^2 e + r\sigma^2_{fl}$
S_1 lines X Loc	(l-1) (s-1)b	$\sigma^2 e + r\sigma^2_{sl}$
checks X Loc	(l-1) (c-1)	$\sigma^2 e + r\sigma^2_{cl}$
S_1 vs checks X Loc	(l-1) (f-1)b - [(l-1)] (s-1)b + (l-1) (c-1)]	
Error	(r-1) (f-1)bl	$\sigma^2 e$
S_1 lines	(r-1) (s-1)bl	$\sigma^2 e_s$
checks	(r-1) (c-1)l	$\sigma^2 e_c$
S_1 vs checks	(r-1) (f-1)bl - [(r-1) (s-1)bl + (r-1) (c-1)l]	

*=l, r, b, f, s, and c are numbers of environments, replications, blocks, entries, S_1 lines and checks respectively. σ^2_{sl} = variance due to interactions of S_1 lines and environments, σ^2_{cl} = variance due to interactions of checks and environments.

TABLE 5

Form of variance analysis and mean square expectations for separate analysis of S_1 lines and hybrid checks at each of 4 environments.

SOURCE	DF*	MEAN SQUARE EXPECTATIONS
Rep	(r-1)	
Block (Rep)	(b-1)r	
Entry (Block)	(f-1)b	$\sigma^2e+r\sigma^2_f$
S_1 lines	(s-1)b	$\sigma^2e+r\sigma^2_{es}$
checks	(c-1)	$\sigma^2e+r[k]^2$
S_1 vs checks	(f-1)b - [(s-1)b + (c-1)]	
Error	(r-1) (f-1)b	σ^2e
S_1 lines	(r-1) (s-1)b	σ^2e_s
checks	(r-1) (c-1)	σ^2e_c
S_1 vs checks	(r-1) (f-1)b - [(r-1) (s-1)b + (r-1) (c-1)]	
Total	(rfb) - 1	

*= r, b, s, and c are numbers of replications, blocks, entries, S_1 lines and checks respectively.

used for the traits flowering, height, yield, 1000-seed weight, percent protein, percent digestibility, percent of tillers retained, and percent of green leaves retained. These traits were measured as either interval or ratio data, so Pearson's r was the appropriate correlation technique to use (Bartz, 1981). Spearman's rank-difference method was used for all correlations involving the traits pericarp color, endosperm texture, endosperm color, endosperm type, presence of a testa, amount of molding, and amount of sprouting.

To determine the relative performance of S_1 lines over environments, the performance of lines at one environment was correlated with their performance at each of the other 3 environments (Guitard, 1960; Campbell and Lefever, 1977).

GENETIC VARIANCE, HERITABILITY AND GENOTYPIC CORRELATIONS

Genetic variance estimates and heritability estimates were calculated for a combined analysis and for each of 4 environments. Genetic variance among S_1 families can be expressed as $\sigma^2_A + 1/4\ \sigma^2_D$, where σ^2_A is the variance due to additive genetic variance and a deviation due to dominance effects, and σ^2_D is variance due to dominance genetic variance (Hallauer and Miranda, 1981). Genetic variance for the combined analysis was calculated as

$$\sigma^2_g = \frac{MS_{entry} - MS_{entryxlocation}}{rl}$$

where r = number of replications and l = number of environments. Genetic variance for each of the 4 environments was calculated as $\sigma^2_g = \frac{MS_{entry} - MS_{error}}{r}$ where r = number of replications.

Heritability for the combined analysis was calculated according to Knapp et al., 1985 as:

$$h^2 = \frac{MS_{entry} - MS_{entryxloc}/rl}{MS_{entry}/rl}$$

where r = number of replications and l = number of environments. The heritabilities for each of the 4 environments was calculated as: $h^2 = \frac{\sigma^2 g}{\sigma^2 p}$

$\sigma^2 g = MS_{entry} - MS_{error}/r$ and $\sigma^2_p = \sigma^2 g + MS_{error}/r$ and r = number of replications.

Confidence intervals were calculated for the heritabilities according to the formula in Knapp et al., 1985, and standard errors for heritabilities were calculated using the formula in Hallauer and Miranda, 1981.

Genotypic correlations between 2 traits were calculated using the formula: $r_{gxy} = \sigma^2_{gxy} / [\sigma^2_{gx} \cdot \sigma^2_{gy}]^{1/2}$ where x = trait x and y = trait y.

SELECTION

Pooled means and environment means were calculated for the top 10% and the bottom 10% of the S_1 lines based on yield and based on digestibility for all 15 traits measured. The means of the S_1 population were also included for a comparison of top and bottom lines with the population means. The LSD for comparing the top and bottom lines to the population means was:

$$LSD = t_{0.05} [(1/rb + 1/rc) MS_E]^{1/2}$$

where $t_{0.05}$ is the tabular value of t at the 0.05 level of significance, r, b, and c equal the number or replications, entries in the S_1 population mean, and entries in the top and bottom 10% of S_1 means, respectively, and the MS_E is the error mean square (Cox et al., 1984; Bramel-Cox et al., 1986).

RESULTS AND DISCUSSION

ANALYSIS OF VARIANCE

The combined analysis of variance for all entries for 6 traits in 4 environments is presented in Table 6 . Effects of environments and entry variances were significant (P=0.01) for all traits. Entry X location interaction was significant (P=0.01) for flowering, height, 1000-seed weight, and percent protein, but was non-significant for yield and percent digestibility. Bartlett's Chi-square test for homogeneity of error variances (Bartlett, 1937) performed on the individual environments making up the combined analysis indicated a large amount of heterogeneity (P<0.001 for flowering, height, yield, percent protein and percent digestibility; P=0.01 for 1000-seed weight) for all traits. Heterogeneity of these mean squares invalidates the F tests to some extent, although the amount of bias is not clear (Schutz and Bernard, 1967). The general effect is that significance will be obtained more frequently than should be the case (LeClerg et al., 1962). A lack of a relationship between mean values and error variances precluded the transformation of the data (Snedecor and Cochran, 1967). The two Olsburg environments, high and low

Table 6. Mean squares from analysis of variance for combined analysis for the traits flowering (FL), height (HT), yield (Y), seed weight (SD WT), protein (PRO) and digestibility (DIG), of 110 entries produced at 4 locations. (**=P=0.01, *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
LOC	3	11335.82**	16814.04**	1772418.11**	73.92**	273.20	0.20100**
REP(L)	4	151.28**	75.46	8077.26	1.69**	60.57**	0.00568**
B(REP)(L)	72	52.81**	173.91**	11679.48**	1.17**	9.74**	0.00571**
ENT(B)	100	136.35**	310.80**	22915.45**	3.55**	1.51**	0.00248**
LXENT(B)	300	15.51**	59.46**	4989.92	0.38**	1.09**	0.00172
ERROR	400	8.26	36.27	5965.84	0.25	0.76	0.00150

nitrogen, contributed to the error variance heterogeneity having a larger error variance for flowering, and lower error variances for percent protein and percent digestibility (Table 7). The Garden City irrigated environment had lower error variances for height and 1000-seed weight, and the highest error variance for yield. A test of homogeneity of error variance was also performed on the S_1 lines and the hybrid checks and as was to be expected, the major portion of the heterogeneity was found to be due to the S_1 lines.

Results of the separate analyses of variance for all 110 entries at each of 4 environments are shown in Table 7. There was significant variability among the entries for days to flowering, plant height and seed weight at all four locations. The entry variance was only significant for protein and digestibility at the two Olsburg environments, but entry variance for yield was significant at all the environments but Garden City irrigated.

Analyses of variance for a comparison of environments within locations were conducted at Olsburg and Garden City (Tables 8 and 9). At Olsburg, variance among entries was significant (P=0.01) for all 6 traits. The only trait with a significant environment effect was yield (P=0.05); in other words, there was a significant difference in

Table 7. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO) and digestibility (DIG) of 110 entries of sorghum at each of 4 environments. (**=P=0.01; *=P=0.05)

ENV.	SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
OLSBURG LOW N	REP	1	351.29**	112.40	8720.09	3.86**	216.64**	0.00900*
	B(REP)	18	99.48**	183.67**	7596.27*	0.94**	4.91**	0.00370*
	ENT(B)	100	61.80**	122.90**	7403.62**	1.05**	1.28**	0.00150*
	ERROR	100	15.92	50.22	4049.58	0.30	0.56	0.00066
OLSBURG HIGH N	REP	1	212.07**	9.20	10727.70	0.64	6.37**	0.00065
	B(REP)	18	64.15**	184.44**	5770.54	1.39**	3.07**	0.00230*
	ENT(B)	100	50.86*	127.82**	8159.73**	1.34**	1.34**	0.00240*
	ERROR	100	11.59	48.19	3698.23	0.24	0.28	0.00085
GARDEN CITY IRR.	REP	1	4.95	44.55	4296.24	0.81*	14.70**	0.01300*
	B(REP)	18	6.10**	129.99**	6023.99	0.39*	28.60**	0.00113*
	ENT(B)	100	24.41**	124.40**	14229.24	1.09**	0.10	0.00230
	ERROR	100	1.00	25.06	12434.70	0.19	1.19	0.00300
GARDEN CITY DRYLAND	REP	1	38.81**	136.04	8565.02	1.47*	4.58*	0.00010
	B(REP)	18	41.50**	197.52**	27327.10**	1.96**	2.38**	0.00560*
	ENT(B)	100	45.80**	78.11**	8092.62**	1.22**	1.17	0.00140
	ERROR	100	3.72	48.04	3680.84	0.27	0.99	0.00130

Table 8. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO), and digestibility (DIG) of 110 entries at the Olsburg location. (**=P=0.01; *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
LOC	1	1361.54	229.83	276151.70*	31.13	261.57	0.05300
REP(L)	2	281.68**	121.25	9723.90	2.25**	111.51**	0.00490**
B(REP)(LOC)	36	81.81**	184.06**	6683.41**	1.17**	3.99**	0.00300**
ENT(B)	100	96.53**	212.88**	12031.99**	2.10**	2.07**	0.00290**
LXENT(B)	100	16.13	37.85	3531.36	0.29	0.55	0.00096
ERROR	200	13.76	49.21	3873.91	0.27	0.42	0.00075

Table 9. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO), and digestibility (DIG) of 110 entries at the Garden City location. (**=P=0.01; *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
LOC	1	1097.78**	47882.15**	4425256.14**	0.0037	346.02*	0.0147
REP(L)	2	20.89**	90.30	6430.63	1.1400	9.65	0.0065
B(REP)(L)	36	23.80**	163.76**	16675.55**	1.1800**	15.49**	0.0084**
ENT(B)	100	64.23**	158.91**	15592.10**	1.9200**	1.23	0.0020
LXENT(B)	100	5.99**	43.61	6729.76	0.3800**	0.94	0.0017
ERROR	200	2.76	36.55	8057.77	0.2300	1.09	0.0022

yield between the low and high nitrogen environments. There was no significant entry X environment interaction for any trait in Olsburg. At Garden City, entries varied significantly (P=0.01) for flowering, height, yield and 1000-seed weight, but not for protein or digestibility. The environmental effects were significant at the P=0.01 level for flowering, height, and yield, and significant at the P=0.05 level for percent protein. Entry X environment interaction was significant (P=0.01) for flowering and 1000-seed weight.

In Table 10, the mean squares for entry, entry X environment and error are separated into S_1, check and S_1 vs. check components, for a comparison of S_1 vs. checks. The F tests for entry were calculated using the appropriate mean squares from entry X environment. The S_1 lines had significant variance for entries for all traits (P=0.01), while the hybrid checks had differences in their means for days to flowering (P=0.05), height (P=0.01) and seed weight (P=0.01). There was no significant S_1 vs. checks comparison. Entry X environment interaction was significant for S_1 lines for days to flowering, seed weight and protein (P=0.01), but significant for only days to flowering (P=0.01) for hybrid checks. This analysis indicates a significant proportion of the variability of the 110 entries is due to the S_1

Table 10. Mean squares from combined analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO) and digestibility (DIG) for a comparison of S_1 lines vs. check hybrids combined over 4 environments. 01; *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
ENT(B)	100	136.35**	310.80**	22915.45**	3.55**	1.51**	0.00250**
S_1	90	131.13**	295.28**	11326.98**	2.30**	1.44**	0.00260**
CHECK	9	16.01*	286.29**	7111.47	4.32**	1.22	0.00064
S_1 VS CH	1	1689.54	1928.19	1208113.79	109.08	9.94	0.00520
LXENT(B)	300	15.51**	59.46**	4989.92	0.38**	1.09**	0.00170
S_1	270	15.92**	61.10	4825.98	0.35**	1.09**	0.00170
CHECK	27	11.95**	22.97	7568.25	0.46	1.27	0.00220
S_1 VS CH	3	10.18	240.27	0	1.91	0.02	0.00067
ERROR	400	8.26	36.27	5965.84	0.25	0.76	0.00150
S_1	360	8.68	35.49	5289.70	0.24	0.78	0.00150
CHECK	36	6.28	32.68	13088.15	0.36	1.29	0.00180
S_1 VS CH	4	0	138.78	2717.82	0	0	0

lines and not to the check varieties.

Table 11 shows a comparison of S_1 lines vs. checks at each of 4 environments. As with the combined analysis, the S_1 lines contributed the most to the overall entry variability.

Results of the analysis of variance for comparing S_1 lines and checks within the Olsburg location are shown in Table 12, and within the Garden City location in Table 13. At Olsburg, the S_1 lines had significant variance among entries for all traits, and hybrid checks differed significantly for only height and seed weight. At Garden City, S_1 lines had significant entry variances for days to flowering, height and seed weight, and checks differed significantly for height only.

In general, there was greater variation among entries for flowering, height and 1000-seed weight in all environments. Percent protein and percent digestibility was significant only at the Olsburg location. As indicated by the analysis of the breakdown into S_1 lines and checks, the S_1 lines have greater significance, with little difference between means for the hybrid checks.

Table 11. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO), and digestibility (DIG) for a comparison of S_1 lines vs. check hybrids at each of 4 environments. (**=P=0.01; *=P=0.05)

ENVIRON.	SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
OLSBURG	ENT(B)	100	61.80**	122.90**	7403.62**	1.05**	1.28**	0.0015**
LOW N	S_1	90	62.04**	125.35**	5100.55	0.76**	1.23**	0.0015**
	CHECKS	9	21.91	67.02	4582.56	1.63*	1.14	0.0024
	S_1 VS CH	1	398.90	405.68	24000.69	29.80	7.10	0
	ERROR	100	15.92	50.22	4049.58	0.30	0.56	0.00066
	S_1	90	16.31	50.63	3933.40	0.28	0.57	0.00066
	CHECKS	9	17.64	40.20	4665.24	0.39	1.36	0.00120
	S_1 VS CH	1	0	103.37	8964.73	0.83	0	0
OLSBURG	ENT(B)	100	50.87**	127.82**	8159.73**	1.34**	1.34**	0.0024**
HIGH N	S_1	90	47.90**	132.70**	5180.01*	1.18**	1.24**	0.0025**
	CHECKS	9	15.20*	84.09*	5964.59	1.38*	1.05	0.0013
	S_1 VS CH	1	639.32	82.83	296000.66	15.23	12.44	0.0070
	ERROR	100	11.59	48.19	3698.23	0.24	0.28	0.00085
	S_1	90	12.63	48.86	3055.58	0.24	0.26	0.00081
	CHECKS	9	4.58	26.42	12395.94	0.40	0.86	0.00080
	S_1 VS C	1	0	283.72	0	0	0	0.00510
GARDEN	ENT(B)	100	24.41**	124.40**	14229.24	1.09**	0.10	0.00230
CITY	S_1	90	23.98**	109.98**	10232.91	0.71**	1.03	0.00230
IRR.	CHECKS	9	9.87**	95.64*	11362.16	2.15**	2.57	0.00200
	S_1 VS CH	1	194.71	1681.12	399702.68	25.40	0	0.01110
	ERROR	100	1.80	25.06	12434.70	0.19	1.19	0.00300
	S_1	90	1.89	25.51	10568.89	0.20	1.29	0.00310
	CHECKS	9	1.78	22.11	31025.96	0.17	1.95	0.00400
	S_1 VS C	1	0	11.32	13037.03	0	0	0
GARDEN	ENT(B)	100	45.80**	78.11*	8092.62**	1.22**	1.17	0.0014
CITY	S_1	90	44.99**	68.44	5290.47*	0.72**	1.21	0.0015
DRYLAND	CHECKS	9	4.89*	108.45	7906.92	0.54	0.25	0.0014
	S_1 VS CH	1	487.19	676.20	261957.73	52.37	5.54	0
	ERROR	100	3.72	48.04	3680.84	0.27	0.99	0.0013
	S_1	90	3.88	48.43	3600.92	0.26	1.03	0.0013
	CHECKS	9	1.11	42.01	4265.45	0.51	0.98	0.0014
	S_1 VS C	1	12.59	67.72	5612.16	0	0	0.0010

Table 12. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO), and digestibility (DIG) for a comparison of S_1 lines vs. check hybrids at the Olsburg location. (**=P=0.01; *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
ENT(B)	100	96.53**	212.88**	12031.99**	2.10**	2.07**	0.0029**
S_1	90	92.88**	218.47**	6898.76**	1.65**	1.90**	0.0031**
CHECKS	9	51.43	134.49**	4653.52	2.68**	1.04	0.0017
S_1 VS CH	1	1155.10	415.36	540428.80	37.58	26.14	0
LXENT(B)	100	16.13	37.85	3531.36	0.29	0.55*	0.00096*
S_1	90	17.06	39.58	3382.80	0.29	0.56*	0.00087
CHECKS	9	21.68	16.62	5893.63	0.32	1.16	0.00210
S_1 VS CH	1	0	73.15	0	0	0	0
ERROR	200	13.76	49.21	3873.91	0.27	0.42	0.00075
S_1	180	14.47	49.75	3494.49	0.26	0.41	0.00074
CHECKS	18	11.11	33.31	8530.59	0.39	1.11	0.00099
S_1 VS CH	2	0	143.55	0	0	0	0.00020

Table 13. Mean squares from analysis of variance for the traits flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), protein (PRO) and digestibility (DIG) for a comparison of S_1 lines vs. check hybrids at the Garden City location. (**=P=0.01; *=P=0.05)

SOURCE	DF	FL	HT	Y	SD WT	PRO	DIG
ENT(B)	100	64.23**	158.91**	15592.10**	1.92**	1.23	0.0020
S_1	90	63.22**	132.95**	9041.87	1.10**	1.31	0.0020
CHECKS	9	10.04	179.47**	7682.33	1.89	1.12	0.0013
S_1 VS CH	1	642.32	2309.83*	676300.89	76.02*	0	0.0064
LXENT(B)	100	5.99**	43.61	6729.10	0.38**	0.94	0.0017
S_1	90	5.74	45.47	6481.51	0.33	0.93	0.0017
CHECKS	9	4.71	24.63	11586.75	0.80*	1.69	0.0021
S_1 VS CH	1	39.58	47.47	0	1.77	0	0.0020
ERROR	200	2.76	36.55	8057.77	0.23	1.09	0.0022
S_1	180	2.89	36.97	7084.90	0.23	1.15	0.0022
CHECKS	18	1.44	32.06	17645.70	0.34	1.46	0.0027
S_1 VS CH	2	3.13	39.53	9324.59	0	0	0

MEANS

Means and ranges for 6 traits of 100 S_1 lines and 10 hybrid checks at each environment and their pooled means are summarized in Table 14. Using yield as a measure of an environment's productivity, the environments can be ranked as follows: Garden City irrigated, Olsburg high nitrogen, Olsburg low nitrogen, and Garden City dryland. The highest yielding environment, Garden City irrigated, was also the earliest, the tallest, the largest seeded, had the lowest percent protein, and had the lowest percent digestibility. Comparing the checks to the S_1 lines over all environments, the checks were earlier, taller, higher yielding, larger seeded, had lower percent protein, and lower percent digestibility than the S_1 lines, but in no case were these differences significant (Table 10).

Comparing checks and S_1 lines at each environment and for the traits flowering, height, yield and 1000-seed weight, the checks were earlier, taller, higher yielding and larger seeded than the S_1 lines in all environments, but none of these differences were significant (Table 11). For the trait percent protein, the checks had lower percent protein than the S_1 lines in the Olsburg low nitrogen and Olsburg high nitrogen and Garden City irrigated environments, but had a higher percent protein in the Garden City dryland environment. The checks had a

Table 14. Means by environment, their ranges and pooled means for 100 S_1 lines and 10 hybrid checks for the traits flowering, height, yield, 1000-seed weight, protein and digestibility.

TRAIT	ENVIRONMENT				
	OLSBURG LOW NITROGEN	OLSBURG HIGH NITROGEN	GARDEN CITY IRRIGATED	GARDEN CITY DRYLAND	POOLED
FLOWERING (days)					
S_1 lines	80.65a	77.15b	65.15d	68.46c	72.85
range	70.50-94.00	68.00-94.00	59.00-73.50	61.00-65.50	
checks	75.30a	71.60b	61.90c	63.50c	68.08
range	72.50-82.00	66.00-76.00	58.50-65.00	61.00-65.50	
HEIGHT (cm)					
S_1 lines	111.64bc	110.13c	117.45a	96.67d	108.97
range	98.0-142.0	92.0-129.0	91.5-137.0	82.5-113.0	
checks	111.70bc	110.90c	124.60a	102.85d	112.51
range	105.0-125.0	102.0-125.5	117.0-142.0	95.0-117.5	
YIELD (kg/ha)					
S_1 lines	3319.1c	3973.6b	5662.8a	3005.9c	3990.3
range	1566.7-4713.3	2246.7-5974.0	3816.7-8704.0	1342.7-5158.0	
checks	4858.8c	5662.0b	7563.9a	4715.5c	5700.0
range	4176.0-6050.7	4540.0-6656.0	6130.0-9665.3	3150.3-6225.3	
1000-SEED WEIGHT (g/1000 seeds)					
S_1 lines	16.67c	18.50b	20.67a	20.50a	19.07
range	11.47-21.73	11.03-26.27	16.60-27.10	14.03-25.13	
checks	20.57c	21.67bc	24.73ab	26.13a	23.27
range	16.20-27.00	18.27-26.97	20.23-30.30	23.40-29.20	
PROTEIN (%)					
S_1 lines	9.88ab	11.43a	9.02b	10.75ab	10.27
range	8.00-12.09	9.22-13.38	6.72-12.50	7.81-13.13	
checks	9.07a	10.50a	8.70b	11.04a	9.83
range	8.22-10.56	9.28-11.81	7.25-10.47	10.47-11.34	
DIGESTIBILITY (%)					
S_1 lines	75.8a	73.8b	63.9d	70.2c	72.3
range	68.7-82.6	61.7-81.0	59.9-78.4	62.2-75.9	
checks	76.0a	71.4b	68.0c	71.2b	71.6
range	68.8-82.0	67.1-75.3	61.7-71.4	67.7-75.6	

Means followed by the same letter in the same row are not significantly different at the P=0.05 level according to Fisher's LSD procedure.

higher percent digestibility than the S_1 lines in the Olsburg low nitrogen environment and in the two Garden City environments, but had a lower percent digestibility than the S_1 lines in the Olsburg high nitrogen environment. None of these differences between checks and S_1 lines were significant (Table 11).

Means were also calculated for S_1 lines and checks for other characters measured and are shown in Table 15. In general, comparing checks to S_1 lines, checks were more often red in pericarp color, more corneous in endosperm texture, more heteroyellow in endosperm color, more waxy in endosperm type, received a higher rating for presence of a testa, were slightly more moldy and slightly less sprouted, had a higher percent of tillers retained, and a higher percent of green leaves retained after anthesis.

PHENOTYPIC CORRELATIONS

The results of phenotypic correlations of 15 traits for 10 hybrid checks are presented in Table 16. The correlations were analyzed primarily to determine which traits had any effect on the digestibilty or the yield of the population, therefore, the discussion will relate to these two major traits of interest.

The phenotypic correlations showed that the traits with significant correlations with digestibility were flowering (r=.62), yield (r=-.44) and 1000-seed

Table 15. Means of S_1 lines and checks and their pooled means for the traits pericarp color, endosperm texture, endosperm color, endosperm type, presence of a testa, amount of molding, amount of sprouting, % tillers and % green leaves retained.

TRAIT	OLSBURG LOW N	OLSBURG HIGH N	GARDEN CITY IRRIGATED	GARDEN CITY DRYLAND	POOLED MEANS
PERICARP COLOR					
S_1	5.07	5.40	5.00	4.75	5.05
Check	5.75	6.25	4.85	4.45	5.33
ENDOSPERM TEXTURE					
S_1	3.59	3.41	3.14	3.33	3.36
Check	3.25	3.40	3.10	3.20	3.24
ENDOSPERM COLOR					
S_1	1.95	1.87	1.70	1.68	1.80
Check	2.20	2.00	2.15	1.95	2.08
ENDOSPERM TYPE					
S_1	1.39	1.15	1.15	1.12	1.20
Check	1.20	1.20	1.20	1.45	1.26
TESTA					
S_1	3.10	2.85	2.91	2.96	2.95
Check	3.20	3.15	3.05	3.10	3.13
MOLDING					
S_1	2.73	2.66	2.06	1.78	2.30
Check	2.90	2.80	2.35	1.65	2.43
SPROUTING					
S_1	1.75	1.93	1.00	1.00	1.42
Check	1.65	1.70	1.00	1.00	1.34
% TILLERS					
S_1	50.7	68.3	75.2	49.0	60.8
Check	60.0	81.4	88.0	55.0	71.1
% GREEN LEAVES					
S_1	52.9	51.7	67.8	33.7	51.5
Check	52.5	56.2	77.9	37.9	56.1

Table 16. Phenotypic correlation coefficients for 10 hybrid checks for the traits days to flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), digestibility (DIG), protein (PRO), % tillers (TL), % green leaves (GL), pericarp color (COL), endosperm texture (TEX), endosperm color (END COL), endosperm type (TYPE), presence of testa (TES), amount of molding (MOLD), and amount of sprouting (SPR) combined over 4 environments. (**=P=0.01; *=P=0.05)

TRAIT	FL	HT	Y	SD WT	DIG	PRO	TL	GL
FL	1.00	-.21	-.45**	-.72**	.62**	-.02	-.04	-.11
HT		1.00	.69**	.18	-.31	-.52**	.17	.50**
Y			1.00	.28	-.44**	-.36*	.39*	.62**
SD WT				1.00	-.34**	.20	-.12	-.07
DIG					1.00	0	-.29	-.24
PRO						1.00	-.10	-.47**
TL							1.00	.44**
GL								1.00

Table 16 (continued). Phenotypic correlation coefficients for 10 hybrid checks for the traits days to flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), digestibility (DIG), protein (PRO), % tillers (TL), % green leaves (GL), pericarp color (COL), endosperm texture (TEX), endosperm color (END COL), endosperm type (TYPE), presence of testa (TES), amount of molding (MOLD), amount of sprouting (SPR) combined over 4 environments. (**=P=0.01; *=P=0.05)

TRAIT	COL	TEX	END COL	TYPE	TES	MOLD	SPR
FL	.16	.21	.13	.04	.02	.60**	.70**
HT	.13	-.07	.12	-.16	.08	.12	-.10
Y	.02	-.20	.03	-.08	.06	.05	-.27
SD WT	.12	-.18	-.16	.22	.30	-.55**	-.55**
DIG	-.07	.16	.09	.17	-.02	.35*	.38*
PRO	.03	-.05	-.10	.18	.05	-.38*	.06
TL	.31	0	-.09	.11	.30	0	-.15
GL	.17	-.01	.17	-.03	.21	.36*	-.13
COL	1.00	.18	-.17	0	.79**	.08	-.21
TEX		1.00	-.29	-.12	.04	.20	-.03
END COL			1.00	-.30	-.13	-.02	.20
TYPE				1.00	.08	-.09	0
TES					1.00	-.11	-.20
MOLD						1.00	.52**
SPR							1.00

weight (r=-.34). This indicates that increased digestibility was associated with later flowering, lower yielding, and smaller seeded lines. Amounts of molding and sprouting also had significant associations with digestibility, and indicated that the higher the amount of molding and sprouting, the more digestible the line. Of the other seed characters scored, none showed a significant correlation with digestibility for the hybrid checks. No significant correlation between percent protein and digestibility was recorded.

Significant correlations with yield were plant height (positive), percent green leaves (positive), flowering (negative), and digestibility (negative), percent tillers (positive), and protein (negative).

Correlations were computed based on S_1 family means at each of the 4 environments and combined over environments. The results are reported in Table 17. As with the checks, the S_1 lines had significant correlations between digestibility and flowering (positive), yield (negative), and seed weight (negative). None of the other seed characters measured had significant correlations with digestibility. In general, the correlations were not consistent from environment to environment, and of all the significant correlations discussed, all of them were found in the two Olsburg environments.

Table 17. Phenotypic correlation coefficients for S_1 lines at each of 4 environments and a combined analysis for the traits days to flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), digestibility (DIG), protein (PRO), % tillers (TL), and % green leaves (GL) with the traits pericarp color (COL), endosperm texture (TEX), endosperm color (END COL), endosperm type (TYPE), presence of testa (TES), amount of molding (MOLD), and amount of sprouting (SPR). (**=P=0.01; *=P=0.05)

TRAIT	ENV	HT	Y	SD WT	DIG	PRO	TL	GL
FL	1	.21*	-.50**	-.60**	.57**	-.25*	-.10	.22*
	2	.21*	-.42**	-.53**	.66**	-.36**	-.10	.25*
	3	.23*	-.19	-.38**	.10	-.01	-.11	.16
	4	.08	-.52**	-.61**	.10	.15	.04	.50**
combined		.12	-.49**	-.72**	.65**	.17**	-.11*	.05
HT	1		.26**	.05	.19	-.07	-.09	.09
	2		.34**	-.07	.30**	-.21*	-.04	.36*
	3		.17	.11	.21*	.10	.06	.06
	4		0	.01	.16	-.01	-.18	.03
combined			.52**	-.08	.18**	-.30**	.09	.55**
Y	1			.49**	-.31**	.28**	.29**	-.19
	2			.42**	-.24*	.15	.18	.07
	3			.21*	.04	.12	.19	.11
	4			.49**	.04	-.06	0	-.15
combined				.39**	-.28**	-.19**	.27**	.49**
SEED WT	1				-.41**	.30**	-.02	-.14
	2				-.45**	.42**	.18	-.03
	3				-.10	0	.05	-.05
	4				-.04	-.15	-.09	-.24
combined					-.51**	.01	.08	-.08
DIG	1					-.24*	-.06	.20*
	2					-.33**	-.10	.28**
	3					.03	.05	.18
	4					.16	.15	0
combined						.09	-.04	.07
PRO	1						.04	-.22*
	2						-.02	-.12
	3						.08	.06
	4						.10	.11
combined							-.01	-.33**

ENVIRONMENTS : 1=Olsburg Low N, 2=Olsburg High N, 3=Garden City Irrigated, 4=Garden City Dryland.

Table 17 (continued). Phenotypic correlation coefficients for S_1 lines at each of 4 environments and a combined analysis for the traits days to flowering (FL), height (HT), yield (Y), 1000-seed weight (SD WT), digestibility (DIG), protein (PRO), % tillers (TL), and % green leaves (GL), with the traits pericarp color (COL), endosperm texture (TEX), endosperm color (END COL), endosperm type (TYPE), presence of a testa (TES), amount of molding (MOLD), and amount of sprouting (SPR). (**=P=0.01; *=P=0.05)

TRAIT	ENV.	COL	TEX	END COL	TYPE	TES	MOLD	SPR
FL	1	-.32**	.29**	.07	.03	-.18	-.22	.24*
	2	-.09	.13	.18	-.27	-.19	-.01	.16
	3	-.09	.02	.14	.04	.13	-.26	.
	4	-.06	.30**	-.05	.10	.07	-.01	.05
combined		-.05	.42**	.16**	.14**	-.02	.46**	.60**
HT	1	-.07	.16	-.13	-.19	-.17	-.13	.14
	2	-.12	.04	-.02	-.21	-.19	.10	.04
	3	-.24*	.10	-.13	-.14	-.13	-.06	.
	4	.04	.06	-.06	.01	.12	-.20*	-.05
combined		-.01	-.01	-.03	-.02	-.07	.20**	.14**
Y	1	.25*	-.30**	.07	-.10	-.06	.14	-.03
	2	-.03	-.16	.03	.05	-.02	.09	-.07
	3	.12	.12	.05	-.11	.17	-.04	.
	4	.15	-.14	.18	-.11	.04	-.17	.10
combined		.10	-.31**	-.03	-.06	-.03	-.07	-.19**
SD WT	1	.03	-.42**	.17	-.02	-.09	.26**	-.01
	2	-.20*	-.30**	.13	.05	-.01	.18	.10
	3	-.20	-.16	.14	.04	-.33**	.12	.
	4	.04	-.26**	.28**	.01	-.11	.01	.07
combined		-.11*	-.45**	.04	-.15**	-.13**	-.30**	-.34**
DIG	1	-.19	.26**	-.06	.05	-.30**	-.05	.14
	2	-.04	.15	.13	-.18	-.27**	.15	.20
	3	.09	.09	-.14	-.06	.01	.02	.
	4	-.07	.01	.24*	-.11	-.01	.03	.14
combined		0	.30**	.13**	.08	-.09	.42**	.47**
PRO	1	.10	-.42**	-.02	-.11	-.02	.10	-.13
	2	-.11	-.13	-.09	-.04	.16	-.13	-.18
	3	.11	-.05	-.13	.11	.15	.13	.
	4	0	.06	-.18	.07	.03	.05	-.13
combined		.06	-.01	-.02	-.07	.05	.14**	.21**

Phenotypic correlation coefficients at each of 4 environments and a combined analysis for the traits pericarp color, endosperm texture, endosperm color, endosperm type, presence of a testa, amount of molding and amount of sprouting are shown in Table 18. The significant correlations were : between pericarp color and endosperm color (negative) and presence of a testa (positive), between endosperm texture and endosperm color (negative), between endosperm color and presence of a testa (negative), and between presence of a testa and molding (negative). Similar to the results of the other traits measured, the direction and significance of the correlations differed among environments, with the greatest number of correlations in the Olsburg environments.

A rank correlation was run for 5 traits to determine the stability of S_1 line performance at various environments (Table 19). The highest r values were for flowering at the two Garden City environments (r=.84), and 1000-seed weight at the two Olsburg environments (r=.68). The correlations among environments for yield were low but significant in all comparisons except Olsburg, both high and low nitrogen, and Garden City Dryland. Correlations among environments were generally non-significant for protein and digestibility, except between the two Olsburg environments. These findings indicate

Table 18. Phenotypic correlation coefficients for S_1 lines at each of 4 environments and a combined analysis for the traits pericarp color (COL), endosperm texture (TEX), endosperm color (END COL), endosperm type (TYPE), presence of testa (TES), amount of molding (MOLD), and amount of sprouting (SPR). (**=P=0.01; *=P=0.05)

TRAIT	ENV.	TEX	END COL	TYPE	TES	MOLD	SPR
COL	1	-.08	-.27**	.09	.56**	-.13	-.25
	2	.30**	-.59**	.23*	.64**	-.49**	-.21*
	3	-.07	-.17	.15	.70**	-.05	.
	4	.36**	-.14	-.03	.70**	-.05	-.02
combined		.10	-.31**	.12*	.61**	-.06	-.05
TEX	1		-.33**	-.09	.09	-.04	.03
	2		-.45**	.05	.17	-.07	-.16
	3		-.30**	.04	-.04	-.04	.
	4		-.19	.01	.42**	.01	.06
combined			-.20**	.08	.17**	.15**	.15**
END	1			.06	-.43**	.23*	.28**
COL	2			-.23*	-.66**	.40**	.17
	3			-.02	-.19	-.07	.
	4			-.01	-.20*	.02	.07
combined				-.01	-.38**	.21**	.23**
TYPE	1				.20*	-.20*	-.15
	2				.26**	-.19	-.17
	3				.25	-.19	.
	4				-.01	-.20*	.02
combined					.21**	.05	.02
TES	1					-.33**	-.39**
	2					-.59**	-.18
	3					-.13	.
	4					-.05	-.06
combined						-.14**	-.13**
MOLD	1						.21*
	2						.17
	3						.
	4						.16
	combined						.56**

ENVIRONMENTS : 1=Olsburg Low N, 2=Olsburg High N, 3=Garden City Irrigated, 4=Garden City Dryland.

Table 19. Rank correlations of S_1 lines for the traits days to flowering, yield, 1000-seed weight, protein, and digestibility in 4 environments.

TRAIT		ENV. 2	ENV. 3	ENV. 4
FLOWERING	ENV. 1	.60**	.59**	.66**
	ENV. 2		.54**	.59**
	ENV. 3			.84**
YIELD	ENV. 1	.24*	.31**	.06
	ENV. 2		.28**	.06
	ENV. 3			.25*
1000 SEED WT.	ENV. 1	.68**	.50**	.46**
	ENV. 2		.52**	.51**
	ENV. 3			.51**
PROTEIN	ENV. 1	.43**	-.23*	-.17
	ENV. 2		-.07	-.02
	ENV. 3			.12
DIGEST-IBILITY	ENV. 1	.48**	-.05	-.10
	ENV. 2		.02	.18
	ENV. 3			.13

ENV. 1=Olsburg Low Nitrogen, ENV. 2=Olsburg High N, ENV. 3=Garden City Irrigated, ENV. 4=Garden City Dryland.

that it would be difficult to correlate environments when selecting testing environments to select for yield, protein and digestibility, and the results obtained in one environment would not be applicable to another environment. The results of the rank correlation in this study indicate that the Garden City dryland environment would be selected as a testing environment, and that any one of the other three environments could be selected as a testing environment to represent those three environments with significant rank correlations. This would reduce the number of testing environments to two, thus allocating resources more efficiently.

GENETIC VARIANCE, HERITABILITIES AND GENETIC CORRELATIONS

Genetic variances and their standard errors, heritabilities and their standard errors and confidence intervals based upon on the combined environment analysis of 6 traits are shown in Table 20.

Heritabilities and their standard errors were calculated on an entry-mean basis (S_1 family) according to the formula presented in Hallauer and Miranda (1981). Heritability estimates may be inflated for the combined analysis because only one year is included in this study (Fehr, 1987). Confidence intervals were also calculated for heritabilities as a measure of precision of the estimate, and calculated according to the formula in

Table 20. Genetic variances, heritabilities, standard errors and confidence intervals for a combined analysis of the traits flowering, height, yield, 1000-seed weight, protein and digestibility.

TRAIT	GENETIC VARIANCE	HERITABILITY	C. I.
FLOWERING	14.40 ± 2.44	0.88 ± 0.149	0.85 - 0.91
HEIGHT	29.27 ± 5.51	0.79 ± 0.149	0.74 - 0.84
YIELD	812.63 ± 216.18	0.57 ± 0.153	0.46 - 0.68
1000-SEED WEIGHT	0.24 ± 0.043	0.85 ± 0.148	0.81 - 0.88
% PROTEIN	0.04 ± 0.029	0.24 ± 0.161	0.04 - 0.43
% DIGEST	.000118 ± .00005	0.36 ± 0.158	0.19 - 0.51

Knapp et al. (1985).

In the combined analysis, heritability estimates were highest for flowering, 1000-seed weight and height and were similar to the h^2 estimates reported by Eckebil et al. (1977). Heritability estimates were moderate for yield, and lowest for digestibility and protein.

Genetic variances, error variances, heritabilities and confidence intervals for each of 4 environments are shown in Table 21. Genetic variances were tested for homogeneity (Steel and Torrie, 1960) and found to be heterogeneous among environments for all traits. This heterogeneity was also found for error variances among environments. Genetic variances did not increase (or decrease) in the same proportion as error variances in relation to the mean, so heritabilities differed among environments (Table 21).

The environments varied considerably for heritability estimates for some traits, such as height, yield, percent protein and percent digestibility. These differences may be due either to actual changes in the genetic variance component or due to changes in the error variance. The former is the case for height, where the error variances are similar but the genetic variance for Garden City dryland is 4 times smaller than for the other environments. The same is true for 1000-seed weight,

Table 21. Error variances, genetic variances, heritabilities and confidence intervals for the traits flowering, height, yield, 1000-seed weight, protein and digestibility at each of 4 environments.

TRAIT	ERROR VARIANCE	GENETIC VARIANCE	HERITABILITY	C.I.
FLOWERING				
Env. 1[x]	16.31	22.87	0.74	.62 - .82
Env. 2	12.63	17.64	0.74	.62 - .82
Env. 3	1.89	11.05	0.92	.87 - .95
Env. 4	3.88	20.56	0.92	.88 - .94
HEIGHT				
Env. 1	50.63	37.36	0.60	.42 - .72
Env. 2	48.86	41.92	0.63	.47 - .74
Env. 3	25.51	42.24	0.77	.67 - .84
Env. 4	48.43	10.01	0.29	-.02 - .59
YIELD				
Env. 1	3933.40	583.58	0.23	-.11 - .46
Env. 2	3055.58	1062.72	0.41	.15 - .59
Env. 3	10568.89	0	0	-.49 - .28
Env. 4	3600.92	844.78	0.32	.02 - .53
1000-SEED WEIGHT				
Env. 1	0.28	0.24	0.63	.47 - .74
Env. 2	0.24	0.47	0.80	.71 - .86
Env. 3	0.20	0.26	0.72	.60 - .81
Env. 4	0.26	0.23	0.63	.47 - .75
% PROTEIN				
Env. 1	0.57	0.33	0.54	.33 - .68
Env. 2	0.26	0.49	0.79	.71 - .86
Env. 3	1.29	0	0	-.81 - .13
Env. 4	1.00	0.10	0.17	-.19 - .42
% DIGESTIBILITY				
Env. 1	0.00066	0.00040	0.55	.35 - .69
Env. 2	0.00081	0.00085	0.68	.54 - .78
Env. 3	0.00310	0	0	-.97 - .05
Env. 4	0.00130	0.00010	0.13	-.25 - .40

x = Env. 1=Olsburg Low Nitrogen, Env. 2=Olsburg High Nitrogen, Env. 3=Garden City Irrigated, Env. 4=Garden City Dryland.

where the genetic variance was twice as large in the Olsburg high nitrogen environment but has a similar error variance. In the case of flowering, yield, protein and digestibility, there were large differences in error variances, usually larger than the change in genetic variance, so more of the differences in heritabilities were due to differences in error variance than due to large changes in genetic variance.

Garden City irrigated had zero estimate of genetic variance for yield, percent protein and percent digestibility. When describing optimum testing environments to select for digestibility or yield, the comparison was made based upon the highest heritability estimate. In this study, the optimum environment for yield based upon the mean was Garden City irrigated, which showed no genetic variance for yield, percent protein and percent digestibility, due to a larger error variance with no proportionate increase in the entry variance. As pointed out by Allen et al. (1978), the literature contains conflicting data about the question of selecting optimum environments for yield testing. This study suggests that when selecting for yield and percent digestibility, the best environment was Olsburg high nitrogen, followed by Olsburg low nitrogen and Garden City dryland, and not the most optimum mean environment, Garden City irrigated.

Genetic correlations for the combined analysis are presented in Table 22. The significant correlations were between protein and digestibility (negative), flowering and digestibility (positive), flowering and 1000-seed weight (negative), flowering and yield (negative), flowering and protein (negative), and yield and 1000-seed weight (positive). The r values for the first four correlations were similar to those reported by Eckebil et al. (1977). The genetic correlation between yield and digestibility was -0.40, a moderate correlation that indicates that simultaneous selection for both traits would be difficult. In general, the genetic correlations are similar to the phenotypic correlations except for the correlation between protein and digestibility; r=0.09 for the phenotypic correlation and r=-0.82 for the genetic correlation. Protein and yield were negatively correlated but non-significant (r=-0.09) as similarly reported by Eckebil et al. (1977).

SELECTION

Pooled means and environment means were calculated for the top 10% and the bottom 10% of the 100 S_1 lines based both on yield and digestibility (Tables 23 and 24). The associated changes in the other traits was measured to predict changes when S_1 families were selected for high yield and low yield, and high digestibility and low

Table 22. Genotypic correlations among the traits flowering, height, yield, 1000-seed weight, protein and digestibility for a combined analysis.

	HEIGHT	YIELD WEIGHT	1000-SEED	PROTEIN	DIGEST
FLOWERING	0.23	-0.58	-0.64	-0.49	0.69
HEIGHT		0.32	0	-0.09	0.21
YIELD			0.49	-0.09	-0.40
1000-SEED WEIGHT				0.49	-0.35
PROTEIN					-0.82

Table 23. Means of top 10% and bottom 10% of 100 S_1 lines based on yield, their pooled means, and the S_1 population means at each of 4 locations.

ENVIRONMENT		FL	HT	Y	SD WT	PRO	DIG
OLSBURG	top 10%	76.55*	117.45*	4477.33*	18.47*	10.19	74.4
LOW N	bottom 10%	87.90*	107.35*	2087.60*	14.77*	9.51	77.7*
	S_1 pop. mean	80.65	111.64	3319.07	16.67	9.88	75.8
OLSBURG	top 10%	74.45*	117.55*	5293.73*	20.57*	11.51	72.8
HIGH N	bottom 10%	81.00*	105.95*	2823.20*	16.87*	10.97*	74.6
	S_1 pop. mean	77.15	110.13	3973.60	18.50	11.43	73.8
GARDEN	top 10%	64.80	120.10	7559.47*	21.20	9.71*	69.6*
CITY	bottom 10%	65.55	114.85	4158.80*	20.43	8.56*	68.7*
IRR.	S_1 pop. mean	65.15	117.45	5662.80	20.67	9.02	63.9
GARDEN	top 10%	65.70*	96.95	4406.53*	21.60*	11.00	70.4
CITY	bottom 10%	73.40*	96.50	1748.13*	18.20*	10.77	69.3
DRYLAND	S_1 pop. mean	68.46	96.67	3005.87	20.50	10.75	70.2
POOLED	top 10%	70.38*	113.01*	5434.27*	20.46*	10.60	71.8
MEANS	bottom 10%	76.96*	106.16*	2704.40*	18.20*	9.96	72.6
	S_1 pop. mean	72.85	108.97	3990.34	19.07	10.27	72.3

* = significantly different from the S_1 population mean at the P=0.05 level.

Table 24. Means of top 10% and bottom 10% of 100 S_1 lines based on digestibility, their pooled means and the S_1 population means at each of 4 environments.

ENVIRONMENT		FL	HT	Y	SD WT	PROT	DIG
OLSBURG	top 10%	87.05*	111.45	2925.60	14.70*	9.39*	80.3*
LOW N	bottom 10%	75.10*	109.45	3914.93*	18.47*	10.28	70.6*
	S_1 pop. mean	80.65	111.64	3319.07	16.67	9.88	75.8
OLSBURG	top 10%	86.05*	111.75	3379.60*	15.77*	10.88*	79.2*
HIGH N	bottom 10%	71.90*	103.65*	4190.80	19.77*	11.73	66.8*
	S_1 pop. mean	77.15	110.13	3973.60	18.50	11.43	73.8
GARDEN	top 10%	64.70	121.30*	5923.87	20.20	9.09	75.7*
CITY	bottom 10%	63.90	116.55	5923.60	21.63*	9.66*	61.9*
IRR.	S_1 pop. mean	65.15	117.45	5662.80	20.67	9.02	63.9
GARDEN	top 10%	63.95*	96.90	2816.80	19.37*	10.85	75.6*
CITY	bottom 10%	69.35	93.05	2693.20	19.63*	10.38	64.4*
DRYLAND	S_1 pop. mean	68.46	96.67	3005.67	20.50	10.75	70.2
POOLED	top 10%	75.44*	110.35	3761.47	17.51*	10.05	77.7*
MEANS	bottom 10%	70.06*	105.68	4180.67	19.88*	10.51	65.9*
	S_1 pop. mean	72.85	108.97	3990.29	19.07	10.27	72.3

* = significantly different from the S_1 population mean at the P=0.05 level.

digestibility. These means of the top 10% and bottom 10% were then compared to the S_1 population means to predict if selection resulted in means that were significantly different than the population means.

Means were also calculated for nine other traits measured, namely pericarp color, endosperm texture, endosperm color, endosperm type, presence of a testa, amount of molding, amount of sprouting, the percent of tillers retained after anthesis, and the percent of green leaves retained after anthesis. Because these were classification traits, no analyses of variance could be performed, and they could not be compared statistically to the S_1 population mean, but they are still of interest.

When S_1 lines were selected for high yield (Table 23), the lines were significantly earlier than the S_1 population mean in all environments except the Garden City irrigated environment, were taller in the two Olsburg environments, were higher yielding in all environments, were larger seeded in all environments except Garden City irrigated, and were significantly higher for protein and digestibility than the S_1 population mean only in the Garden City irrigated environment. When selected for low yield, the S_1 lines were significantly later than the S_1 population mean in all environments except Garden City irrigated, shorter in the two Olsburg environments, lower

yielding in all environments, smaller seeded in all but Garden City irrigated, and had significantly lower protein in Olsburg high nitrogen and Garden City irrigated, and significantly higher digestibility in Olsburg low nitrogen and Garden City irrigated. In general, selection for high yield resulted in changes that were opposite in tendency from the lines that were selected for low yield. Little significant change in height, protein and digestibility was observed when the lines were selected based on yield.

Based on selection for high digestibility (Table 24), S_1 lines were later in all environments except Garden City irrigated, not significantly different than the S_1 population mean for height in all environments except Garden City irrigated, were significantly lower yielding only in Olsburg high nitrogen, were smaller seeded in all environments except Garden City irrigated, had significantly lower protein in the two Olsburg environments, and had significantly higher digestibility in all environments than the S_1 population mean. When selected for low digestibility, the lines were earlier in the two Olsburg environments, shorter in Olsburg high nitrogen only, higher yielding in Olsburg low nitrogen only, larger seeded in all environments, had higher protein in Garden City irrigated only, and had significantly lower digestibility in all environments than

the S_1 population mean. In general, selection for high digestibility resulted in opposite changes in traits than when selected for low digestibility. There was little significant change in height, yield or protein when selection for digestibility was practiced.

Comparing the changes in traits upon selection for yield and selection for digestibility, selection for high yield resulted in changes in traits that were similar to selection for low digestibility. Similarly, selection for low yield and high digestibility resulted in similar changes in traits. In addition, the relationship between yield and digestibility was non-significant; in other words, when selecting for yield there was no significant change in digestibility, and when selecting for digestibility, there was no significant change in yield. To summarize the effect of selection for digestibility on the other 9 traits measured (Table 25), the most digestible lines were generally : more yellow in pericarp color, more floury in endosperm texture, similar in endosperm color, less waxy, less likely to have a testa, more moldy and sprouted, lower in percent of tillers after anthesis, and higher in percent of green leaves after anthesis than the least digestible lines.

Table 25. Means of top 10% and bottom 10% of 100 S_1 lines based on digestibility their pooled means, and the S_1 population mean for 9 other traits at each of 4 locations.

ENVIRONMENT		COL	TEX	END COL	TYPE	TES	MOLD	SPR	TL	GL[x]
OLSBURG	top 10%	4.85	4.00	1.45	1.65	3.00	2.65	1.60	54.8	56.2
LOW N	bottom 10%	7.20	3.25	2.00	1.40	3.95	2.70	1.40	61.2	40.6
	S_1 pop. mean	5.07	3.59	1.95	1.39	3.10	2.73	1.75	50.7	52.9
OLSBURG	top 10%	5.35	3.60	1.55	1.00	2.50	2.70	2.40	35.8	57.5
HIGH N	bottom 10%	6.25	3.45	1.50	1.40	3.38	2.45	1.85	78.1	44.9
	S_1 pop. mean	5.40	3.41	1.87	1.15	2.85	2.66	1.93	68.3	51.7
GARDEN	top 10%	4.30	3.20	1.50	1.05	2.50	2.20	1.00	79.4	67.1
CITY	bottom 10%	3.95	3.05	1.55	1.30	2.95	2.30	1.00	65.8	65.2
IRR.	S_1 pop. mean	5.00	3.14	1.70	1.15	2.91	2.06	1.00	75.2	67.8
GARDEN	top 10%	4.50	3.35	1.70	1.10	2.95	1.90	1.05	55.0	40.6
CITY	bottom 10%	4.90	3.35	1.25	1.15	3.40	1.80	1.00	25.0	38.9
DRYLAND	S_1 pop. mean	4.75	3.33	1.68	1.12	2.96	1.78	1.01	49.0	33.7
POOLED	top 10%	4.75	3.54	1.55	1.20	2.74	2.36	1.51	56.3	55.4
MEANS	bottom 10%	5.51	3.28	1.58	1.31	3.42	2.31	1.31	57.5	47.4
	S_1 pop. mean	5.05	3.36	1.80	1.20	2.95	2.30	1.42	60.8	51.5

x = COL= pericarp color, TEX= endosperm texture, END COL= endosperm color, TYPE= endosperm type, TES= presence of testa, MOLD= amount of molding, SPR= amount of sprouting, TL= % of tillers after anthesis, GL= % of green leaves after anthesis.

Conclusions

The combined analysis of variance for the overall population of 110 entries showed significant variance among entries for all the traits flowering, height, yield, seed weight, digestibility and protein. The separate analysis of each environment showed significant variance among entries for protein and digestibility only in the two Olsburg environments and no significant variation among entries for protein and digestibility in the Garden City environments.

Comparing the S_1 lines to the hybrid checks, S_1 lines had significant variance among entries for all traits including digestibility, whereas checks had significant variability for flowering, height and seed weight but not for digestibility.

In general, more significant variation was detected in the Olsburg location than the Garden City location. This was due in part to the lower error variances for digestibilty, protein, seed weight and yield in Olsburg.

Based on the mean yield, the environments were ranked as Garden City irrigated, Olsburg high nitrogen, Olsburg low nitrogen and Garden City dryland for productivity. The highest yielding environment was also earlier, taller, larger seeded, lower in percent protein and lower in percent digestibility than the other

environments.

The significant phenotypic correlations between digestibility and the other traits were with flowering (positive), seed weight (negative), and yield (negative), but varied considerably among environments. There were no significant correlations between digestibility and the other seed characteristics. Significant correlations between endosperm texture and flowering and seed weight were recorded. This suggests that in the environment with the latest flowering dates and the smallest seeds, Olsburg low nitrogen, the seeds did not reach full maturity, contributing to the highest digestibility. This location was also heavily frosted before reaching maturity, and this may have had the largest influence on digestibility, reducing the seed size and resulting in lower yield, thereby confounding these traits with maturity.

When the top 10% of S_1 lines were selected for digestibility, they were later, lower yielding, smaller seeded, more yellow in pericarp color, more floury in texture and more molded. If a breeder selected for improved digestibility, a lower yielding population could be expected because of the negative correlation between yield and digestibility ($r=-.40$). The population would tend to be later and smaller seeded, all undesirable traits in an agronomically acceptable sorghum population.

The results of this study indicate that it would be difficult to genetically improve the digestibility of this population through selection because of the low heritability of digestibility and the negative correlation wth yield.

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BREEDING SORGHUM FOR IMPROVED DIGESTIBILITY AND FEEDING EFFICIENCY

by

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ABSTRACT

Fifteen traits were measured to study their effect on the digestibility of grain sorghum. The effect of environment on sorghum digestibility was also evaluated. Two replicates of 110 entries, 100 S_1 lines and 10 hybrid checks, were sampled from four environments in two locations, Olsburg and Garden City, Kansas in 1986. Traits measured were days to flowering, plant height, grain yield, 1000-seed weight, percent protein, percent digestibility, percent tillers retained, percent green leaves retained, pericarp color, endosperm texture, endosperm color, endosperm type, presence of a testa, amount of molding, and amount of sprouting. Significant variability for digestibility was observed in the combined analysis of the population, and a separate environment analysis showed that the variability was found in Olsburg and not in Garden City. Comparing S_1 lines and hybrid checks showed that the S_1 lines contributed the most variability to the overall population. The strongest phenotypic correlations between digestibility and other traits were flowering (r=0.65), seed weight (r=0.51),

sprouting (r=0.47) and molding (r=0.42). None of the other seed characteristics had strong correlations with digestibility. Genetic variances and heritabilities were low to moderate for digestibility in a combined analysis (h^2 =0.36), and variable from environment to environment, ranging from 0 in the Garden City irrigated environment to 0.68 in the Olsburg high nitrogen environment. The low genetic correlation between digestibility and yield (r=-0.40) coupled with relatively low heritability for digestibility suggests that it would be difficult to select for improved digestibility and high yield simultaneously.