

DIVERGENT SELECTION FOR GRAIN PROTEIN IN A GRAIN

SORGHUM [SORGHUM BICOLOR (L.) MOENCH]

RANDOM-MATING POPULATION

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INTRODUCTION

A long range objective for cultivated grain sorghum [Sorghum bicolor (L.) Moench] is improved nutritional quality. Higher quality sorghum grain would partially alleviate the protein deficiency of the indigeneous population in areas where sorghum is a major food grain. One of the major problems in breeding for improved nutritional quality is its quantitative nature of inheritance.

Discovery and utilization of male sterility has enabled sorghum breeders to adapt cross-pollinated breeding techniques to sorghum. Use of random-mating populations and their improvement by recurrent selection is one such technique. With such a system a large number of elite lines and introductions can be combined and advanced by population breeding. Population improvement occurs when plants are selected for a particular objective and either they or their progeny intermated to form a new population. Selection cycles may be repeated as many times as required to accomplish the program objectives. Populations appear to be particularly useful with quantitative traits.

This dissertation is composed of two studies initiated in a high protein population. Part I deals with results of the divergent selection program. The major objectives were to determine the effect of divergent selection for protein in a sorghum random-mating population, to study the effect of divergent selection on other favorable agonomic traits, and to learn something about the genes governing the

inheritance of protein.

Part II examines the effect of Gardner's grid system. The effect of the use of grids with two selection intensities is discussed.

A brief summary of the experimental results for Part I and II is given in Part III. Part IV contains appendix tables. Data presented in these tables is not discussed in the text but is pertinent to the research results and conclusions.

Parts I and II are presented in a form suitable for publication by the Crop Science Society of America.

PART I

POPULATION IMPROVEMENT

Divergent Selection for Grain Protein in a
Grain Sorghum [Sorghum bicolor (L.) Moench]

Random-Mating Population

I. Population Improvement

ABSTRACT

A divergent selection study for grain protein was initiated in a grain sorghum [Sorghum bicolor (L.) Moench] random-mating population composed of high protein lines which had been composited and random-mated. Initial high and low protein populations were formed by application of a 30% selection intensity to each end of the population distribution from base population selections. During subsequent years the 30% selection intensity was applied to high protein selections in each grid of the low populations. Equal amounts of seed were bulked each year to form new populations.

Analyses of variance of the data from the replicated trials indicated significant differences due to selection for grain protein, 100 kernel weight, days-to-50%-bloom, and height. Responses for yield, yield per panicle, and protein yield were inconsistent. Kernel number was not significant. Mean of high protein populations decreased although the response was inconsistent. Yield of high populations was decreased slightly but protein yield increased. Increased yield and protein yield of the low populations was attributed to significantly larger kernels. Both populations became later and shorter,

the low populations exhibiting greater response. Grain protein was significantly negatively correlated with yield. Correlations between grain and protein yield were small and insignificant.

Inconsistent correlations were found between grain protein and the remaining characters. Yield exhibited a highly significant positive correlation with protein yield, yield per panicle, and kernel number. The correlations of protein yield with grain protein and yield indicated that selection for protein yield could achieve small positive gains for grain protein and yield. There was no apparent decrease in genetic variability during the selection program.

Additional index words: Recurrent selection, Grain quality, Selection response, Grain yield, Kernel number.

INTRODUCTION

Cultivated grain sorghum [Sorghum bicolor (L.) Moench] is the worlds fourth largest food grain produced. In many areas of sorghum consumption, the indigenous population suffers from a protein deficiency. Production of grain sorghum varieties or hybrids with improved nutritional qualities would thus benefit the human and animal population.

Application of cross-pollinated breeding techniques in sorghum became possible with the discovery of genetic male-sterility (9). Genetic male-sterility is conditioned by a single recessive gene pair and is unaffected by either modifying factors or the type of cytoplasm present. In an intensive breeding program, S_1 progeny testing gives increased variation among lines, and higher heritabilities, so that selection progress should be increased (24). Since more plants may be observed, selection for desirable agronomic traits is more effective. The low amount of outcrossing in sorghum allows open pollinated heads to be treated as selfed heads so S_1 seed is readily obtained for testing.

Doggett (10) postulated that genetic gain in one cycle of selection of alternating female choice (male-sterile) and fertile heads in fields subdivided into grids would be equivalent to two cycles of mass selection using female choice alone. He selected an equal number of heads per grid. Male-steriles were selected for agronomic characters, yield, and gene recombination, while fertile panicles were selected for yield

alone. In a subsequent paper, Doggett (11) evaluated three selection systems (female choice, alternating, and S_1 testing), and proved each to be effective in increasing yield. A recombination generation was effective in all systems in substantially increasing yield. The usefulness of recurrent selection techniques for improved quality is implied, provided selection is properly applied in adequate intensity.

Ross (22) noted that sorghum resembles both naturally self and cross-pollinated species. The basic plant breeding goal in both pollination types is the isolation, accumulation, and perpetuation of favorable genes in a population.

The genetic nature of a grain sorghum random-mating population was evaluated utilizing half-sib, full-sib, and S_1 families by Jan-orn et al. (17). Additive genetic variance was greater than dominance genetic variance. The S_1 families exhibited more total genetic variance than either full-sib or half-sib families. Improvement of highly heritable traits appeared possible with S_1 family selection usually giving a larger single trait response. Eckebil et al. (13) evaluated three random-mating populations of differing genetic background utilizing S_1 heads. The broad based population exhibited more genetic variance than narrower based populations. Genetic correlations indicated a negative relationship between grain protein and other characters studied except days to 50% bloom. Although grain protein heritabilities were high, ranging from 0.71 to 0.80, expected gain for grain protein was low. However, the gain represented significant progress if achieved. The negative relationship between yield and protein indicated that selection for protein yield may be a means to achieve slow gains in both characters.

Kofoed et al. (18) determined that populations have slightly higher mean yields than hybrids in more and less favorable environments. Population crosses exhibited greater overall stability than F_1 hybrids, although all three types displayed a genotype x environment interaction. A population yield level of 5.1% less than the F_1 hybrids indicated improved population yielding ability would allow the extraction of lines comparable in yield with F_1 hybrids.

Ross et al. (23) found divergent selection for grain protein to be significant, actual gains being approximately one-half of the predicted gain. In the experimental material, six populations tracing to the same source but selected for different objectives had strong negative correlations with protein and grain yield. A correlated response between grain protein and grain yield was apparent. Little yield response to protein selection was found with the low protein population outyielding the high protein population in each of two selection cycles. Populations selected for yield exhibited a higher protein yield (protein per hectare) than when selection was for protein. Positive correlations of protein yield with grain protein and grain yield indicated that selection for protein yield should allow for yield increases without decreases in grain protein. Small changes were made in protein content through the selection process illustrating the effectiveness of mass selection for high and low protein levels in grain sorghum.

Investigations into the genetic nature of sorghum grain protein indicated the feasibility of selection for protein in random-mating populations. Malm (21) utilized elite lines of exotic origin crossed onto adapted lines to determine that additive gene action was important for grain protein. Using the ratio of mean squares as a measure

indicated that general combining ability effects were 17.5 times greater than specific combining ability effects. A negative correlation (-0.26) existed between protein and yield.

Liang et al. (19) found the genetic control of protein was by at least two groups of partially dominant genes. Although lower protein expressed some dominance, a moderate heritability (0.43) indicated potential for increased protein. Liang et al. (20) found a significant negative correlation (in excess of -0.50) between protein and yield. Simultaneous improvement appeared difficult. A positive correlation was found only between protein and germination percentage indicating protein selection per se was more effective than selection for other characters as indications of protein.

Collins and Pickett (4,5) found general combining ability and thus additive gene action important for grain yield, grain protein, and grain lysine. Grain protein was negatively correlated with grain yield. Protein ranged from 9.2 to 18.2% and, although high protein was not consistently transmitted between generations, the hybrids of higher protein parents generally possessed higher than average protein.

Crook and Casady (7) found specific combining ability and thus nonadditive gene action significant for protein. The nonadditive genetic variance appeared stable across environments. Heritability, depending on the method of calculation, ranged from 0.75 to 0.90. Wilson et al. (27) found dominance for higher yield and lower protein, high protein being controlled by recessive alleles of low frequency. Highly significant estimates of general and specific combining ability were found for all traits, with specific combining ability and thus dominant genes more important.

Finkner et al. (14) used divergent selection to study the inheritance of grain sorghum grain yield and grain protein. Divergent selection effect was highly significant. Several genes were involved in the dominance or partial dominance of low protein to high protein. Favorable recessive genes appeared to be responsible for high protein. Additive gene action accounted for 82% of the protein genetic variance. Protein was moderately heritable ($h_{ns}^2 = 0.35$) but simultaneous improvement in grain yield and protein appeared difficult due to a significant negative correlation of -0.53.

The classical study in long-term two-way selection studies in crop plants is the Illinois oil and protein corn selection study initiated by Hopkins in 1896. Following 28 generations of selection Winter (28) indicated there was no apparent limit to future progress in the high protein and high oil strain. The low oil line was approaching a physiological limit to further progress and the low protein line had remained fairly constant for the last 20 years. Protein content in the original 'Burr White' cultivar was 10.9% and it had been increased 50% and decreased 23.3%. From an original oil level of 4.7% an increase of 109.8% and a decrease of 67.9% were apparent. Woodworth et al. (29) following 50 generations of selection reported a 19.5% protein content in the high line and 4.9% in the low line. The oil was increased to 15.4% in the high line and decreased to 1.0% in the low line. Although the low protein and high oil lines were still responding to selection, the high protein and low oil lines showed no response for 15 generations. The high oil, as well as the high and low protein lines, retained a considerable amount of genetic variability following two generations of reverse selection. Dudley and Lambert (12) following 65 generations of

selection detected a significant amount of genetic variability in all populations. While indicating that additional progress should be possible in each population, the low oil line may have reached its physiological limit. Small positive correlated responses in percent oil and protein were found with the magnitude varying with selection direction.

Gardner (16) selected for grain yield utilizing a modified mass selection technique, and subsequently formed two advanced populations which outyielded their open-pollinated parent 'Hays Golden' by approximately 40%. Two populations were started from random seed samples - "Control" and "Irradiated". Both populations were treated identically except for the "Irradiated" population having been irradiated by thermal neutrons prior to the first and third selection cycles to induce mutations and increase genetic variability. Yield gains for 13 selection cycles have averaged 2.93% per cycle.

Davis and Crane (8) utilized three cycles of recurrent selection to increase stalk rind thickness and to study the associated response of other characters in a synthetic maize (Zea mays L.) population. Lodging decreased approximately 20% in the population per se and in the topcrosses of the selected populations. The respective yield decline was approximately 20 and 5%.

Allen and Darrah (1) evaluated the effect of three cycles of reciprocal recurrent selection for yield on the nitrogen and plant population responses of two maize hybrids. A variety cross of the two populations yielded 8.5% more per cycle. A significant response to nitrogen and population density was found in the variety cross and the topcross hybrid with the same male parent.

Brim and Burton (2) increased protein percent in two soybean populations an average of 0.59% for each of six cycles utilizing recurrent selection. While selection significantly decreased yield, the change in total protein produced per unit area was nonsignificant. In a subsequent paper, Burton and Brim (3) discussed selection for increased oil in a population segregating for male sterility. On a per cycle average, selection increased oil 0.35%, decreased protein 0.52%, and did not significantly change yield. Realized heritability from the observed response to mass selection was approximately 0.28%.

Vogel et al. (26) found one cycle of divergent selection for in vitro dry matter digestibility (IVDMD) in switchgrass to cause an approximate 6% change in each direction. The increased IVDMD was achieved without yield loss or decreased protein content. Additional changes were expected in subsequent cycles. Realized heritabilities were 0.59 and 0.55 for the high and low IVDMD strains respectively.

Foster et al. (15) applied a 10% divergent selection intensity to three characters (seed weight, plant height, and days to flower) in the inbred sorghum population 'Double Dwarf Yellow Milo 38'. Significant changes were made in each character with response per cycle ranging from 0.25% for early flowering to 3.4% for increased seed weight. Low character heritability (ranging between 0.08 and 0.17) indicated a small amount of present genetic variability. Populations developed utilizing male sterility should possess larger heritability estimates and allow larger predicted gains.

Cortez-Mendoza and Hallauer (6) found 10 generations of divergent mass selection for corn ear length to cause a significant response per cycle per direction. The response to selection for decreased ear length,

was attributed to the directional dominance of genes and unequal gene frequencies in the original population. Selection for shorter ears significantly reduced yield, but selection for longer ears produced no change in yield per plant. No significant changes occurred in cob diameter, kernel row number, and weight of 300 kernels. Ear diameter and kernel depth were significantly decreased as ear length was increased with selection.

The objectives of this research were to determine the effectiveness of divergent selection for grain protein in a grain sorghum random mating population and to determine the effect of divergent selection on associated plant characters.

MATERIALS AND METHODS

The original protein random-mating population was obtained from the Nebraska Agricultural Experiment Station. It depended on the 'antherless' character for random-mating. At the Oklahoma Agricultural Experiment Station the cytoplasmic-genetic male-sterility system was introduced through the use of an A-line, AOK15, a Redlan-like line with higher protein than Redlan. In a subsequent cycle of random mating, seed from a number of lines with high protein was mixed with the planting seed. The high protein lines were identified by screening a large number of advanced pedigree lines from the Oklahoma breeding nursery.

The source material for the current study had undergone several cycles of random mating where the original planting seed consisted of 43% from protein population male-sterile panicles, 43% a composite of the six highest protein fertile panicles and approximately 50 F_3 high protein panicles from crosses to high protein parents and, 14% from AOK15 panicles. The population was advanced by planting a bulk composed of equal amounts of seed from male-sterile, male-fertile, and AOK15 panicles. Male-sterile panicles were identified and tagged at anthesis.

The grain protein population was planted at Lake Carl Blackwell, Oklahoma, in 1978 on a Teller very fine sandy loam (a fine-loamy, mixed, thermic Udic Argiustolls). Rows were 91 cm apart with plants

15 cm apart within a row following thinning. During anthesis, male-sterile panicles were identified and tagged. At harvest, 221 open pollinated fertile panicles were chosen from the population based on favorable agronomic appearance. Each fertile panicle was threshed separately and measured for:

1. Panicle grain yield - weight in grams of the threshed cleaned grain from each panicle.
2. 100 kernel weight - weight in grams of a cleaned sample of good whole kernels representative of an entire sample.
3. Kernel number - total number of kernels on each panicle as calculated by the formula:

$$(\text{panicle grain yield} \times 100) / 100 \text{ kernel weight}$$
4. Grain protein - protein percent obtained by the Udy dye binding procedure (25).
5. Protein yield - total amount of protein (expressed in grams) produced by each plant as calculated by the formula:

$$(\text{panicle grain yield} \times \text{grain protein}) / 100.$$

Thirty percent of the analyzed fertile samples from each end of the population distribution for grain protein were selected to form two new grain protein populations - high (H) and low (L). Equal amounts of seed (approximately 4 g) from each fertile selection were bulked to form the new populations.

In subsequent years (1979, 1980, and 1981) grids were imposed on the experimental area and plants were chosen within the grids. The utilization of 'grids' divided the experimental area into smaller plots from which the plants were chosen. The experimental procedure

was identical for each population. The 1979 experimental area was on a Port Loam soil (a fine-silty, mixed, thermic Cumulic Haplustolls) at Lake Carl Blackwell, Oklahoma. In 1980 and 1981 the experimental area was at Perkins, Oklahoma, on a Teller loam soil (a fine, loamy, mixed, thermic Udic Argiustolls).

The 13.7 x 68.6 m experimental area was divided into three 13.7 x 22.9 m plots prior to planting. To prevent pollen movement between populations the center plot was a corn fill. The other plots were subdivided into nine 4.6 x 7.6 m plots (Figure 1) and sampled for soil nutrients. An additional sample was taken from the entire 13.7 x 22.9 m area. Based upon the soil test recommendation, ammonium nitrate (34-0-0) fertilizer was applied broadcast preplant at a rate of 56 kg/ha in 1979 and at a rate of 78 kg/ha in 1980 and 1981. In 1980, 560 kg/ha of hydrated lime was broadcast to alleviate a low soil pH. Water was applied by sprinkler irrigation as needed in 1980 and 1981. Rows were 91 cm apart, and the within row plant spacing was approximately 15 cm. The ideal plant stand was 250 plants per grid.

At anthesis, male-sterile panicles were identified and tagged. Following maturation, the tagged male-sterile panicles and approximately 25 selected male-fertile panicles were harvested from each grid. After harvest, panicles chosen from the populations were handled as previously described, except the 30% selection intensity was applied within each grid. Choice of parents for each new population alternated each year between male-fertile and male sterile panicles.

Two studies, one composed of population head rows and one of population bulks, were undertaken at Perkins, Oklahoma, in 1981 to determine the effectiveness of divergent selection for grain protein. Seven populations were analyzed in each study: Base, H and L (1978), HH and LL (1979) and HHH and LLL (1980). From the base source population, initial high (H) and low (L) grain protein selections were made in 1978. Populations HH and LL represent second cycle selections, and HHH and LLL represent third cycle selections. Selections for a given cycle were from the populations (high or low) formed by compositing equal amounts of seed from the preceding cycle selections. In subsequent discussions, the populations will be referred to according to the above designations.

The population head row study was composed of the base population and the selected fertile panicles following grain protein analysis from each improved population. Each selection was present in two progeny rows, and the base population in 8 progeny rows in a completely randomized design. In the population bulk study, the base population and fertile seed composites (selected after grain protein analysis) for each improved population were planted in a randomized complete block design with 10 replications. The experimental area was a Teller loam soil (a fine-loamy, mixed thermic Udic Argiustolls).

Plots were 4.57 m long and 0.91 m apart. The intra-row plant spacing was approximately 15 cm. During anthesis, days-to-50%-bloom were noted for each row and male-sterile panicles were identified and tagged. Days-to-50%-bloom is a relative measure of maturity and is

that time when approximately 50% of the plants are blooming. Prior to harvest, rows were observed for plant height, panicle exertion, plant color, and presence or absence of awns.

Following maturity a 1 m section of row was harvested and weighed (in grams). Sterile panicles were replaced with fertile panicles selected at random from outside the measured area. This was done because sterile panicles yield less and produce more grain than fertile panicles. Grain samples (2 to 3 branches) were selected from the middle of each fertile panicle in the row and threshed in bulk. A common threshing percentage was calculated from a random sample of rows by dividing threshed grain weight by the panicle weight at harvest and adjusting for moisture. Yield was calculated by multiplying the panicle gram weight at harvest by the threshing percentage and converting to quintals/hectare. The bulked sample of all fertile panicles was used to obtain 100 kernel weight (in grams), grain protein (expressed as a percent), kernel number, and protein yield (in quintals/hectare).

Data for all agronomic and quality traits from both experiments were subjected to an analysis of variance. An F-test was utilized to determine significance of the source components. Significant differences between means in the population bulk study were determined with a 0.05 level LSD. Phenotypic correlations were calculated for all traits in both experiments. Estimates of broadsense heritability were calculated for all traits in both experiments.

RESULTS AND DISCUSSION

Results of the analyses of variance for the population head rows are found in Table 1. Divergent selection for grain protein resulted in a nonsignificant population x selection interaction for the population head rows indicating the populations changed in the same direction and in the same magnitude as the selections. Selection did produce changes in either direction as evidenced by a highly significant selection mean square. Divergent selection for grain protein did produce a significant selection response for yield, yield per panicle, and 100 kernel weight indicating that high and low selections were different for these characters. There was no significant change in kernel number as a result of selection.

A significant population x selection interaction for protein yield indicated the character did not change in the same direction or the same magnitude as grain protein selection. Due to the nature of the characteristic the change in protein yield is a result not only of selection for grain protein but also the associated response to such selection in yield. There were no significant differences among populations and selections for days-to-50%-bloom. Height response to selection was indicated by highly significant population x selection and selection terms.

Analyses of variance for the replicated bulk study are presented in Table 2. Study of the table reveals that divergent selection for grain protein resulted in a significant selection response. This indicated that significant differences for grain protein existed among the high and low populations. Among the other quality and yield related traits, a significant selection response was noted only for 100 kernel weight. This indicated kernel size changed with grain protein selection. Lack of change in the yield related and quality traits is encouraging since selection for higher grain protein often produces negative responses in these characters. Significant differences were found in days-to-50%-bloom for population and selection, and in height for population and population x selection.

Performance of the population head rows for measured traits (Table 3) is expressed as a mean in each population. The mean is the average performance of all rows resulting from single panicle selections in a particular year and population. Due to an unequal number of entries composing each population an LSD was not calculated. It is possible to observe the general trends. Divergent selection for grain protein produced inconsistent trends for the high and low populations. Yield decreased in the high population and increased in the low population although response was inconsistent. Protein yield did not change following the initial selection in the low populations. Response in the yield related traits of 100 kernel weight, yield per panicle, and kernel number has been inconsistent. Selection has resulted in both the high and low populations becoming later, as measured by days-to-50%-bloom, with the low populations exhibiting greater response.

Performance of the population bulks for yield and quality characteristics is shown in Table 4. Each high population contains significantly more protein than the base. Although significant differences were not indicated between the three high populations, a positive response was achieved with each selection cycle. Grain protein content decreased in the low populations although response was less than for high protein. While the response was inconsistent, the LL population was significantly different from the base population.

The genetic control of grain protein is governed by two groups of genes, dominant genes conditioning low protein and favorable recessive genes conditioning high protein. Dominant gene control of low protein is consistent with its positive relationship with high yield, also controlled by dominant genes. Greater response for high protein would indicate that favorable recessive genes governing character expression accumulate at a faster rate than do dominant genes governing expression of low protein.

An inverse relationship exists between high protein and high yield. An increase in quality (grain protein) decreases yield, and the amount of protein produced per acre (protein yield). Significant yield differences were found only when comparing the base and LLL population, and the H and LLL population. While yield in the high populations has not been consistent, the yield of the HH and HHH populations was actually higher than that of the base.

The yield response could result from the selection criteria utilized in the population improvement program. Male-sterile panicles were selected for genetic recombination in addition to high or low

protein. Fertile panicles were selected for phenotypic expression of favorable agronomic traits, i.e. a good plant of medium height with a large full panicle and no apparent disease or insect problems. The 30% selection intensity was applied to plants within a grid for high or low grain protein, respectively. Yield was involved in the selection criteria for population improvement.

Total protein production, or protein yield, is largely dependent on yield for its value. A yield decrease in higher protein lines usually results in the same or less total grain protein production than low protein lines with higher yield. Protein yield of the high population has changed with the corresponding yield changes. The low population protein yield increase reflects the steady yield increase. However, the high and low populations were not significantly different. Only the HH population differed significantly from the base. This population produced the highest yield of the three high populations.

Agronomic characteristics of the population bulks are also shown in Table 4. There was little change in 100 kernel weight for the high populations. With each selection cycle the 100 kernel weight for the low populations increased. Each low population possesses significantly larger kernels than the corresponding high population. The LL and LLL populations possess significantly larger kernels than the base. The consistent increase in yield and yield per panicle of the low populations, each population yielding more per panicle than the prior cycle, is due to a slow, steady increase in kernel size. This consistent increase is a plant breeding gain in the selection program. Response of kernel number to grain protein selection has been inconsistent. Yield per panicle for high protein lines has been inconsistent although

each is less than the base. The only significant yield difference is between the two third cycle populations - HHH and LLL.

Divergent selection delayed the days-to-50%-bloom of all populations compared to the base. Change in the low population is consistently later with each selection, and each low population is significantly later than the base. Height response to selection has been inconsistent although both high and low selections are shorter than the base.

Phenotypic correlations calculated from the head row data (Table 5) indicated a significant negative relationship between grain protein and yield. Higher correlation values for the low populations were expected. Grain protein has shown no consistent positive or negative correlation with protein yield. Inconsistency as to sign indicates the feasibility of simultaneous improvement. Significant positive correlations in the low populations between grain protein and 100 kernel weight were expected due to the steady increase in kernel size. The yield related traits of yield per panicle and kernel number were usually negatively correlated with grain protein. Correlations with days-to-50%-bloom were inconsistent and of small magnitude, while height is negatively correlated with grain protein.

The correlations between the latter two traits were unexpected as both showed a fairly consistent response to protein selection. Magnitude of the correlations supports the data in Table 3, the low populations exhibiting a more positive relationship with the traits. Apparently, sorghum will produce more grain protein with material of intermediate height and maturity.

Positive correlations between grain yield and the yield related traits of protein yield, yield per panicle, and kernel number were highly significant. This was not unexpected since yield is a component used in calculating each trait. Correlations with 100 kernel weight were small and consistently negative for the low population. An insignificant relationship, usually negative, exists between grain yield and days-to-50%-bloom while a positive relationship usually exists between yield and height.

Since the components used in calculating protein yield, yield per panicle, and kernel number are similar the large significant positive correlations would be expected. The correlations with 100 kernel weight and days-to-50%-bloom are very small and, except for one case, nonsignificant. Height is usually positively correlated with protein yield although the value varies considerably with selection cycles.

Phenotypic correlations between population bulk traits are presented in Table 6. A significant negative correlation between grain protein and yield existed only in the HHH population. This provides supporting evidence that except in the one case on appreciable yield decline has followed selection for increased protein. While protein has become more negatively correlated with protein yield and the remaining traits, there appears to be potential for simultaneous improvement. A large significant positive correlation between yield and protein yield was expected because of the way yield was calculated. The large positive correlations between yield and yield per panicle, and between protein yield and the yield related characters of yield per panicle and kernel number were expected because of the way the traits were calculated. Yield per panicle and kernel number (not shown)

were also positively correlated. The yield and protein yield correlations with 100 kernel weight, days-to-50%-bloom, and height were inconsistent as to sign and, with one exception, nonsignificant. This indicates a lack of consistent response to the selection process.

Estimates of broadsense heritability are shown in Table 7. Calculated from variance components, such estimates are probably inflated from the true values. Protein is a trait of moderate heritability and appears to be easily improved in a breeding program. Yield appears to be of low to moderate (0.10-0.47) heritability and should be closely watched to maintain or increase its present level. Of the other yield related traits, 100 kernel weight exhibited high heritability. This is consistent with its constant performance in the high populations, and increased performance in the low populations. Protein yield is a trait of very low (0.03) to moderate (0.38) heritability. Due to the nature of the relationship between protein yield and yield the heritability of protein yield was expected to resemble that of yield. This did not occur. Despite its low heritability, protein yield may be the proper trait to select for increased grain protein and yield.

The estimated heritability of yield per panicle and kernel number varied considerably with selection cycles and showed no consistent pattern in relation to yield. However, these are secondary characters, being selected for in grain yield. The heritability for days-to-50%-bloom and height exhibited stability over cycles and appears to be highly heritable.

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Table 1. Analysis of variance of population head row traits.

Source	df	Mean Squares							
		Grain protein	Yield	Protein yield	Yield per panicle	100 Kernel weight	Kernel number	Days-to-50%-bloom	Height
Population (P)	3	1.46	182.91*	1.66	188.80	0.15	232190.29	25.98*	57.15
Selection (S)	1	200.26**	1788.09**	0.17	1016.03**	2.24**	1113.26	380.84**	2009.56**
P x S	2	1.58	127.14	2.57	375.68	0.02	368197.71	16.07	1643.78**
Error	400	0.94	57.35	0.74	136.78	0.12	173750.93	8.57	234.20

*, ** Significant at the 0.05 and 0.01 levels, respectively

Table 2. Analysis of variance of population bulk traits.

Source	df	Mean squares							
		Grain protein	Yield	Protein yield	Yield per panicle	100 Kernel weight	Kernel number	Days-to-50%-bloom	Height
Reps	9	0.82	112.60**	1.67*	358.83**	0.04	2233001.80*	2.55	88.52
Populations (P)	3	0.21	34.44	0.61	11.29	0.06	8108.29	14.04*	230.26*
Selection (S)	1	28.84**	95.74	0.05	449.80	1.29**	7116.54	109.35**	247.74
P x S	2	0.77	9.89	0.34	50.66	0.05	50806.69	9.65	261.61*
Error	54	0.45	32.37	0.51	129.87	0.06	187630.21	4.14	76.91

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 3: Mean performance and standard errors of population head rows for measured traits.

Population	Grain protein	Yield	Protein yield	100 Kernel weight	Yield per panicle	Kernel number	Days-to- 50%-bloom	Height
	%	q/ha		g	g			cm
HHH	13.47 \pm 0.04	33.1 \pm 0.87	4.4 \pm 0.12	2.84 \pm 0.04	55.8 \pm 1.38	1987 \pm 48.53	62.3 \pm 0.26	109.7 \pm 1.30
HH	13.23 \pm 0.12	37.0 \pm 0.90	4.8 \pm 0.11	2.78 \pm 0.04	57.4 \pm 1.33	2095 \pm 48.99	62.0 \pm 0.30	116.1 \pm 1.62
H	13.31 \pm 0.12	32.9 \pm 0.85	4.3 \pm 0.10	2.83 \pm 0.03	54.0 \pm 1.43	1921 \pm 48.73	61.9 \pm 0.27	114.9 \pm 1.84
Base	12.45 \pm 0.13	38.5 \pm 4.19	4.8 \pm 0.52	2.99 \pm 0.06	62.0 \pm 3.24	2078 \pm 104.08	60.8 \pm 0.67	113.3 \pm 2.63
L	12.13 \pm 0.08	38.0 \pm 0.73	4.6 \pm 0.09	2.97 \pm 0.03	58.0 \pm 1.24	1968 \pm 43.21	63.1 \pm 0.33	109.2 \pm 1.44
LL	11.79 \pm 0.08	39.1 \pm 0.78	4.6 \pm 0.09	2.91 \pm 0.03	57.0 \pm 0.97	1981 \pm 37.17	64.0 \pm 0.28	105.4 \pm 1.21
LLL	11.85 \pm 0.08	38.7 \pm 0.83	4.6 \pm 0.09	3.02 \pm 0.03	61.9 \pm 1.43	2070 \pm 51.19	64.9 \pm 0.34	112.9 \pm 1.17

Table 4. Mean performance of population bulks for measured traits.

Population	Trait							
	Grain protein	Yield	Protein yield	100 Kernel weight	Yield per panicle	Kernel number	Days-to-50%-bloom	Height
	%	q/ha		g	g			cm
HHH	13.84	26.9	3.7	2.61	42.3	1637	60.3	107.4
HH	13.81	28.2	3.9	2.59	45.5	1777	59.7	112.0
H	13.39	24.9	3.4	2.60	44.5	1698	61.2	105.9
Base	12.84	25.8	3.3	2.65	46.1	1747	59.6	114.3
L	12.43	28.0	3.5	2.78	47.5	1725	62.3	103.4
LL	12.08	29.1	3.5	2.94	49.9	1694	63.3	100.1
LLL	12.37	30.4	3.7	2.96	51.4	1757	63.7	109.7
LSD .05	0.50	4.2	0.5	0.18	8.5	324	1.5	6.6

Table 5. Phenotypic correlations in head rows.

Population	Trait						
	Yield	Protein yield	100 Kernel weight	Yield per panicle	Kernel number	Days-to-50%-bloom	Height
Grain protein							
HHH	-0.20*	0.04	-0.13	-0.10	-0.04	-0.07	-0.04
HH	-0.40**	-0.12	-0.34**	-0.32**	-0.14	0.15	-0.22**
H	-0.49**	-0.19*	-0.52**	-0.36**	-0.11	-0.16	-0.23**
Base	0.03	0.11	-0.18	0.11	-0.02	-0.36	-0.02
L	-0.28**	0.06	0.03	-0.08	-0.09	-0.09	-0.09
LL	-0.36**	-0.06	0.18*	0.01	-0.12	0.16	-0.13
LLL	-0.26**	0.04	0.30**	0.13	0.03	0.06	-0.09
Yield							
HHH		0.97**	-0.03	0.54**	0.55**	0.06	-0.00
HH		0.95**	0.14	0.62**	0.52**	-0.14	0.32**
H		0.94**	0.10	0.59**	0.56**	0.21*	0.34**
Base		0.97**	-0.07	0.34	0.39	-0.03	0.01
L		0.94**	-0.04	0.55**	0.55**	-0.03	0.11
LL		0.59**	-0.06	0.39**	0.44**	-0.10	0.17**
LLL		0.94**	-0.01	0.49**	0.46**	-0.10	0.05
Protein yield							
HHH			-0.07	-0.07	0.52**	0.55**	0.04
HH			-0.03	0.58**	0.53**	-0.11	0.25**
H			0.08	0.53**	0.58**	-0.20*	0.30**
Base			-0.08	0.33	0.38	-0.01	0.01
L			-0.03	0.53**	0.54**	-0.07	0.08
LL			-0.09	0.44**	0.44**	-0.06	0.14
LLL			-0.09	0.56**	0.49	-0.09	0.01

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 6. Phenotypic correlations in population bulks.

Trait and Population	Trait						
	Yield	Protein yield	100 Kernel weight	Yield per panicle	Kernel number	Days-to-50%-bloom	Height
Grain protein							
HHH	-0.74*	-0.56	-0.53	-0.39	-0.50	-0.58	0.22
HH	-0.49	-0.27	-0.52	-0.21	-0.01	0.07	-0.08
H	0.33	0.51	0.13	0.28	0.29	0.39	-0.41
Base	-0.24	0.00	-0.09	-0.14	-0.08	-0.62	-0.34
L	0.12	0.22	0.28	0.10	0.01	0.16	0.62
LL	-0.36	-0.14	0.23	-0.16	-0.26	-0.23	-0.14
LLL	-0.62	-0.49	0.18	-0.38	-0.27	-0.14	-0.09
Yield							
HHH		0.97**	0.08	-0.68	0.53	0.00	-0.22
HH		0.97**	0.07	0.81**	0.70*	0.48	0.19
H		0.98**	0.35	0.71*	0.70	0.52	-0.35
Base		0.97**	0.38	0.75*	0.58	-0.47	-0.44
L		0.99**	-0.20	0.94**	0.92*	-0.56	0.30
LL		0.97**	0.42	0.75*	0.68*	0.46	0.60
LLL		0.99**	-0.47	0.91**	0.85**	-0.47	-0.48
Protein yield							
HHH			-0.08	0.73*	0.66*	-0.22	-0.20
HH			-0.06	0.85**	0.79**	0.54	0.18
H			0.35	0.71*	0.70*	0.56	-0.40
Base			0.36	0.73*	0.58	-0.64*	-0.53
L			-0.16	0.93**	0.91**	-0.53	0.36
LL			0.50	0.76**	0.67*	0.45	0.54
LLL			-0.50	0.94**	0.89**	-0.55	-0.51

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 7. Estimates of broad sense heritability in six sorghum populations calculated from variance components.

Population	Trait							
	Grain protein	Yield	Protein yield	100 Kernel weight	Yield per panicle	Kernel number	Days-to-50%-bloom	Height
HHH	0.43	0.19	0.10	0.78	0.09	0.07	0.37	0.68
HH	0.67	0.38	0.26	0.76	0.43	0.39	0.50	0.64
H	0.67	0.17	0.05	0.78	0.21	0.08	0.59	0.71
L	0.29	0.47	0.39	0.51	0.35	0.32	0.47	0.73
LL	0.60	0.10	0.03	0.54	0.24	0.36	0.53	0.60
LLL	0.41	0.21	0.08	0.70	0.01	0.11	0.32	0.58

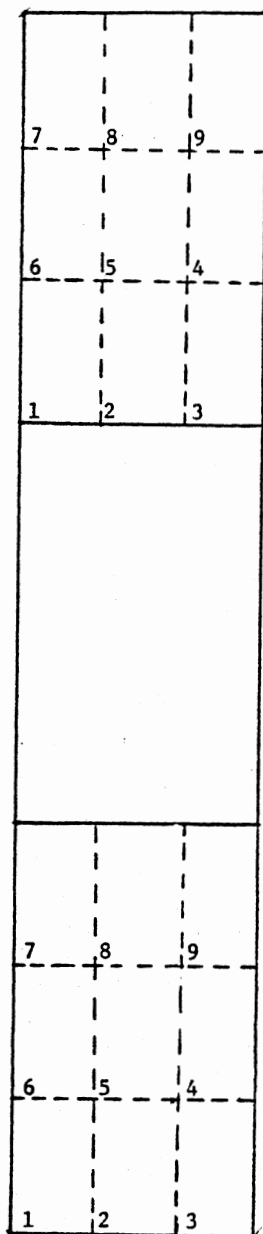


Figure 1. Diagram of field plot design for high and low grain protein populations in 1979, 1980, and 1981.

PART II

EFFICIENCY OF GARDNER'S GRID SYSTEM

Divergent Selection for Grain protein in a
Grain Sorghum [Sorghum bicolor (L.) Moench]
Random-Mating Population

II. Efficiency of Gardner's Grid System

ABSTRACT

A divergent selection study for grain protein was initiated in a grain sorghum [Sorghum bicolor (L.) Moench] random-mating population. High protein lines were composited and allowed to random mate to form the base population. The initial high and low protein populations were formed by applying a 30% selection intensity to each end of the population distribution from the base population. During subsequent years the 30% selection intensity was applied to high protein selections in each grid of the high population and to low protein selections in each grid of the low population. Equal amounts of seed were composited from individual selections each year to form new populations.

The analysis of variance indicated that grids significantly enhanced the selection process in 1979 and 1980. Little benefit was found in 1981 selections. Comparison of the predicted efficiency of grid vs. no grid selection for fertile panicles indicated an increased response of up to 3.6% for grids. Predicted selection efficiency for sterile panicles was increased up to 13.8% by the use of grids. Grids did not significantly enhance selection in the 1981 high population and contributed only 0.7% in the 1981 low population for sterile

panicles.

Additional index words: Recurrent selection, Selection response,
Grain quality.

INTRODUCTION

Gardner (2) discussed the division of field plots into several small areas with the selection intensity being applied to each "grid" independent of the other "grids". The main advantage of this system was increased selection efficiency due to reduction of the environmental effect on the plants. Selection was practiced with two populations, "Control" and "Irradiated", of the open-pollinated corn variety "Hays Golden". Both populations were treated identically with the exception of the "Irradiated" population being subjected to thermal neutrons prior to the first and third selection cycles. After four selection cycles for yield the "Control" population achieved a total gain of 22.8% with no evidence of decreasing additive genetic variance or rate of gain. Yield gain in the "Irradiated" population was 20.2% despite an initial yield decrease due to the irradiation treatment.

After six generations of selection Lonnquist et al. (5) showed significantly increased productivity in the "Control" and "Irradiated" populations, 12.7 and 10.9%, respectively over the original population. No decline in additive genetic variance was apparent. Following 14 generations Gardner (3) realized a more or less linear trend of 2.93% per cycle per yield gain. Like earlier reports, there was no appreciable decline in additive genetic variance.

Johnson (4) divided a white dent corn plot into 300 plant subplots. Mass selection was practiced for yield. A total gain of 33% or 8.25% per cycle was realized after three cycles of selection.

Working with cotton Meridith and Bridge (6) reported the effectiveness of Gardner's system on a crop other than corn. A randomized complete block design with 8 replications was used to analyze the relationship between F_2 and selected F_3 performance. Each plot in each replication was considered a grid with 10 F_2 progenies visually selected for yield. This procedure resulted in an F_3 yield increase of 5.7%.

Verhalen et al. (8) conducted an experiment to select for increased and decreased fiber length in a field of 'Westburn' cotton which was divided into three equal sized areas. Selection intensity was 10%. Grid reduced phenotypic variation by 22% and selection differentials by 11 to 14%, while increasing selection responses 20 to 35%. Selection utilizing grids produced estimated "realized" or narrow-sense heritabilities 41 to 52% higher than selection without grids. The method appeared particularly useful with traits of low heritability which show small inconsistent differences.

Burton (1) applied "recurrent restricted phenotypic selection" on 'Pensacola' bahiagrass. Following division of the experimental area into 25-plant square plots, selection was practiced for increased forage yield. Four cycles of selection increased yield 17.7% over the commercial check. Use of the system with a narrow-gene population (which had been previously selected) and a wide-gene population (which had not been previously selected) resulted in progress at the rate of approximately 2 and 6%, respectively, per 2-year cycle.

Redden and Jensen (7) divided wheat and barley plots into groups of 10 or 20 plants, respectively. The F_2 and F_3 generations of one cross each of spring wheat and spring barley with two cycles of mass

selection under two mating systems were studied. Selection was practiced for the number of green tillers prior to head emergence. Mean response in barley per cycle compared to the unselected check was 6.3%, while in wheat the response was 10.3% per cycle. Comparison of the selfed versus the hybrid selection series indicated greater response for the hybrid series. Selections in each cycle were random mated to form the hybrid selection series. Results showed mass selection with concurrent random-mating to be a useful breeding strategy in self-pollinated crops.

MATERIALS AND METHODS

This experiment was conducted in conjunction with the population improvement program described in the previous paper. A divergent selection study for protein was initiated on a Port Loam soil (a fine-silty, mixed, thermic Cumulic Haplustolls) in 1979 and continued on a Teller loam soil (a fine-loamy, mixed thermic, Udic Argiustolls) in 1980 and 1981. From the base population, a 30% selection intensity was applied for selected heads at each end of the population distribution for protein. Selections at the upper end of the distribution were bulked to form the initial high (H) population while selections at the lower end of the distribution were bulked to form the initial low (L) population. During subsequent years, the 30% selection intensity was applied to high protein selections in each grid of the high population and to low protein selections in each grid of the low population. Further details concerning the initial population, selection criteria, and experimental methods may be found in the previous paper.

To evaluate the effectiveness of Gardner's grid system for grain protein selection in grain sorghum statistical analyses were conducted of the high and low populations of 1979, 1980, and 1981. Six populations were involved in the analyses - H and L (1979), HH and LL (1980), and HHH and LLL (1981). The analyses of variance were conducted separately on fertile and sterile panicles from each population

to determine if stratification of the field into grids exerted a significant effect on the selection process. The within grid mean square (σ_w^2) was used as the error term in an F-test with the among grid mean square ($\sigma_w^2 + n\sigma_B^2$).

The predicted efficiency (E) of selection with grids versus selection over grids was estimated by the equation:

$$E = \frac{R_G}{R_N} = \sqrt{(\sigma_w^2 + \sigma_B^2) / \sigma_w^2}$$

where R_G represents the response with grids and R_N the response with no grids. The phenotypic variance is represented by σ_w^2 and $\sigma_w^2 + \sigma_B^2$ for within and over grids, respectively. A value of 1.0 indicates grids did not enhance the selection process. A value greater than 1.0 indicates grids were more effective by the amount greater than 1.0.

Selection differentials for fertile and sterile panicles from each population were calculated as the mean of the selections minus the population mean. Calculations were done within and over grids at two selection intensities, 10 and 30%.

RESULTS AND DISCUSSION

The utilization of two selection methods (with grids and over grids) resulted in the selection of particular plants by only one method. Since there were plant selections not in common with both methods, a breeder should be able to determine which method would provide greater response in a breeding program. The contribution of each grid to a particular selection method varied with the year, population, and panicle type (fertile or sterile) selected.

Significance of an F-test in an analysis of variance indicated whether grids produced a significant effect. The error term is the within grid component (σ_w^2) and contains both genetic and environmental variation. The between grid component ($\sigma_w^2 + n\sigma_B^2$) contains mostly environmental variation.

Results of the analyses of variance for plant selections made in 1979, 1980, and 1981, are found in Table 1. For purposes of the experimental fertile and sterile selections within a population were analyzed separately. Data analysis in this manner will give slightly different results than a combined fertile-sterile analysis for a particular population.

In eight of the twelve cases investigated grids exerted a significant effect on the selection process as indicated by significance of the F-test. A significant effect was not found for selection of 1980 high fertiles, 1981 high fertiles and high steriles, and 1981 low steriles. When grids produced a significant response the between grid

component was at least 4% of the phenotypic variation for the whole experiment. With phenotypic variance reduced by at least 4% selection should have been more effective utilizing grids.

The major benefit expected of grids is reduced environmental effect. This would allow for more accurate sampling of the genetic potential of the experimental material. As the micro-climate of the experimental area becomes less variable the benefits of imposing and selecting within grids are reduced. A general assessment of the environmental conditions involved in the three years of testing may help in interpreting the results. Material in 1979 was planted in an area where sorghum had not been recently grown. Planting at an acceptable time, there was temperature and moisture stress during the growing season. In this environment grids were effective for all selections.

Experimental material in 1980 was planted late in an area where sorghum had not been grown. The soil had a lower than desired pH and the ambient air temperature was higher than normal. Water was applied by sprinkler irrigation when needed to insure adequate moisture. In this environment, grids were effective in three of four selections. The 1981 experimental site was the same as the 1980 site. Planting time was at an optimum time with environmental stress during the growing season almost negligible. Grids were effective in one of four selections.

Greater selection efficiency indicates grids enhanced the selection progress (Table 2). In ten of twelve examples grids were more efficient than straight mass selection. Increased effectiveness ranged from 0.7% for the 1981 low steriles to 13.8%

for the 1979 low steriles. For 1981, the selection in grids for high protein (high panicle selection), grids provided no greater response. than straight mass selection. This supported the analysis of variance for 1981 fertile selections. Two of the calculated efficiencies (1980 high fertiles and 1981 low steriles) appeared to conflict with the analyses of variance by showing greater selection efficiency's with grids. This will occur occasionally due to the nature of the calculation, $\sqrt{\frac{\text{Between grid mean square}}{\text{Within grid mean square}}}$.

Selection differentials for two selection intensities (10 and 30%) and two selection methods (with grids and over grids) are shown in Table 3 for fertile panicles and in Table 4 for sterile panicles. As expected, selection differentials were larger at the 10% selection intensity. Use of the more stringent selection intensity should achieve a faster rate of progress.

In 10 of the 12 populations investigated the total variance with grids was smaller than the total variance over grids. The selection differentials should then be smaller with grids. Fertile panicles (Table 3) confirmed this expectation, with all selection differentials smaller with grids than over grids. Selection differentials for sterile panicles (Table 4) were smaller with grids for all comparisons at both selection intensities. More progress should be made by selection with grids rather than over grids.

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Table 1. Results of grid vs. no-grid analysis of variance for 1979, 1980, and 1981 grain protein selections in two sorghum populations.

Source	Mean squares			
	High		Low	
	Fertile	Sterile	Fertile	Sterile
1979				
Between grids	3.669*	5.636**	2.808**	12.384**
Within grids	1.843	1.338	0.945	1.526
1980				
Between grids	1.868	4.917**	3.159**	5.645**
Within grids	1.487	2.047	1.224	1.524
1981				
Between grids	2.350	1.489	2.986**	1.710
Within grids	3.699	2.620	1.163	1.511

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 2. Predicted efficiency of grain protein selection with grids in two sorghum populations.

Year	Population	Fertile Panicles	Sterile Panicles
1979	High	1.019	1.076
	Low	1.036	1.138
1980	High	1.007	1.036
	Low	1.032	1.097
1981	High	1.000	1.000
	Low	1.030	1.007

Table 3. Selection differentials for fertile panicles from six sorghum populations with two selection intensities and two selection methods.[†]

Year and Population	10% Selection intensity		30% Selection intensity	
	With grids	Over grids	With grids	Over grids
1979				
High	2.50	2.70	1.52	1.56
Low	1.63	1.93	1.09	1.17
1980				
High	2.12	2.23	1.38	1.51
Low	1.66	1.75	1.25	1.27
1981				
High	3.69	4.13	2.17	2.34
Low	1.50	1.68	1.12	1.21

[†] Selection differential for base population selections was 2.83.

Table 4. Selection differentials for sterile panicles from six sorghum populations with two selection intensities and two selection methods.†

Year and Population	10% Selection intensity		30% Selection intensity	
	With grids	Over grids	With grids	Over grids
1979				
High	1.84	2.18	1.17	1.40
Low	2.02	2.18	1.37	1.60
1980				
High	2.47	2.71	1.56	1.60
Low	1.70	2.08	1.20	1.45
1981				
High	2.47	2.71	1.75	1.78
Low	1.90	2.19	1.32	1.44

† Selection differential for base population selections was 2.83.

PART III

CONCLUSIONS

CONCLUSION

Population improvement by recurrent selection appears to be a suitable technique for divergent grain protein selection in grain sorghum. Although the genetic response was not consistent between generations the level of grain protein in the high populations was increased over the base. The low protein populations showed decreased levels of grain protein following selection. Yield response in the high populations was inconsistent and nonsignificant. Increased yield in the low populations was a result primarily of significantly larger kernels. Protein yield exhibited an inconsistent positive response in the high populations, and a slight positive response in the low populations.

Selection for high and low protein both resulted in shorter populations which were later maturing than the base population. The low protein populations expressed these tendencies to a greater degree than the high populations. Yield per panicle changed in a similar fashion as yield, with inconsistent response in the high populations and a consistent increase in the low populations. The kernels per panicle were not changed significantly with selection.

Selection utilizing grids appeared to be a positive force in the selection program. While the effect of grids was greater early in the program, there was some advantage throughout. When grids were more efficient, their effectiveness varied from 0.1 to 14%. Since total

variance with grids was smaller than total variance over grids in all but two populations, selection differentials should have been smaller with grids. This was the situation in all of the investigated situations. Greater progress should be made by selection with grids than by selection over grids.

APPENDIX

(TABLES 1-4)

Table 1. Phenotypic correlations in population head rows.

Trait and Population	Trait			
	Yield per panicle	Kernel number	Days-to- 50%-bloom	Height
100 Kernel weight				
HHH	0.24**	-0.29**	0.32**	0.23**
HH	0.23**	-0.34**	0.19*	0.19*
H	0.29**	-0.18*	0.09	0.37**
Base	0.29	-0.14	0.47	-0.74*
L	0.17	-0.26**	0.16	0.20*
LL	0.19*	-0.46**	0.21*	0.07
LLL	0.04	-0.32	0.32	0.02
Yield per panicle				
HHH		0.85**	0.32**	-0.11
HH		0.82*	0.01	0.19*
H		0.88*	0.01	0.32**
Base		0.90**	0.34	-0.23
L		0.90**	0.11	0.05
LL		0.77**	0.08	0.11
LLL		0.93**	0.08	-0.05

Table 1. (cont.) Phenotypic correlations in population head rows.

Trait and Population	Trait	
	Days-to- 50%-bloom	Height
Kernel number		
HHH	0.16	-0.23
HH	-0.12	0.08
H	-0.04	0.16
Base	0.13	0.06
L	0.05	-0.04
LL	-0.06	0.06
LLL	-0.04	-0.07
Days-to-50%-bloom		
HHH		0.05
HH		-0.20*
H		-0.22*
Base		-0.22
L		-0.14
LL		-0.15
LLL		-0.06

*,** Significant at the 0.05 and 0.01 levels, respectively.

Table 2. Phenotypic correlations in population bulks.

Trait and Population	Trait			
	Yield per panicle	Kernel number	Days-to-50%-bloom	Height
100 Kernel weight				
HHH	0.01	-0.50	0.52	0.23
HH	0.01	-0.40	0.04	0.57
H	0.47	0.24	0.82*	0.35
Base	0.12	-0.23	0.21	-0.53
L	-0.10	-0.34	0.69	0.30
LL	0.35	0.06	0.59	0.19
LLL	-0.66*	-0.79**	0.67*	0.53
Yield per panicle				
HHH		0.86**	-0.29	-0.50
HH		0.91**	0.53	0.17
H		0.97**	0.80**	0.18
Base		0.94**	-0.46	-0.12
L		0.97**	-0.52	0.36
LL		0.95**	0.46	0.83**
LLL		0.98**	-0.69*	-0.64

Table 2. (cont.) Phenotypic correlations in population bulks.

Trait and Population	Trait	
	Days-to- 50%-bloom	Height
Kernel number		
HHH	-0.54	-0.54
HH	0.47	-0.09
H	0.65*	0.07
Base	-0.51	0.07
L	-0.65	0.27
LL	0.30	0.81**
LLL	-0.74*	0.65*
Days-to-50%-bloom		
HHH		-0.24
HH		0.21
H		0.36
Base		0.44
L		-0.09
LL		0.45
LLL		0.52

*,** significant at the 0.05 and 0.01 levels, respectively.

Table 3. Partition of total variance into its between and within grid components for 1979, 1980, and 1981 selections.

Source	Fertile		Sterile	
	High	Low	High	Low
1979				
Between grids	1.84 + 24.74(0.07)	0.95 + 26.74(0.07)	1.34 + 20.55(0.21)	1.53 + 24.40(0.45)
Within grids	1.84	0.95	1.34	1.53
1980				
Between grids	1.49 + 23.20(0.02)	1.22 + 24.75(0.08)	2.05 + 19.68(0.15)	1.52 + 13.23(0.31)
Within grids	1.49	1.22	2.05	1.52
1981				
Between grids	0.00	1.16 + 24.78(0.07)	0.00	1.51 + 12.40(0.02)
Within grids	3.70	1.16	1.16	1.51

Table 4. Results of grid vs. no-grid analysis of variance for grain protein selections in two sorghum populations.

Source	Mean Squares					
	1979		1980		1981	
	Low	High	Low	High	Low	High
Between grids	16.080**	4.002	6.336**	5.634*	3.298*	3.142
Within grids	1.814	2.194	1.397	2.720	1.564	3.486

*,** Significant at the 0.05 and 0.01 levels, respectively.

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