QUANTITATIVE GENETIC STUDIES OF A SORGHUM CROSS

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CHAPTER I

INTRODUCTION

Sorghum, Sorghum bicolor (L.) Moench, was introduced into the United States prior to 1853 from Africa via the West Indies. Brown and white durra were brought from Egypt to California in 1874. Subsequent introductions were: white and red kafir from south Africa in 1876, milo from northeast Africa about 1885, shallu from India about 1890, and feterita and hegari from northeast Africa in 1906 and 1908, respectively (40). However, sorghum was not of major economic importance in the United States until the invention of suitable mechanical harvesting devices during the nineteen thirties.

Much of the early breeding of sorghum was accomplished by farmers selecting within the above mentioned introductions. Gradually, types were developed to fit various needs, e.g., forage, syrup, and grain types. Within those types, further selection resulted in varieties superior to the older ones in several aspects. As sorghum gained prominence in the economy of United States agriculture, systematic sorghum research and breeding began. The first efforts of the early researchers were in the realm of qualitative genetics, i.e., researchers were interested in easily described and distinguishable characters. With the discovery of genetic-cytoplasmic male sterility, commercial hybrids in grain sorghum became a possibility, then a reality. The next phase, that of quantitative genetics, in sorghum breeding followed two paths. Large numbers of hybrids were screened to find desirable hybrid combinations. In addition, selections were made following hybridization within segregating populations for genetically superior pure-lines.

Knowledge of the relative magnitudes of the various genetic and environmental parameters for characters of economic importance is important before more efficient breeding and selection procedures can be employed. Since economically important characters are largely, if not entirely, quantitative in inheritance, they are described in terms of first and second order statistics, i.e., means, variances, and covariances, instead of in terms of classification into categories as is done with qualitative characters. The use of first and second degree statistics permits the estimation of genetic population parameters such as means, several genetic variances, heritabilities, genotypic correlations, expected genetic advances, environmental correlations, and phenotypic correlations. Judicious use of these estimates permits the plant breeder to construct selection indexes for more effectively selecting the genetically superior plants or families. Knowledge of the heritabilities allows him to employ the more efficient breeding procedure in order to gain the desired objective in the shortest time possible. The magnitudes of genotypic correlations will indicate to the breeder the extent to which various characters are inherited together and how selection for one of them is likely to affect others.

The purpose of this investigation was to estimate the phenotypic and genetic parameters of thirteen characters in a sorghum cross. The characters are node number, flower date, plant height, head length, peduncle length, flagleaf height, vegetative height, plant yield, kernel weight, number of kernels per head, per cent fertility of head, head weight, and plant vigor. Selection indexes for various combinations of characters were constructed and evaluated, and two breeding procedures were compared.

CHAPTER II

REVIEW OF LITERATURE

Most characters of economic importance in sorghum as well as in other crops appear to be influenced by many genes or gene groups. Their phenotypic expression cannot be classified into discrete classes but rather exhibit a more or less continuous distribution. The plant breeder is faced with the problem of how to choose genetically superior individuals or groups of individuals from the population. According to Comstock and Robinson (16), the main considerations of practically all breeding programs are selection within a base population of genetically variable individuals or families and utilization of the selected material as either potential commercial varieties or the base for a new cycle of selection. Population genetic theory in conjunction with statistical analysis provides a firm foundation for the modern plant breeder to effectively plan and execute selection programs.

Since the phenotype of individuals is the only indication of their genetic potential, some procedure must be employed to determine to what extent differences between individuals or groups are due to genetic constitution, to environmental influences and to interactions between them.

The phenotype, P, of an individual may be expressed as follows:

$$P = G + E + GE$$

where G is the genotypic value, E is the environmental deviation and GE is the genotypic-environmental interaction. The genotypic value may be further partitioned into the following components:

$$G = A + D + I$$

where A is breeding value, D is dominance deviation or intra-allelic interaction, and I is the epistatic or inter-allelic interaction. Falconer (21) defines breeding value as the value of an individual judged by the mean value of its progeny or in terms of average effects of genes, the breeding value of an individual is equal to the sum of the average effects of the genes it carries, the summation being made over the pair of alleles at each locus and over all loci. Mather (47) describes this type of effect as fixable since it depends on differences in average character expression associated with the homozygotes for each of the gene pairs involved. Deviations arising from the difference between the expression of heterozygote and the average of the two corresponding homozygotes are unfixable. This deviation is that previously defined as the effect due to dominance or intra-allelic interaction. The concept of additive variance does not carry with it the assumption of additive gene action; additive variance can arise from genes with any degree of dominance or epistasis; and only if all the genetic variance is additive, can it be concluded that the genes show neither dominance nor epistasis (21).

Epistatic variance is very difficult to estimate and is usually discounted as a source of variation although plant breeders have trouble forgetting it. Horner, cited by Comstock and Robinson (16), states that epistatic relations among genes may have large effects on the genetic variances in any kind of family and on covariances between any two kinds of related families that can be formed. Mather (47) suggested the use of scaling techniques to eliminate epistatic effects. However, this is difficult because a proper scale may not be found in many cases. These results leave then the estimation of genetic variance as a sum of its two "major" components, i.e., additive genetic variance and dominance genetic variance.

Estimates of the variances due to the different sources of variation contributing to differences between individuals as discussed above are important so that the plant breeder may properly plan his breeding programs. Comstock and Moll (15) give three advantages of knowing the true magnitudes of genetic variation: 1) overestimation of genetic variation would in some cases lead to investment of time and effort not justified by the real potential for improvement of genetic stocks employed, 2) optimum procedures may vary significantly depending on the magnitude of genetic variance, and 3) there is danger that sound breeding programs may be abandoned prematurely or unwisely because of results that are disappointing relative to unwarranted expectations based on erroneous estimates of genetic variance. Dudley and Moll (20) and Matzinger (48) indicate that if genetically variable material is grown in a randomized block experiment adequately replicated in time and space, the data analysis provides a reliable estimate for genetic variability and can also provide an estimate of broad sense heritability. They further point out that the more diverse the environmental population the smaller the estimate of genetic variance since more of the genotype-environment interaction variance is removed from the estimate of genetic variance. Estimates of variance components to be used in heritability estimates should come from experiments grown in an adequate sample of the environments to which the predictions will apply so that the estimate of genetic variance will be free as much as is possible of genotype-environment interaction and so that the appropriate fractions of the various genotype-environment interaction components can be included in the estimate of phenotypic variance (15).

Various procedures have been employed by plant breeders to obtain estimates of the phenotypic, genetic, and environmental variances. Since in self-pollinated crops the inbred parents and their F_1 hybrids are largely genetically homogeneous within lines, the variance between plants within lines has commonly been used to estimate environmental variance (1, 21, 22, 47). The common practice is to develop some system of relatives and from the analysis of variance of these individuals or of family means obtain estimates of genetic variance (1, 14, 16, 21). For example, two inbred lines may be crossed to produce an F_1 population which is selfed to produce the F_2. The phenotypic variance among plants in the F_2 is composed of both genotypic and environmental variance. The mean between plant variance for both parents and their F_1 is used as the estimate of environmental variance and is subtracted from the F_2 phenotypic variance to obtain the estimate of genotypic variance. This same procedure may be extended to later generations of selfing to obtain estimates of between family and within family genetic variance which may be partitioned into additive and dominance variances (1, 21, 22, 47). Relatives need not be developed to obtain estimates of genetic variance, but the estimates obtained by using several different inbred lines cannot be partitioned into components. Estimates of genotypic variance so obtained should be used with caution since they may contain large proportions of dominance and epistatic variance. If present, such estimates would cause the plant breeder to expect erroneously larger estimates of expected genetic advance than he should since these sources of variation cannot be fixed in the genotype. Therefore, considerable time and expense might be wasted pursuing a breeding program in which expected progress does not justify the effort necessary to attain that progress

(1, 13, 20).

Estimation of genotypic variance by comparing several inbred lines has been accomplished in oats (32) and sorghum (61). Johnson and Frey (32) used 27 inbred oat strains to estimate genotypic variance under varying environmental conditions. They found oat strains grown under non-stress environments had higher grain yield heritabilities than when grown under stress environments. This indicated that the non-stress environments permitted a greater degree of expression of the genotypic differences among these strains than did the stress environments. Swarup and Chanugale (61) used 70 inbred varieties of sorghum to obtain estimates of genotypic variance for 13 characters. The error and the variety mean squares were taken as environmental and phenotypic variances, respectively. The genotypic variance was obtained by subtracting the environmental variance from the phenotypic variance and broad sense heritability estimates were obtained for each character. The genotypic variance estimates obtained for all characters were high as reflected by the large heritability estimates, i.e., none of the heritability estimates were less than 70 per cent.

Robinson and Comstock (56) employed sib analyses to obtain estimates of genetic variances in open-pollinated varieties of corn. This procedure allowed the partitioning of the genetic variance into additive and dominance variance for several quantitative characters. All progenies were grown with two replications in each of two years.

Principle findings were that all characters exhibited less dominance variance, less than 0.6 as large for all traits, than additive variance and that a considerable amount of additive variance, two to three times the amount of dominance variance, existed for grain yield.

Differences between relatives were used in soybeans by several investigators to obtain estimates of genetic variances and in some instances to partition those variance estimates (3, 8, 33, 67). Anand and Torrie (3) used the regression of the F_4 family means on the F_3 parents to obtain heritabilities for various characters and concluded that the magnitude of the additive variance was not large for yield and the yield components studied. Brim and Cockerham (8) using F_3 , F_4 , and F_5 plants concluded that additive genetic variance was the principle component of genetic variance for all characters studied. Weber and Moorthy (67) employed the F_2 phenotypic variance and the average of the P_1 , P_2, and F_1 variances to obtain broad sense heritability estimates for six soybean characters. Their heritability estimates were all above 50 per cent. Differences between relatives have been used in other self-pollinated crops, e.g., cotton (49), oats (51), and barley (53), to obtain estimates of genetic variance. Rasmusson and Glass (53) studied 80 lines of barley in the F_5 , F_6 , and F_7 to obtain estimates of genetic and environmental variability. They were particularly concerned with the number of replications needed to give accurate estimates. They concluded that under the conditions of their study, a single trial with three replicates gave sufficient information for each character studied to permit favorable odds of including the elite lines if the top 25 per cent were selected.

Variance between F_2 plants has been used in sorghum to estimate genotypic variance (5, 38). As usual, the mean between-plant variance for the parents and the F_1 was used to estimate environmental variance. Beil and Atkins (5) obtained broad sense heritability estimates of 88 and 75 per cent for plant height and 75 and 59 per cent for seed weight in two different populations. Khan (38) obtained broad sense heritability estimates for eight of nine characters of less than 50 per cent in two different F_2 populations whose parents had similar origin.

Mather's procedure (47) of using the F_2 and the two first backcross generations has been employed to a considerable extent in self-pollinated crops to obtain estimates of additive and dominance variance. Ramey (52) examined 11 characters in cotton and found substantial amounts of additive variance for nine characters and small positive dominance variances for all characters except three. Application of Mather's procedure has been made by several investigators in sorghum (26, 35, 44, 63). Hadely (26) reported that dominance variance for plant height was suggested but not statistically significant. Liang and Walter (44) examined grain yield, kernel weight, number of kernels per head, half bloom, plant height, stalk diameter, and germination percentage in three different crosses. The parents of the crosses were similar in origin and had been employed in commercial hybrid production. Additive effects were significant for grain yield, head weight, kernel weight, and number of kernels per head in only one cross. These investigators concluded that dominance effects were more important than additive effects for yield and the yield components. However, Voigt et al. (63) found a heritability for seed size of 60 per cent.

Extensive use has been made of diallel crosses to estimate genetic variance and its components in sorghum (6, 11, 12, 26, 36, 41, 42, 45, 50). Beil and Atkins (6) investigating grain yield, number of heads per plant, weight of 100 kernels, and number of seeds per head reported significant general combining ability effects (GCA) for all characters, but significant differences for specific combining ability effects (SCA) were expressed only for 100-seed weight. Chiang and Smith (12) found additive effects to be high for head length, number of tillers, threshing percentage, and leaf length. GCA and SCA were important for all of the characters studied by Kambel and Webster (36). However, they noted that GCA effects were considerably more important than SCA effects. Liang (41) found significant GCA for all characters studied except kernel weight and germination percentage while SCA was not significant for leaf area, germination percentage, threshing percentage, and protein content.

Liang et al. (42) used the diallel to obtain variances of both GCA and SCA in sorghum and concluded that SCA effects were more important for yield than GCA effects. Narrow sense estimates for yield, anathesis time, and protein content were 13, 64, and 43 per cent, respectively. Malm (45) and Niehaus and Pickett (50) concluded that additive effects were much more important for yield and yield components than dominance effects.

Estimates of genetic variance and its additive and dominance variance components as well as phenotypic variance are used by plant breeders to make estimates of heritability. Heritability in a general sense has been defined as the portion of the observed variance for which difference in heredity is responsible by Knight as cited by Hanson (28). More specifically, heritability is defined in two different ways, i.e., broad sense heritability as the ratio of the genetic variance to phenotypic variance and narrow sense heritability as the ratio of additive genetic variance to phenotypic variance. Broad sense estimates contain both additive and dominance variance in the numerator as well as epistatic variance. However, it is not so apparent that estimates commonly assumed to be narrow sense heritabilities may, in fact, contain fractions of dominance variance if determined in self-pollinated species. This is true for estimates determined by regression of progeny values either as family means or as individual plants on their parental values. It is important to realize that heritability is a property not only of the character under consideration but also of the population and of the environmental circumstance to which the population is subjected. A change in any one of these factors will affect heritability estimates (21, 28).

Heritabilities may be estimated by at least four techniques: 1) use of nonheritable variance from genetically homogeneous populations subtracted from phenotypic variance estimates of segregating populations to estimate total genotypic variance, 2) variance components from an analysis of variance, 3) parent-offspring regression, and 4) difference between twice the F_2 genotypic variance and the sum of the variances of both first backcross generations as an estimate of the additive variance (65). The last-mentioned procedure has the advantage of growing all material during the same season thus eliminating the necessity of obtaining environmental variance estimates and estimates of total genetic variance. The parent-offspring method has the disadvantage that the two generations under consideration must be grown in different environments. Frey and Horner (24) proposed a method, standard unit heritability, to largely eliminate this difficulty. It is determined by calculating regressions on data after it is coded in terms of standard deviation units. The resulting regressions are identical to correlation coefficients on the original data and have an approximate ceiling of 100 per cent. They concluded that this method tended to eliminate those environmental effects of different years which increase or decrease the range of the progenies relative to that of the parent (24). Another problem arising from the use of parent-offspring regression to estimate heritability is the failure to take into account the degree of inbreeding of the parent (59). Smith and Kinman (59) have pointed out that heritability estimates based on offspring-parent regressions in self-pollinated crops should be adjusted by dividing the regression coefficient by twice the degree of relationship between the parent and its offspring. The major problem encountered in using the variance component method to estimate heritability is that the estimate of additive variance so obtained is quite likely to contain fractions of epistatic variances and genotype-environment interactions which, if present would inflate the estimate.

Heritability estimates derived by taking the difference between the variances of segregating populations and nonsegregating populations and dividing by the variance of the segregating population have been reported by investigators working with several crops. In oats, Johnson and Frey (32) and Petr and Frey (51) reported relatively high heritability estimates for various characters. Rasmusson and Glass (53) found heritabilities in barley to be highest for heading date and diastatic power; intermediate for kernal plumpness, height, and barley extract; and lowest for yield. They indicated that inflated estimates are not serious if the researcher recognizes the limitations associated with heritability estimates made in self-pollinated crops. Johnson et al. (34) and Weber and Moorthy (66) in soybeans reported fairly low heritability estimates for yield but relatively high ones for the other characters studied. In sorghum, several investigators have made similar studies (5, 38, 44, 61, 63). The magnitudes of the heritabilities reported by these investigators were discussed previously when estimation of variances was under consideration and will not be reiterated.

Robinson et al. (54) applied the regression and variance component techniques in corn to obtain estimates of heritability. They compared three methods of estimation: 1) regression of progeny means on the female parent, 2) regression of progeny means on the male parent, and 3) variance component method. In general, the heritabilities of plant height, ear height, husk extension, and husk score were relatively high while number of ears per plant, ear length, ear diameter, and yield had considerably lower values. Regression estimates for ear number, ear length, ear diameter, and yield were significantly less than those computed for the other characters by similar methods. These differences were attributed to the fact that progenies were grown in different environments from the parents. Anand and Torrie (3) compared heritability estimates determined by regression of the F_4 family means on the F_3 with estimates obtained from variance components in soybeans. They found estimates obtained in these manners were generally similar in magnitude. Estimates of heritability for seed yield, pods per plant, and seeds per pod were low. The estimate for seed weight was high but uncorrelated with seed yield.

Aside from the fact that heritability measures the reliability of the phenotype as an indication of genotypic merit, it plays a role in determining which breeding procedure to employ for selection purposes and in making predictions concerning expected advance under selection. For example, high heritability, in the narrow sense, in the F_2 indicates effective selection is possible on an individual plant basis. Genetic advance is defined as the product of the intensity of selection, the estimate of the phenotypic standard deviation, and the heritability estimate (21). The proportion of the population saved determines the intensity of selection which is calculated as the height of the normal curve at the point of truncation divided by the proportion of the population selected. The primary component of the prediction formula which determines whether selection will be effective or not is the heritability estimate (20).

Khadr and Frey (37) and Frey (23) estimated genetic advance in oats. Khadr and Frey (37) concluded that opportunity for progress from selection in the pedigreed and the recurrent selection populations are nearly equal. Frey (23) compared three methods of selection; random, stratified, and tandem. The tandem selection system provided greater expected gain than either the random or stratified systems. The degree of superiority of the tandem system was determined by the heritability of the character under selection.

Some investigators (5, 44, 61) have used the prediction formula to estimate expected genetic advance but have not determined the degree of correspondence between actual and expected gains. Beil and Atkins (5) determined expected genetic advance for several characters in sorghum for various proportions of the population selected. When 10 per cent of the population was selected, the expected genetic advances for the characters studied expressed as a per cent of the mean were as follows: days to mid-bloom, 15.2 per cent; plant height, 25.2 per cent; weight per 100 seeds, 18.2 per cent; and grain yield, 66.6 per cent. Swarup and Chanugale (61) give the following expected genetic advances for the characters studied expressed as a per cent of the mean: plant height, 108.5 per cent; leaf number, 114.9 per cent; peduncle length, 127.1 per cent; panicle length, 120.08 per cent; panicle weight, 139.77 per cent; grain yield, 203.82 per cent; and 100-seed weight, 124.3 per cent.

When a character is under selection, it is important to determine the effect that selection for that character will indirectly have on other characters. For this reason, genetic relationships between quantitative characters are of considerable interest to plant breeders. Falconer (21) also states two additional reasons for determining such relationships, i.e., to study the genetic causes of correlation through the pleiotropic action of genes, and to examine the relationship between a metric character and fitness of that character in a natural population. Knowledge of the correlation between complex characters of low heritability, such as yield, and less complex characters which may have much higher heritabilities would benefit the breeder to the extent that it may be easier to select for the complex character indirectly by practicing selection on the highly heritable character. The genetic and phenotypic variances and covariances of correlated characters provide the basis for constructing selection indexes. Phenotypic, genetic and environmental correlations have been reported by many investigators. Robinson et al. (55) discussed the application of genetic and phenotypic correlations as they apply to selection in corn. Various genetic and phenotypic variances and covariances were employed in the construction of several selection indexes involving different sets of characters. Miller et al. (49) did essentially the same thing in cotton. They reported that lint yield is highly positively correlated with lint percentage and bolls per plant. Burton (10) working with millet stated that the correlations he obtained involving plant yield indicated that high yielding plants tended to have more stems, larger stems, wider leaves, and to be taller than their less productive associates. Petr and Frey (51) concluded that yield of oats was most closely associated with plant height, panicle length, number of spikelets per panicle, and number of panicles per plant. Wallace et al. (64) working with oats reported that the most important aspect of their study was that there was no evidence that a selection index, based on the characters they considered, would have enough advantage over selection based only on yield to be of practical significance. Breeders of soybeans have found that genetic correlations usually exceed phenotypic correlations in magnitude (3, 33, 34, 66, 67). In sorghum many investigators have reported genetic and phenotypic correlations. Some have been interested in finding a character highly correlated with yield that could more easily be determined than yield (4, 31, 38, 57). All reported a high positive correlation between panicle weight and threshed grain weight. Beil and Atkins (5) reported genetic correlations involving grain yield usually were among the highest obtained with the largest correlation obtained being for the association of plant height and yield. Kirby and Atkins (39) found that seeds per head was the character most highly associated with yield. Liang et al. (43) stated that head weight and half bloom date appear to be the best indicators for yield. Swarup and Changale (62) examined the possible associations of seven characters considered two at a time and concluded that in general the genetic correlation coefficients were higher than the phenotypic and environmental correlation coefficients. They constructed selection indexes employing various combinations of the characters studied and determined their relative efficiencies compared to that of selection for yield alone.

When the plant breeder is faced with the actual responsibility of choosing individuals in a selection program, he is faced with a difficult problem since the worth of individuals normally depends upon more than one character. One might select for one character at a time, i.e., tandem selection, or one might select for all characters at the same time but independently, rejecting all individuals that fail to come up to a certain standard for each character regardless of their values for any other of the characters, i.e., independent culling levels (21). Hazel and Lush (30) compared the efficiency of three methods of selection, the two just mentioned and the total score or index method. They found most rapid improvement of economic value from selection applied simultaneously to all characters. Appropriate weight must be given to each character according to its relative economic importance, its heritability, and the genetic and phenotypic correlations between the different characters. If the characters that determine economic worth of an organism are uncorrelated, then each character is simply weighted by the product of its economic value and its heritability (21). However, if the genetic correlations are present and known, the efficiency of the index can be improved.

Smith (58), Griffing (25), and Hazel (29) have presented theoretical considerations involved in the proper construction of selection indexes. The first consideration is the definition of the merit, economic worth, or aggregate worth of the organism, i.e., what characters contribute to the worth of the organism. Then the aggregate breeding value is defined as the sum of the breeding values for each character after each is multiplied by the relative increase in net worth expected from a one unit improvement in that character. Since only phenotypes of individuals can be measured, the index used is a linear function of the phenotypic values.

Attempts have been made by several plant breeders to develop selection indexes in various crop species. Robinson et al. (55) constructed six indexes using four characters in corn, and compared their relative efficiencies to the index developed for yield alone. Theoretically, an index composed of a subset of the characters considered in another index should have a lower efficiency than the index which considers all characters determined to be of economic value (29). This was true for the indexes constructed by Robinson et al. (55). Manning (46) and Miller et al. (49) constructed various selection indexes for different characters in cotton. Manning (46) used this method to bring about yield improvement in a cotton grown extensively in Uganda and realized a selection response of 36 per cent after six generations of selection. After examining the correlations between various characters in cotton, Miller et al. (49) selected four characters and constructed various indexes containing different combinations of the characters. The most efficient index was the one that included all four characters, though one index composed of only three characters had nearly the same efficiency. Wallace et al. (64) constructed ten different indexes using various combinations of five characters in oats but concluded after looking at their relative efficiencies as compared to that for yield alone that there was no evidence that a selection index based on the characters considered would have enough advantage over selection based on yield alone to be of practical significance. Brim et al. (9) examined selection indexes by changing the economic values. That is, they constructed one set of indexes using one set of economic values then changed the economic values and constructed another set of indexes. Changing the price ratio in one population had little effect on the relative values of the weights for any index. However, in another population changing the price ratio had an appreciable effect on the relative values of the weights. In sorghum Swarup and Chaugle (62) concluded that results from the indexes they constructed gave almost the same or lower efficiencies than that obtained from selection for grain yield alone.

Another aspect of selection indexes that should be considered is the time and expense involved in the construction of the index and the fact that for each generation a new index should be constructed from new estimates of the phenotypic and additive variances and covariances. However, the thought of Brim et al. (9) may be very applicable here. They state that while one is pessimistic about the use of indexes, the alternatives are even less desirable. Alternatives, such as independent culling levels, visual appraisals, or mental thumbrules, do not overcome any of the objections to indexes.

When selection within a genetically variable population is contemplated, the breeder is faced with the choice of breeding procedures under which selection will be practiced. If the magnitude of the heritability is known, the problem is more easily resolved. If the heritability is high for a particular character, h^2 greater than .2, then individual or mass selection is the easiest and probably the most economical procedure to employ and adequate response may be expected (21). However, if the heritability is low, h^2 less than .2, a system that makes use of relatives should be used because the mean value of a number of relatives often provides a more reliable guide to breeding value than the individual's own phenotypic value. Often, the actual gain under selection does not approximate the expected. This may be due to over estimates of heritability. However, the question still remains in the breeder's mind as to which procedure will give the maximum gain. Bilbiro (7) states that the relative effectiveness of a breeding method should be evaluated in terms of progress accomplished and also in terms of time and labor required to make this progress. Therefore, progeny testing must, in general, result in more than twice the gain of mass selection since it takes twice as long to accomplish.

From a theoretical standpoint, Comstock et al. (17) compared three breeding procedures under which selection may be practiced. The procedures compared were reciprocal recurrent selection, recurrent selection, and selection based on general combining ability with a common tester series. The comparison indicated that under no circumstances would reciprocal recurrent selection be more than slightly inferior to the better of the other two. However, it would definitely be superior to selection for general combining ability at loci where there is over-dominance or if a situation analogous to that with over-dominance exists because of linkage. Reciprocal recurrent selection would definitely be superior to recurrent selection for loci at which there is partial dominance.

Sprague et al. (60) contrasted recurrent selection and selection within selfed lines of corn for their relative efficiencies in increasing the oil percentage of corn grain. At the end of the test period, the recurrent series had passed through two complete cycles and the inbred series had been self-pollinated for five generations. Recurrent selection was 1.3 to 3.0 times more effective depending upon the particular contrast used. Duclos and Crane (19) developed a synthetic population from 45 introduced strains and allowed it to mate randomly for three generations. Some plants were then chosen and crossed to a double cross tester. The top 11 per cent in the S_1 based on S_1 performance and based on the top cross progeny were selected. These were developed into two subsynthetics in which random mating was practiced for three generations. In the next cycle, mean yields were significantly higher in S_1 progeny from the synthetic based on S_1 progeny performance than from the synthetic based on top cross performance. However, mean yields were significantly higher in the top crosses from the synthetic based on S_1 line performance. The next generation of each subsynthetic was propagated by intermating the top-yielding 21 per cent based on S_1 performance and top cross performance, respectively. Seed samples were drawn from each and tested at two locations. A highly significant yield improvement was made with the first cycle of selection by both methods of evaluation, but there was no significant difference between the two methods.

In cotton, Bilbro (7) compared recurrent selection, selection-while-inbreeding, and mass selection. Considering the time and labor required, mass selection was the most efficient with selection-while-inbreeding and recurrent selection following in that order. However, when considered in light of actual breeding progress, the selection-while-inbreeding method was superior to the recurrent selection method. Recurrent selection and mass selection did not differ significantly in progress gained.

Frey (23) working with oats and barley compared the following testing schemes: random - seeds for family propagation were drawn at random from bulked seed of all individuals in a family; stratified - one or two seeds were taken from each individual in a family and bulked for family propagation, and tandem pedigree system practiced in F_2 with progeny from a selected plant being carried as a bulk like with no intra-line selection in subsequent generations until the line was readied for release. Six species - character cases, three characters in oats and three characters in barley, were tested. The tandem selection system provided greater expected genetic progress than either of the other methods for five of them. Heading date in oats was equal in all three situations. The inputs of testing resources were the same for all three selection systems. The degree to which the tandem system proved superior to the other two systems was determined by the relative heritability of the character under selection. If heritability is 100 per cent, all three systems give equal genetic gain; but as the heritability becomes lower, the tandem system becomes more and more superior.

CHAPTER III

MATERIALS AND METHODS

Segregating material used in this investigation was the result of making the following cross:

A Combine Kafir 60 x Brown Kaoliang.

The female parent, Combine Kafir 60, is a short, relatively high yielding, white seeded, inbred line. It is a genetic-cytoplasmic male-sterile line and has frequently been used as a female parent in the commercial production of hybrid material. The center of origin of the kafirs is probably Africa. Brown Kaoliang, the male parent, is a tall, relatively high yielding, brown seeded, inbred line. Its seeds have a bitter taste and largely for this reason this line has not been used in hybrid production. Brown Kaoliang was introduced to the United States from Manchuria where every part of the plant from the seed to the stalk is utilized in some manner (40).

The parents had been self-pollinated for many generations and should be genetically homozygous. The vegetative plant characters were measured in centimeters. Yield and its components were recorded in grams. Flower date was measured as the number of days from June 1 until the first flowers appeared on each plant. Node number was determined by counting the number of leaves produced by each plant from the seedling stage until the plant matured. Plant height was measured as the height from ground level to the tip of the head. Head length was recorded as the length from the lowest branch on the inflorescence to the tip of the head. Peduncle length was assessed as the length from the first node below the head to the lowest branch of the head. Flagleaf height was calculated as length of the plant from the ligule of the first leaf below the head to ground level. Vegetative height was measured as the length of the plant from the first node below the head to ground level. Plant yield was recorded as the weight of the threshed grain from the main culm. Head weight was determined to be the weight of the unthreshed main head with 20 centimeters of the peduncle attached. Weight per kernel $= \frac{\text{weight of X kernels}}{\text{X kernels}}$, kernels per head $= \frac{\text{plant yield}}{\text{weight of X kernels}}$ (X), fertility $= \frac{\text{plant yield}}{\text{head weight}}$ (100), and vigor $= \frac{\text{flower date}}{\text{number of nodes}}$.

During the summer of 1966, the parents, F_1, F_2, and a homozygous inbred line, Wheatland, were grown at the Oklahoma Agricultural Experiment Station at Perkins, Oklahoma. Each F_2 plant was used as a pollinator on one or more plants of Wheatland. The progenies which resulted from these crosses have been designated as topcrosses. At the same time, more F_1 seed was obtained by crossing the parents of the original F_1, and all material was self-pollinated. Of 283 Wheatland x F_2 crosses, only 49 produced enough seed to be included in the study over a two-year period with three replications each year. The F_2 plants used as the parents for the F_3 families did not constitute the F_2 population which was analyzed to estimate the F_2 phenotypic, genetic, and environmental variances. Both F_2 populations were from the same F_1 and were considered random samples.

In 1967 and 1968, three replications were planted each year. Each replication included the parents, F_1, F_2, F_3 families, and topcross families. One replication was composed as follows: two rows of each parent, two rows of the F_1, four rows of the F_2, one row for each of the 49 F_3 families, and one row for each of the 49 topcross families giving a total of 108 rows. Each entry was assigned to each replication at random and a new randomization was used for each replication in each year. Although multiple rows of the parents, F_1, and F_2 were grown in each replication, the rows of any single entry were not planted side-by-side unless they so occurred by chance. The 49 F_3 families were obtained from the F_2's which when used as pollinators on Wheatland produced enough seed for the 1967 and 1968 tests.

Estimates of phenotypic, genotypic, and environmental variances for each character were obtained from analyses of variance of the F_2, parents, and F_1. These estimates were based on two years data at one location. For the F_2 the model utilized is as follows:

$$X_{ijkl} = \mu + y_i + r_{ij} + l_{ijk} + p_{ijkl}$$

where

X_{ijkl} = observation from the i^{th} year, the j^{th} replication, the k^{th} row, and the l^{th} plant.

μ = effect due to the over-all mean.

y_i = effect due to the i^{th} year, $i = 1, 2, \ldots, T$

r_{ij} = effect due to the j^{th} replication in the i^{th} year, $j = 1, 2, \ldots, U$.

l_{ijk} = effect due to the k^{th} row in the j^{th} replication in the i^{th} year, $k = 1, 2, \ldots, V$.

p_{ijkl} = effect due to the l^{th} plant in the k^{th} row in the j^{th} replication in the i^{th} year, $l = 1, 2, \ldots, W$.

The form of the analysis of variance for the parents, F_1, and F_2 is presented in Table I. The plants in rows in replications in years mean square is an unbiased estimate of $\hat{\sigma}_p^2$. This estimate is composed of genotypic and environmental variance in the analysis of F_2 data and only the environmental variance in the analysis of the F_1 and parental data assuming no genotypic-environmental interaction. The plants in rows in replications in years mean squares for the parents and F_1 were pooled and used as the estimate of environmental variance. The estimate of genotypic variance for each character was obtained by subtracting the environmental variance estimate from the mean square for plants in rows in replications in years in the F_2. This estimate is composed of the additive, dominance, and epistatic variance estimates.

TABLE I

ANALYSIS OF VARIANCE TABLE FOR THE PARENTS, F_1 AND F_2

Source	d.f.	MS	EMS
Total	TUVW-1		
Yrs	T-1	MS_4	$\sigma_p^2 + W\sigma_1^2 + VW\sigma_r^2 + UVW\sigma_y^2$
Reps + Reps x Yrs	T(U-1)	MS_3	$\sigma_p^2 + W\sigma_1^2 + VW\sigma_r^2$
Rows in Reps in Yrs	TU(V-1)	MS_2	$\sigma_p^2 + W\sigma_1^2$
Plts in Rows in Reps in Yrs	TUV(W-1)	MS_1	σ_p^2

By making the following assumptions, the analysis of variance of the F_3 data from 1967 and 1968 permits the estimation of additive and dominance variance: (1) normal diploid inheritance, (2) no linkage, or equilibrium with respect to linkage relations, (3) no epistasis, (4) gene frequency of one-half, and (5) no genotype-environment interaction (20). The model assumed for the F_3 is as follows:

$$X_{ijkl} = \mu + y_i + r_j + b_k + (yb)_{ik} + e_{ijk} + w_{ijkl}$$

where

X_{ijkl} = observation from the i^{th} year, j^{th} replication, k^{th} family, and the l^{th} plant.

μ = effect due to the over-all mean.

y_i = effect due to the i^{th} year, $i = 1, 2, \ldots, T$.

r_j = effect due to the j^{th} replication, $j = 1, 2, \ldots, U$.

b_k = effect due to the k^{th} family, $k = 1, 2, \ldots, F$.

$(yb)_{ik}$ = effect due to the interaction between the i^{th} year on the k^{th} family.

e_{ijk} = error associated with the k^{th} family in the j^{th} replication in the i^{th} year.

w_{ijkl} = effect due to the l^{th} plant in the k^{th} family in the j^{th} replication in the i^{th} year, $l = 1, 2, \ldots, V$.

The analysis of variance of the F_3 based on the above model is shown in Table II. The estimates of variance

TABLE II

ANALYSIS OF VARIANCE TABLE FOR THE F_3

Source	d.f.	MS	EMS
Total	TUFV-1		
Years	T-1	MS_6	$\sigma_w^2 + V\sigma_e^2 + UV\sigma_{yf}^2 + UFV\sigma_y^2$
Reps.	U-1	MS_5	$\sigma_w^2 + V\sigma_e^2 + TFV\sigma_r^2$
Between Families	F-1	MS_4	$\sigma_w^2 + V\sigma_e^2 + UV\sigma_{yf}^2 + TUV\sigma_b^2$
Yr. x Fam.	(T-1)(F-1)	MS_3	$\sigma_w^2 + V\sigma_e^2 + UV\sigma_{yf}^2$
Experimental Error	(U-1)(TF-1)	MS_2	$\sigma_w^2 + V\sigma_e^2$
Within Families	TUF(V-1)	MS_1	σ_w^2

components for within families ($\hat{\sigma}^2_w$), experimental error ($\hat{\sigma}^2_e$), year x family ($\hat{\sigma}^2_{yf}$), between families ($\hat{\sigma}^2_b$), replications ($\hat{\sigma}^2_r$), and year ($\hat{\sigma}^2_y$), were found by equating the mean squares to their expectations and solving for the unknowns. The within families estimate of variance, $\hat{\sigma}^2_w$, is an estimate of within families genetic variance as well as plant-to-plant variance. The estimate of between families variance, $\hat{\sigma}^2_b$, is an estimate of between families genetic and row-to-row variance. The within and between row variances were estimated from the analysis of variance of the parents and F_1. The within row estimates for the parents and F_1 were pooled and subtracted from the F_3 within families variance estimate. The between rows variance estimates for the parents and F_1 were pooled and subtracted from the between families estimates of variance in the F_3. The between rows estimate for the parents and F_1 were obtained by $\frac{MS_2 - MS_1}{TUV}$ from Table I.

The assumptions of no epistatic variance in the F_3 and gene frequency of one-half permits the use of the following two equations to obtain estimates of additive and dominance variance:

$$(\hat{\sigma}^2_{w}F_3 - \hat{\sigma}^2_{w}H) = \tfrac{1}{2}\hat{\sigma}^2_A + \tfrac{1}{2}\hat{\sigma}^2_D$$

$$(\hat{\sigma}^2_{b}F_3 - \hat{\sigma}^2_{b}H) = \hat{\sigma}^2_A + \tfrac{1}{4}\hat{\sigma}^2_D$$

where

$\hat{\sigma}^2_w F_3$ = estimate of F_3 within families variance.

$\hat{\sigma}^2_{wH}$ = estimate of pooled within rows variance for the parents and F_1.

$\hat{\sigma}^2_{bF_3}$ = estimate of F_3 between families variance.

$\hat{\sigma}^2_{bH}$ = estimate of pooled between rows variance for the parents and F_1.

$\hat{\sigma}^2_{A}$ = estimate of additive genetic variance in the F_2.

$\hat{\sigma}^2_{D}$ = estimate of dominance genetic variance in the F_2.

After some modification in notation, these equations are the same as those presented by Mather (47). An estimate of the environmental variance was determined as:

$$\hat{\sigma}^2_{E} = \hat{\sigma}^2_{wH} + \hat{\sigma}^2_{bH} + \hat{\sigma}^2_{eF_3} + \hat{\sigma}^2_{rF_3} + \hat{\sigma}^2_{yF_3}$$

where $\hat{\sigma}^2_{wH}$, $\hat{\sigma}^2_{bH}$, $\hat{\sigma}^2_{eF_3}$, $\hat{\sigma}^2_{rF_3}$, $\hat{\sigma}^2_{yF_3}$ assume the previous definitions for each. The total genetic variance estimate in the F_3 was estimated as $\hat{\sigma}^2_{G} = \hat{\sigma}^2_{A} + \hat{\sigma}^2_{D}$. An estimate of the genotype-environment interaction variance was made by $\hat{\sigma}^2_{GE} = \hat{\sigma}^2_{yfF_3}$. The estimates of genetic, environmental, and genotype-environment interaction variances were summed to obtain an estimate of the F_3 phenotypic variance. All estimates were determined on an individual plant basis.

An analysis of variance of F_3 family means (3) was made according to the following model:

$$X_{ijk} = \mu + y_i + r_j + b_k + (yb)_{ik} + e_{ijk}$$

where

X_{ijk} = observation from the i^{th} year, the j^{th}

replication and the kth family.

μ = effect due to the over-all mean.

y_i = effect due to the ith year, $i = 1, 2, \ldots, T$.

r_j = effect due to the jth replication, $j = 1, 2, \ldots, U$.

b_k = effect due to the kth family, $k = 1, 2, \ldots, F$.

$(yb)_{ik}$ = effect due to the interaction between the ith year and the kth family.

e_{ijk} = error associated with the kth family in the jth replication in the ith year.

Table III presents the form of the analysis of variance based on this model. The error mean square, MS_1, was used as the estimate of the environmental variance for family means, $\hat{\sigma}^2_{E\bar{F}_3}$. Mean square one, MS_2, and MS_3 were set equal to their respective expectations and solved for estimates of $\hat{\sigma}^2_{e\bar{F}_3}$, $\hat{\sigma}^2_{yf\bar{F}_3}$, and $\hat{\sigma}^2_{b\bar{F}_3}$, respectively. The F_3 family mean phenotypic variance was found as follows:

$$\hat{\sigma}^2_{p\bar{F}_3} = \hat{\sigma}^2_{b\bar{F}_3} + \frac{\hat{\sigma}^2_{yf\bar{F}_3}}{T} + \frac{\hat{\sigma}^2_{e\bar{F}_3}}{TU}.$$

This analysis will be discussed further when F_3 correlations are considered.

Heritability was determined in the F_2 and the F_3 in several ways. In the F_2, heritability was estimated by approximating the environmental variance from homogeneous material, subtracting it from the F_2 phenotypic variance estimate to obtain the total genetic variance in the F_2, and

TABLE III

ANALYSIS OF VARIANCE TABLE FOR F_3 FAMILY MEANS

Source	d.f.	MS	EMS
Total	TUF-1		
Yrs.	T-1	MS_5	$\sigma_e^2 + U\sigma_{yf}^2 + UF\sigma_y^2$
Reps.	U-1	MS_4	$\sigma_e^2 + TF\sigma_r^2$
Families	F-1	MS_3	$\sigma_e^2 + U\sigma_{yf}^2 + TU\sigma_b^2$
Yr. X Fam.	(T-1)(F-1)	MS_2	$\sigma_e^2 + U\sigma_{yf}^2$
Experimental Error	(U-1)(TF-1)	MS_1	σ_e^2

dividing that variance by the phenotypic variance; regression of F_3 family means on their respective F_2 parents ($b_{F_2, \bar{F}_3}$); and regression of topcross family means on their respective F_2 parents ($b_{F_2, \overline{TO}}$). The first method is the broad sense heritability estimate. The second method is not strictly a narrow sense estimate because a fraction of the dominance variance is included. The covariance of F_2 and F_3 family means is composed of $\hat{\sigma}_A^2 + \frac{1}{2}\hat{\sigma}_D^2$ which with some modification in notation is the same as that reported by Mather (47). To this investigator's knowledge, the expectation of Cov(F_2, $\overline{TO}$) has not been previously reported. Therefore, the expectation of that covariance has been derived and is as follows. Let the number of loci of an organism, in this case sorghum, be N. The notation used by Falconer (21) will be employed. Consider first one locus only.

F_2

Genotype	Freq.	Genotypic value
BB	$\frac{1}{4}$	a
Bb	$\frac{1}{2}$	d
bb	$\frac{1}{4}$	-a

The Cov(F_2, $\overline{TO}$) $= \sum_i f_i V_{F_2} V_{\overline{TO}} - (\sum_i f_i V_{F_2})(\sum_i f_i V_{\overline{TO}})$ where V_{F_2} = genotypic value for the given genotype in the F_2 and $V_{\overline{TO}}$ = the genotypic value for the same genotype in the topcross. The summation, $\sum_i$, is performed over all different genotypes at that locus.

Now consider that particular locus as B, b and that the female parent has the genotype bb, then

Wheatland X F_2, where the female parent is considered bb

Genotype	Freq.	Mean Genotypic Value
Bb	$\frac{1}{4}$	d
$\frac{1}{2}$Bb $\frac{1}{2}$bb	$\frac{1}{2}$	$\frac{d}{2} - \frac{a}{2}$
bb	$\frac{1}{4}$	$-a$

$$\begin{aligned}
\mathrm{Cov}(F_2,\overline{TO}) &= [(\tfrac{1}{4})(a)(d) + (\tfrac{1}{2})(d)(\tfrac{d}{2}-\tfrac{a}{2}) + (\tfrac{1}{4})(-a)(-a)] \\
&\quad - [(\tfrac{1}{4})(a) + (\tfrac{1}{2})(d) + (\tfrac{1}{4})(-a)] \\
&\quad\quad [(\tfrac{1}{4})(d) + (\tfrac{1}{2})(\tfrac{d}{2} - \tfrac{a}{2}) + (\tfrac{1}{4})(-a)] \\
&= [\tfrac{1}{4}ad + \tfrac{1}{4}d^2 - \tfrac{1}{4}ad + \tfrac{1}{4}a^2] - [\tfrac{1}{4}a + \tfrac{1}{2}d - \tfrac{1}{4}a] \\
&\quad [\tfrac{1}{4}d + \tfrac{1}{4}d - \tfrac{1}{4}a - \tfrac{1}{4}a] \\
&= [\tfrac{1}{4}d^2 + \tfrac{1}{4}a^2] - \tfrac{1}{2}d[\tfrac{1}{2}d - \tfrac{1}{2}a] \\
&= \tfrac{1}{4}d^2 + \tfrac{1}{4}a^2 - \tfrac{1}{4}d^2 + \tfrac{1}{4}ad \\
&= \tfrac{1}{4}a^2 + \tfrac{1}{4}ad.
\end{aligned}$$

Now consider N loci and assume no epistasis, then the $\mathrm{Cov}(F_2,\overline{TO}) = \frac{1}{4}\sum_{j=1}^{N} a_j^2 + \frac{1}{4}\sum_{j=1}^{N} a_j d_j$. Since gene frequency is one-half and assuming no epistasis, the $\mathrm{Cov}(F_2,\overline{TO}) = \frac{1}{2}\sigma_A^2$, since in this case $\sigma_A^2 = \frac{1}{2}\sum_{j=1}^{N} a_j^2$.

If it were assumed that the female parent, Wheatland, used to make the topcrosses had the opposite homozygous genotype, BB, the expectation of the covariance would be very similar. Only the sign of the interaction term would be changed. Since no epistasis was assumed, the expectations would be identical. Consequently, twice the regression of the topcross family means on their respective F_2 parents provides a narrow sense heritability estimate in the absence of epistasis.

Heritability estimates in the F_3 were obtained from the analysis of variance as narrow sense estimates using the estimate of additive genetic variance determined on an individual plant basis and a heritability estimate using the between family variance estimate, $\hat{\sigma}^2_{b \cdot \bar{F}_3}$, determined on a family mean basis, i.e., variance component method (16).

The heritability estimates in each generation were used to calculate expected genetic advance, ΔG, for each character under consideration by the following formula:

$$\Delta G = i \, \hat{\sigma}_p \hat{h}^2$$

where

i = the intensity of selection = z/p.

z = the height of the ordinate of the normal curve at the point of truncation for the proportion of the population selected.

p = the proportion of the population selected.

$\hat{\sigma}_p$ = estimate of the phenotypic standard deviation.

$\hat{h}^2$ = estimate of heritability.

For this investigation, the 10 per cent most desirable plants for each character were selected which results in the intensity of selection taking the value of 1.76 (1).

Phenotypic, genetic, and environmental correlations among five of the characters studied were determined for the F_2 and F_3 generations. Phenotypic correlations were calculated in the F_2 by the following formula:

$$r_p = \frac{\hat{C}ov\ (X,Y)}{\sqrt{\hat{\sigma}^2_x F_2\ \ \hat{\sigma}^2_y F_2}}$$

where

$\hat{C}ov(X,Y)$ = estimate of the phenotypic covariance of character X and character Y in the F_2. These covariances were estimated from an analysis of covariance of the same form as the analysis of variance presented previously for F_2.

$\hat{\sigma}^2_x F_2$ = estimate of phenotypic variance for character X in the F_2.

$\hat{\sigma}^2_y F_2$ = estimate of phenotypic variance for character Y in the F_2.

The environmental correlation was calculated by using the following formula:

$$r_e = \frac{\hat{C}ov_H(X,Y)}{\sqrt{\hat{\sigma}^2_{xH}\ \hat{\sigma}^2_{yH}}}$$

where the subscript, H, indicates pooled $\hat{C}ov(X,Y)$ and variance estimates from the parents and F_1. To obtain genotypic correlations in the F_2, the genotypic variance estimates and genotypic covariance estimates were calculated by subtracting the environmental variance and covariance estimates from the respective phenotypic variance and covariance estimates.

The phenotypic, environmental, and genetic correlations in the F_3 were based on family means. The form of the analysis of variance for F_3 family means has been presented previously. The analysis of covariance for F_3 family means was of the same form as the analysis of variance and the expectation of the mean products was the same as that for the respective mean squares. The mean product of families for traits X and Y, obtained from the analysis of covariance, was considered an estimate of the phenotypic covariance for the two characters. The phenotypic variance estimate for each character was the mean square for between F_3 families, MS_3. Thus, the phenotypic correlation between traits X and Y was calculated by the following formula proposed by Anand and Torrie (3).

$$r_p = \frac{MP_3\,(X,Y)}{\sqrt{MS_3\,(X)\;MS_3\,(Y)}}$$

where

$MP_3\,(X,Y)$ = between family mean product for X and Y.
$MS_3\,(X)$ = between family mean square for X.
$MS_3\,(Y)$ = between family mean square for Y.

Environmental correlations were determined by the following formula:

$$r_e = \frac{MP_1\,(X,Y)}{\sqrt{MS_1\,(X)\;MS_1\,(Y)}}$$

The genetic correlation based on F_3 family means was obtained by the following formula:

$$r_g = \frac{\hat{C}ov_b\,(X,Y)}{\sqrt{\hat{\sigma}^2_{bx}\;\hat{\sigma}^2_{by}}}$$

where

$$\hat{C}ov_b\,(X,Y) = [MP_3\,(X,Y) - MP_2\,(X,Y)]/TU$$

$$\hat{\sigma}^2_{bx} = [MS_3\,(X) - MS_2\,(X)]/TU$$

$$\hat{\sigma}^2_{by} = [MS_3\,(Y) - MS_2\,(Y)]/TU$$

and T and U are the number of years and replications, respectively.

Covariances between breeding values of two characters were calculated for all possible combinations of four characters taken two at a time and were used in construction of various selection indexes. The additive and dominance covariances were determined from an analysis of covariance for each pair of characters considered. The analysis of covariance was of the same form as the analysis of variance presented previously for the F_3 on an individual plant basis. The expectations of the mean products were the same as for the respective mean squares. Thus, two equations similar to those presented previously for the between F_3 family variance estimate minus the between row environmental estimate and for the within F_3 family variance estimate minus the within row environmental variance estimate were formed using the corresponding covariance estimates. The two equations were the following:

$$\hat{C}ov_{b\,F_3}(X,Y) - \hat{C}ov_{b\,H}(X,Y) = \hat{C}ov_A(X,Y) + \tfrac{1}{2}\hat{C}ov_D(X,Y)$$

$$\hat{C}ov_{w\,F_3}(X,Y) - \hat{C}ov_{w\,H}(X,Y) = \tfrac{1}{2}\hat{C}ov_A(X,Y) + \tfrac{1}{4}\hat{C}ov_D(X,Y)$$

where

$\hat{C}ov_{b\,F_3}(X,Y)$ = estimate of between F_3 family covariance for X and Y.

$\hat{C}ov_{b\,H}(X,Y)$ = estimate of pooled between rows covariance of X and Y for the parents and F_1.

$\hat{C}ov_{w\,F_3}(X,Y)$ = estimate of within F_3 family covariance for X and Y.

$\hat{C}ov_{w\,H}(X,Y)$ = estimate of pooled within rows covariance of X and Y for the parents and F_1.

$\hat{C}ov_A(X,Y)$ = estimate of additive covariance for characters X and Y.

$\hat{C}ov_D(X,Y)$ = estimate of dominance covariance for characters X and Y.

The two equations were solved to obtain estimates of the additive covariance between pairs of characters. The additive correlation between two characters, X and Y, was found by the following formula:

$$r_A = \frac{Cov_A(X,Y)}{\sqrt{\hat{\sigma}^2_{AX}\ \sigma^2_{AY}}}$$

Selection indexes were constructed for all possible combinations of four characters. The four characters that were considered to contribute to the economic worth of grain sorghum were: plant height, plant yield, kernels per head, and vigor. Worth, W, for sorghum was then defined to be

$$W = V_1X_1 + V_2X_2 + V_3X_3 + V_4X_4$$

where X_1, X_2, X_3, and X_4 are the phenotypic values for plant height, plant yield, kernels per head, and vigor, respectively, and V_1, V_2, V_3, and V_4 represent the relative increase in net worth expected from one unit of improvement for plant height, plant yield, kernels per head, and vigor, respectively. The economic value, V_i, for each character should be determined as accurately as possible. This is often accomplished by studying past records for the economic return each unit of the character contributes to the economic worth of the organism. However, this task is time consuming and even if the economic return for each unit increase of a character can be determined accurately there is no assurance that the economic value so obtained will be correct at the end of the breeding program. The V_i used in this investigation were determined after consulting with other sorghum breeders and discussing the importance, in their opinion, of each character to the economic worth. The values used were: $V_1 = -0.1$, $V_2 = 0.5$, $V_3 = 0.2$, and $V_4 = -0.2$.

If it is assumed that the aggregate breeding value of an individual is the sum of the individual breeding values for each character, the aggregate breeding value, A, is

$$A = V_1 A_1 + V_2 A_2 + V_3 A_3 + V_4 A_4$$

where the V_i are defined as above and the A_i are the breeding values for the characters.

The form of the selection index used was:

$$I = b_1 X_1 + b_2 X_2 + \ldots + b_n X_n$$

where the b_i are weights to be given to the various phenotypic values, X_i. The weights should be such that both:

1. the correlation between A, the aggregate breeding value, and I is a maximum, and
2. the sum of squares of deviations, $\sum_i (A_i - I_i)^2$ is a minimum.

These may be accomplished by taking the partial differential of $\sum_i (A_i - I_i)^2$ with respect to each b_i and setting the result equal to zero. By doing so a set of normal equations is obtained which may be solved by the Abbreviated Doolittle method after the appropriate estimates of the phenotypic and additive variances and covariances have been placed into the equations. As an example, if only three characters were included in the definition of worth, the result of differentiation of $\sum_i (A_i - I_i)^2$ and finding the covariance between the phenotypic value of each character included in worth and the aggregate breeding value would result in the following three normal equations:

$$b_1 \hat{\sigma}^2_{p_1} + b_2 \hat{\sigma}_{p_{12}} + b_3 \hat{\sigma}_{p_{13}} = V_1 \hat{\sigma}^2_{a_1} + V_2 \hat{\sigma}_{a_{12}} + V_3 \hat{\sigma}_{a_{13}}$$

$$b_1 \hat{\sigma}_{p_{12}} + b_2 \hat{\sigma}^2_{p_2} + b_3 \hat{\sigma}_{p_{23}} = V_1 \hat{\sigma}_{a_{12}} + V_2 \hat{\sigma}^2_{a_2} + V_3 \hat{\sigma}_{a_{23}}$$

$$b_1 \hat{\sigma}_{p_{13}} + b_2 \hat{\sigma}_{p_{23}} + b_3 \hat{\sigma}^2_{p_3} = V_1 \hat{\sigma}_{a_{13}} + V_2 \hat{\sigma}_{a_{23}} + V_3 \hat{\sigma}^2_{a_3}$$

where

$\hat{\sigma}^2_{p_i}$ = estimate of the phenotypic variance for the i^{th} character.

$\hat{\sigma}_{p_{ij}}$ = estimate of the phenotypic covariance between the i^{th} and j^{th} character.

$\hat{\sigma}^2_{a_i}$ = estimate of additive variance for the i^{th} character.

$\hat{\sigma}_{a_{ij}}$ = estimate of additive covariance between the i^{th} and j^{th} character.

V_i = economic value for the i^{th} character.

b_i = partial regression coefficient for the i^{th} character.

Before the equations can be solved for the b_i, estimates must be obtained for the other variables in the equations. For each index considered, different b_i's must be obtained. The indexes then may be compared to each other to determine their relative efficiency by determining the correlation between the index and the aggregate breeding value, R_{AI}, as follows:

$$R_{AI} = \sqrt{\hat{\sigma}^2_I / \hat{\sigma}^2_A}$$

where

$\hat{\sigma}^2_I$ = estimate of the variance of the index.

$\hat{\sigma}^2_A$ = estimate of the variance of the aggregate breeding value.

As an example, if three characters were under consideration, the two variances may be determined, using previous notation, in the following manner:

$$\hat{\sigma}_I^2 = b_1^2\hat{\sigma}_{p_1}^2 + b_2^2\hat{\sigma}_{p_2}^2 + b_3^2\hat{\sigma}_{p_3}^2 + b_1 b_2 \hat{\sigma}_{p_{12}} + b_1 b_3 \hat{\sigma}_{p_{13}} + b_2 b_3 \hat{\sigma}_{p_{23}}$$

$$\hat{\sigma}_A^2 = V_1^2\hat{\sigma}_{a_1}^2 + V_2^2\hat{\sigma}_{a_2}^2 + V_3^2\hat{\sigma}_{a_3}^2 + V_1 V_2 \hat{\sigma}_{a_{12}} + V_1 V_3 \hat{\sigma}_{a_{13}} + V_2 V_3 \hat{\sigma}_{a_{23}}$$

The pedigree and topcross breeding procedures by which selection was practiced in the F_2 were compared. Selection under the pedigree method was done strictly on the phenotypic value of the most desirable ten per cent of the 49 F_2 plants for each character. Selection for the most desirable ten per cent of the 49 F_2 individuals under the topcross procedure was accomplished indirectly based on the character means of topcross families. Thus, a progeny test was conducted for each F_2 individual and F_2 plants were chosen on the basis of the performance of their progeny. The base population for which heritability estimates were made consisted of the 49 F_2 plants having enough F_3 and topcross seed considered necessary for this investigation.

Two regression heritability estimates, $b_{F_2,\bar{F}_3}$ and $2b_{F_2,\overline{TO}}$, were made for the base population and were previously discussed. Expected genetic advance for each character in the F_2 for each breeding procedure was determined using the corresponding heritability estimates. Expected genetic advance was compared with actual advance for each character under each procedure. Actual response was determined by subtacting the character mean of the progeny of the selected F_2 individuals from the character mean of the total F_3 population. The level of inbreeding is the same for the progeny and for the total F_3 population. Thus, the above comparison should result in the actual response being free of inbreeding depression. Actual gains under the pedigree procedure were compared with those obtained using the topcross procedure after one cycle of selection. For the topcross method to be more effective per unit of time than the pedigree procedure, it must result in actual gains that are more than twice as large as the actual gains obtained from pedigree selection since the topcross requires two years per cycle compared to only one per cycle for the pedigree.

CHAPTER IV

RESULTS AND DISCUSSION

Selection programs employed for the purpose of crop improvement must utilize variability existing within the available plant populations. If insufficient variability exists in the populations at the breeder's disposal, then it must be introduced. Introduction may be accomplished in a population by mutation, migration or plant introduction, or hybridization. The material used in this investigation resulted from the cross of the two lines previously described. Various estimates of the population parameters were made to determine the likelihood and extent of success should selection for particular plant characters be conducted in the population. Selections were actually practiced on all characters to measure the reliability of the various estimates that were calculated and used to predict gains through selection.

Character means over the test period for the parents and F_1 are presented in Table IV. For plant height, head length, peduncle length, flagleaf height, vegetative height, weight per kernel and vigor dominance in the direction of the high parent was indicated in the complete or overdominant range. Flower date and node number were near the

TABLE IV

PARENTAL AND F_1 CHARACTER MEANS

Character	Combine Kafir 60 Mean	Brown Kaoliang Mean	F_1 Mean
Flower Date	71.6	65.9	66.0
Node Number	19.4	17.7	18.3
Plant Height (cm)	99.7	224.2	237.2
Head Length (cm)	23.2	15.3	23.9
Peduncle Length (cm)	39.7	39.1	45.1
Flagleaf Height (cm)	72.6	198.3	204.8
Vegetative Height (cm)	36.4	169.7	167.8
Plant Yield (gm)	44.4	53.3	40.4
Head Weight (gm)	63.7	66.7	60.7
Weight Per Kernel (gm)	0.027	0.025	0.031
Kernels Per Head	1671.6	2124.3	1283.6
Fertility (%)	68.9	79.6	61.8
Vigor	3.7	3.7	3.6

midparent value indicating little or no dominance. Plant yield, kernels per head, head weight, and fertility had lower mean values than the low parent, i.e., indicating overdominance in the direction of the low parent.

Estimates of the phenotypic, genotypic, and environmental variances were determined for the F_2. The estimates are presented in Table V. The environmental estimates obtained were relatively small compared to their respective phenotypic variance estimates except for peduncle length, plant yield, head weight, and kernels per head. The environmental variance estimates for these latter characters were approximately one-half the magnitude of their respective phenotypic variance estimates. Except for the four characters just mentioned the genotypic variance estimates were relatively high, i.e., almost of the same magnitude as their respective phenotypic variance estimates. Genotypic variance estimates obtained from the F_2 indicated that considerable amounts of genetic differences existed among individuals in the population. Consequently, significant selection progress could be expected for most of the characters in this population. It must be emphasized, however, that the genotypic variance estimates obtained included, if present, additive, dominance, and epistatic variance components. In addition, the estimates of genotypic and phenotypic variance were inflated to an undetermined degree by inclusion of a genotype-location effect. The relative magnitude of the environmental variance estimate for kernels

TABLE V

ESTIMATES OF VARIANCE FOR THE F_2

Characters	Estimate		
	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
Flower Date	12.49	9.12	3.37
Node Number	2.88	2.35	0.53
Plant Height	1893.12	1783.38	109.74
Head Length	14.98	12.27	2.71
Peduncle Length	54.19	32.91	21.28
Flagleaf Height	1969.37	1864.61	104.76
Vegetative Height	1947.27	1833.72	113.55
Plant Yield	542.94	309.51	233.43
Head Weight	729.75	411.67	318.08
Weight Per Kernel	0.0001	0.0001	0.00001
Kernels Per Head	718995.27	435801.07	283194.20
Fertility	0.08	0.07	0.01
Vigor	0.05	0.03	0.02

per head compared to the phenotypic variance estimate for that character suggested that environmental factors accounted for much of the phenotypic differences among individuals for that character. This also seemed to be true for plant yield and head weight.

Phenotypic differences among F_2 individuals would be the basis for practicing selection. However, not all the phenotypic differences are transmitted to the next generation. In fact, only a fraction of the genotypic differences would be transmitted to the next generation. The portion of genotypic differences transmitted to the next generation would be the additive effects and one-half of the dominance deviations. Therefore, estimates of the components of genotypic variance, additive and dominance genetic variance, were obtained to more accurately predict progress under selection.

Estimates of additive, dominance, genotypic, environmental, and phenotypic variances were obtained from analyses of the F_3, F_1, and parents. The estimates are presented in Table VI. Estimates of between rows and within rows variance from the analyses of variance of the parents and F_1 were pooled and subtracted from the between and within F_3 families variance estimates to obtain estimates free of row-to-row and plant-to-plant variation.

F_3 phenotypic variance estimates followed the same trend, character-by-character, set by the F_2 estimates except for plant yield, head weight, and kernels per head.

TABLE VI

ESTIMATES OF THE VARIANCE COMPONENTS FOR THE F_3 [a]

Characters	Estimates				
	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$ [a]
Flower Date	0.00[b]	9.49	9.49	40.77	50.31
Node Number	0.12	3.59	3.71	0.69	4.49
Plant Height	587.72	1476.44	2064.16	250.02	2326.99
Head Length	10.82	0.00[b]	10.82	5.03	15.90
Peduncle Length	6.57	30.20	36.77	27.83	68.09
Flagleaf Height	789.45	1136.25	1925.70	216.73	2149.21
Vegetative Height	831.53	1041.70	1873.23	244.41	2123.48
Plant Yield	67.15	94.27	161.42	255.74	424.90
Head Weight	110.76	73.61	184.37	351.77	545.64
Weight Per Kernel	0.00[b]	0.00	0.00	0.00	0.00
Kernels Per Head	88104.62	238432.05	326536.67	313283.89	648383.58
Fertility	0.00	0.07	0.07	0.01	0.08
Vigor	0.01	0.04	0.05	0.14	0.19

[a] Estimates were determined on a per plant basis. Differences between $\hat{\sigma}^2_P$ and $\hat{\sigma}^2_G + \hat{\sigma}^2_E$ are due to genetic-environmental interaction variance.

[b] Estimates actually obtained were negative.

The only difference was the larger magnitudes of the F_3 phenotypic variance estimates compared with the respective F_2 phenotypic variance estimates. The estimate of phenotypic variance for weight per kernel was zero. This was true for all estimates of variance for this character. Differences did exist in this trait, but the instrument used to make the determinations could not be read accurately enough to detect them. When this was considered, it was thought practical to consider the various estimates of variance for this character to be zero.

The estimate of the environmental variance for each character was made by the procedure discussed previously. Estimates of environmental variance for the F_3 were larger than in the F_2 for all characters. In general, the trend set by the F_2 environmental variance estimates was followed in the F_3.

Knowledge of the magnitude of the additive genetic variance relative to the phenotypic variance for each character is required before accurate predictions can be made of genetic advance through selection. Although in some cases the estimates of additive genetic variance were rather small or zero, it was thought that some progress under selection should be expected for most of the characters. The estimate of dominance variance for head length was zero indicating that gene action for this character was entirely additive. For the other characters, the estimates of dominance variance exceeded the estimates of additive variance except for head weight.

Estimates of genetic variance were determined by adding the estimates of the additive and dominance variance for each character. Significant is the fact that the estimates of genetic variance for all the vegetative characters except head length, the first seven listed in Table VI and vigor, increased in magnitude compared with the estimates of genetic variance for the same characters in the F_2. This would be expected if additive effects were more important for these characters. However, when compared to the F_2 estimates of genotypic variance, the estimates of genetic variance for yield and the yield components decreased in magnitude. Again this would be expected if dominance effects were more important for these characters. Dominance effects are reduced by one-half with each generation of inbreeding. Based on the above comparisons, it was concluded that progress could be realized when selection was practiced for the vegetative characters and vigor even though all these characters, except head length, exhibited dominance variance. Similarly, progress could not be realized to the same extent for yield and its components.

Heritability estimates for all characters were determined for the F_2 and F_3. Three different estimates were made in the F_2 except for weight per kernel, and two estimates were made for each in the F_3. All estimates are presented in Table VII. The F_2 broad sense heritability estimates were determined from the F_2 population used in the

TABLE VII

ESTIMATES OF HERITABILITY PERCENTAGE DETERMINED FROM THE F_2 AND F_3

Characters			F_2[a]				F_3[b]
	(BS)	b_1	SD	$2b_2$	SD	(IPB)	(FMB)
Flower Date	73	33	6	43	7	0	92
Node Number	81	44	5	48	7	3	92
Plant Height	94	55	4	84	9	25	97
Head Length	82	62	4	72	7	68	98
Peduncle Length	61	45	6	42	9	10	85
Flagleaf Height	95	53	5	87	8	37	98
Vegetative Height	94	56	4	86	8	39	98
Plant Yield	57	21	7	3	16	16	91
Head Weight	56	25	6	8	14	20	92
Weight Per Kernel	91	–	–	–	–	0	64
Kernels Per Head	61	23	7	5	12	14	93
Fertility	87	61	7	55	57	0	95
Vigor	56	46	6	39	8	3	90

[a] BS, b_1, $2b_2$, and SD: Estimates of heritability in the broad sense, regression of F_3 family means on F_2 parent, regression of topcross family means on F_2 parent and standard deviation, respectively.

[b] IPB and FMB Estimates of heritability on an individual plant basis and on a family mean basis, respectively.

analysis of variance of the F_2, F_1, and parents. For the vegetative characters, broad sense estimates were high, the lowest estimate being 61 per cent for peduncle length. These characters would be expected to show significant progress under selection. The broad sense heritability estimates for yield, yield components, and vigor were lower, except for weight per kernel and fertility, than the estimates for the vegetative characters. However, they were still high enough to indicate that some progress could be made by selection.

Estimates of heritability were made by regressing the F_3 family means on their respective F_2 parents and by regressing topcross family means on their respective F_2 parents. Assuming no epistasis, the expectation of Cov(F_2, $\bar{F}_3$) is $\frac{1}{2}a^2 + \frac{1}{8}d^2$ where $\frac{1}{2}a^2$ is the variance of breeding values and $\frac{1}{8}d^2$ is the variance of dominance deviations. Since gene frequency was one-half, the expectation of Cov(F_2, $\bar{F}_3$) becomes $\sigma_A^2 + \frac{1}{2}\sigma_D^2$. The expectation of Cov(F_2,$\overline{TO}$) was demonstrated previously. With gene frequency of one-half and no epistasis, the expectation of Cov(F_2,$\overline{TO}$) would be $\frac{1}{2}\sigma_A^2$. Consideration of these facts helps explain the differences between the two regression estimates for each character. Heritability estimates determined by $b_{\bar{F}_3, F_2}$ followed the same trend set by the broad sense estimates of heritability but were of considerably lower magnitude. The estimates for plant yield, head weight, and kernels per head were more in line with estimates of heritability for reproductive characters in other organisms. Heritability estimates determined by the regression of topcross family means on their respective F_2 parents, $2b_{\overline{TO},F_2}$, varied erratically for vegetative characters. A rather large significant difference was obtained between the estimates of heritability for yield and its components using this method compared with their respective estimates using the broad sense and $b_{\overline{F}_3,F_2}$ methods. The estimates for these characters were very low, and their standard deviations exceeded the estimates in every case. The estimate obtained for fertility was relatively high, but its standard deviation also exceeded the estimate. When a comparison of the two breeding procedures is presented later, the estimates of heritability obtained by the regression techniques will be considered further.

Two estimates of heritability for each character were made in the F_3. A narrow sense estimate of heritability was calculated on an individual plant basis by dividing the estimate of additive genetic variance by the estimate of phenotypic variance. Only one estimate, head length, was higher than 50 per cent. Estimates of narrow sense heritability for the other characters were less than or equal to 40 per cent. Three of the estimates, flower date, weight per kernel and fertility, were zero. Heritability estimates were also determined on the family mean basis using the variance component method, a method used extensively in cultivated plants. All estimates obtained were above 80 per cent except for weight per kernel. These estimates appeared to over estimate the differences between families due to heredity. A possible reason for this may be that all of the row-to-row and plant-to-plant variation was not removed from the estimates of heritability. Both estimates indicated that significant progress for most of the characters would result under selection.

Estimates of heritability apply, strictly speaking, to the population, generation, and set of environmental conditions from which the estimates were obtained. If selection is to be practiced in the F_2, then the three procedures previously mentioned may be employed. Care should be exercised, however, in their use. Broad sense heritability estimates contain all of the dominance deviations, which are not fixable, in addition to all the additive variance. The estimates obtained by regression of the F_3 family means on their F_2 parents must also be used with caution because they contain a fraction of the dominance variance. The regression estimates of topcross family means on their F_2 parents contain no dominance and are narrow sense estimates when it is assumed that epistatic effects are absent. Both regression procedures have one serious limitation, i.e., that of having the progeny grown in a different year than are the parents.

Selection in the F_3 is frequently on the family mean basis. Therefore, the heritability estimates employed should be on the same basis. These estimates include both dominance and additive genetic variance as well as row-to-row and plant-to-plant variation. They should be used with these facts clearly in mind. If F_3 individuals are selected, then the narrow sense heritability estimates should be employed for predictive purposes.

Expected genetic advances for each character for each estimate of heritability expressed in the original units of measurement and as a per cent of the mean are presented in Table VIII. The means used for the broad sense F_2 heritability estimates were the character means of the F_2 population from which the analyses of variance were made. The means used when the regression estimates were employed were the character means for the F_2's used as parents for the F_3 and topcross families. Character means were the same for both estimates in the F_3.

Expected response expressed as a per cent of the mean based on broad sense estimates of heritability in the F_2 were generally high. The highest was 100 per cent for kernels per head; and the lowest were six and seven per cent for vigor and flower dates, respectively. Expected response based on the regression of F_3 family means on their F_2 parents estimates expressed as a per cent of the mean were considerably lower than those based on broad sense estimates. However, only three of these were lower than 10 per cent. Expected progress based on these estimates would be acceptable for most of the characters. Expected genetic advances expressed as a per cent of the mean based on heritability estimates determined by twice the regression of

TABLE VIII

EXPECTED GENETIC ADVANCE AND ITS PER CENT OF THE MEAN FOR THE F_2 AND F_3

Characters	F_2[a]						F_3[b]			
	BS	%	b_1	%	$2b_2$	%	IPB	%	FMB	%
Flower Date	4.54	7	2.24	3	2.87	4	0.00	0	3.16	5
Node Number	2.43	13	1.74	9	1.70	8	0.10	1	1.75	9
Plant Height	72.14	37	49.59	22	77.33	35	21.45	12	53.83	30
Head Length	5.58	26	5.05	22	5.57	24	4.78	23	5.69	28
Peduncle Length	7.87	18	5.63	14	5.56	13	1.40	3	6.22	15
Flagleaf Height	73.95	45	50.00	26	83.24	44	29.97	20	57.22	38
Vegetative Height	73.14	56	53.38	34	83.51	54	31.76	27	57.74	49
Plant Yield	23.38	94	7.49	12	1.07	2	5.73	23	17.12	68
Head Weight	26.82	64	10.81	13	3.81	5	8.35	21	20.11	49
Weight Per Kernel	0.02	84	–	–	–	–	0.00	0	0.0037	15
Kernels Per Head	904.57	100	330.01	15	70.27	3	192.60	20	676.99	69
Fertility	43.00	93	7.49	10	6.87	9	0.00	0	22.44	44
Vigor	0.23	6	0.20	6	0.17	5	0.03	1	0.27	7

[a] BS, b_1, and $2b_2$ are estimates of expected genetic advance calculated using broad sense, regression of F_3 family means on their F_2 parent, and regression of topcross family means on their F_2 parent heritability estimates, respectively.

[b] IPB and FMB are expected genetic advance calculated using heritability estimates determined on an individual plant and the family mean basis, respectively.

topcross family means on their F_2 parents were low for yield and its components. For the vegetative characters the expected responses were lower than those based on broad sense estimates, but high enough to indicate satisfactory progress except for flower date and vigor.

Narrow sense heritability estimates in the F_3 were also used to calculate expected genetic advance. The expected genetic advances for flower date, node number, peduncle length, weight per kernel, and vigor were low. The values for the other characters indicated that significant selection progress for them would be expected. Expected genetic advances determined by using heritability estimates based on F_3 family means were relatively high for most characters. Flower date, node number, and vigor were less than ten per cent. The expected genetic advances for the other characters were in most cases fairly high indicating significant progress would be expected.

Plant height, plant yield, weight per kernel, kernels per head, and vigor were used to obtain estimates of the phenotypic, genetic, and environmental correlation coefficients in the F_2 and F_3 . In the F_2 the correlations were estimated on a per plant basis and in the F_3 on the family mean basis. The correlation coefficients obtained for the five characters taken two at a time in both generations are presented in Table IX. For the F_2 and F_3 phenotypic and environmental correlation coefficients tests of significance were made at the 0.05 and 0.01 levels of probability. The

TABLE IX

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS DETERMINED ON THE F_1, F_2, PARENTS, AND ON THE F_3 FAMILY MEANS

Correlation of		F_2			F_3	
	P[a]	G	E[b]	P[c]	G	E[d]
Plant Height and						
Plant Yield	0.21**	0.26	0.14**	0.38**	0.39	0.26**
Weight Per Kernel	0.24**	0.23	U	0.56**	0.62	-0.05
Kernels Per Head	0.17**	0.20	0.13**	0.31*	0.32	0.26**
Vigor	-0.35**	-0.41	-0.35**	-0.05	-0.04	-0.14*
Plant Yield and						
Weight Per Kernel	0.47**	0.55	U	0.58**	0.61	0.30**
Kernels Per Head	0.98**	1.00	0.95**	0.98**	0.98	0.97**
Vigor	0.10	-0.07	-0.13**	-0.21	-0.21	-0.16*
Weight Per Kernel and						
Kernels Per Head	0.43**	0.53	U	0.46**	0.48	0.17*
Vigor	0.08	-0.06	U	-0.34*	-0.26	0.00
Kernels Per Head and						
Vigor	-0.09	-0.07	-0.12*	-0.17	-0.17	-0.14

*Significant at the 0.05 level.

**Significant at the 0.01 level.

[U] Undefined mathematical operation, i.e., denominator was zero.

[a] Significant values are 0.098 and 0.128 for the 0.05 and 0.01 levels, respectively, for 335 degrees of freedom.

[b] Significant values are 0.099 and 0.129 for the 0.05 and 0.01 levels, respectively, for 395 degrees of freedom.

[c] Significant values are 0.277 and 0.359 for the 0.05 and 0.01 levels, respectively, for 47 degrees of freedom.

[d] Significant values are 0.141 and 0.185 for the 0.05 and 0.01 levels, respectively, for 194 degrees of freedom.

degrees of freedom for testing the non-existence of the phenotypic correlation coefficient in the F_2 were obtained by subtracting one, for the covariable, from the degrees of freedom for the plants in rows in replications in years entry. The degrees of freedom for testing the significance of the environmental correlation coefficients in the F_2 were determined by subtracting one from the pooled F_1 and parents degrees of freedom from the same entry. To test the significance of the phenotypic and environmental correlation coefficients in the F_3, one was subtracted from each of the families and experimental error degrees of freedom, respectively. No test of significance exists for the genetic correlation coefficients.

Phenotypic correlation coefficients in the F_2 varied considerably in magnitude. Two of the correlation coefficients, plant height and vigor and kernels per head and vigor, were negative. The largest correlation coefficient was for plant yield and kernels per head. The environmental correlation coefficients which could be determined followed the same trend as the phenotypic correlation coefficients except that the environmental correlation coefficient for plant yield and vigor was negative. The largest environmental correlation coefficient was again for plant yield and kernels per head. The trend set by the phenotypic correlation coefficients was also followed by the genetic correlation coefficients. The highest genetic correlation coefficient was again for plant yield and kernels per head.

This is in agreement with results reported by other investigators in sorghum (6, 38, 39, 43, 50). Genetic correlation coefficients for plant yield and weight per kernel and kernels per head and weight per kernel were high and positive. Another significant aspect of the F_2 genetic correlation coefficients was that each one involving vigor was negative. This indicated that selection for an increase in this character would result in a decrease in the others and vice versa. With respect to plant height, this would be desirable under most conditions, but not for the other characters. However, the low genetic correlation coefficients of vigor with each of the other traits seemed to indicate that selecting for increased vigor would have a negligible effect on those characters.

Phenotypic correlation coefficients in the F_3 tended to be higher than the respective F_2 phenotypic correlation coefficients. The only exceptions were the correlation coefficients for plant height and vigor and for plant yield and kernels per head. The phenotypic correlation coefficients involving vigor were again all negative. This was also true for the genetic correlation coefficients in the F_3. The F_3 genetic correlation coefficients followed the same trend as the phenotypic correlation coefficients and in every case but one equaled or exceeded the corresponding phenotypic correlation coefficients. The genetic correlation coefficients that were high in the F_2 were repeated in the F_3.

It appeared that kernels per head and plant height were influenced by genes common to each or by linked genes. The same appeared to be true for plant yield and kernels per head, plant yield and weight per kernel, and weight per kernel and kernels per head. Therefore, selection for an increase in any one character of the ones mentioned above should result in an increase of its correlated character. Environmental correlation coefficients fluctuated widely. The lowest was zero for weight per kernel and vigor and the highest was for plant yield and kernels per head.

Characters used in the determinations of the phenotypic, genetic, and environmental correlation coefficients above were used to calculate correlation coefficients between the breeding values of those characters. These coefficients are presented in Table X. The correlation coefficients involving weight per kernel could not be determined because the estimate of additive genetic variance for that character was zero. All of the correlation coefficients involving vigor were negative. The absolute values of all the breeding value correlations were above 0.5 and were considered to be significant. Consequently, it was thought pleiotropic gene action existed for these characters. The positive correlations indicated that some genes increased both characters. The negative correlations indicated that some genes increased one character and at the same time reduced another character.

All possible selection indexes between plant height,

TABLE X

CORRELATIONS OF BREEDING VALUES DETERMINED FROM THE F_3

Correlation of	r_a
Plant Height and	
Plant Yield	1.23
Weight Per Kernel	U[a]
Kernels Per Head	1.04
Vigor	-0.53
Plant Yield and	
Weight Per Kernel	U
Kernels Per Head	3.08
Vigor	-0.62
Weight Per Kernel and	
Kernels Per Head	U
Vigor	U
Kernels Per Head and	
Vigor	-0.65

[a] U: Undefined mathematical operation, i.e., denominator was zero.

plant yield, kernels per head, and vigor were determined and compared by the magnitudes of correlation coefficients for the index and aggregate breeding value. The indexes and correlation coefficients are presented in Table XI. Properly constructed indexes have proven superior to other selection methods (30). Objections raised against their use are that new estimates of the phenotypic and additive genetic variances and covariances should be obtained for each new generation and that solutions for the normal equations required to obtain the weights to be given each character are difficult to solve, especially when several characters are included. Theoretically, the best index would be one utilizing all characters included in the definition of worth. However, by comparing the index-aggregate breeding value correlation coefficients, an index containing a subset of the characters defining worth may be as satisfactory as the index containing all the characters. The index-aggregate breeding value correlation coefficient for the index considering all characters was 0.40. Two indexes that included only one character, the index for plant height and the one for plant yield, had correlation coefficients as large or larger than the index for all characters. It was thought that these correlations were in error although, no computational errors could be found. They were not used to select F_2 individuals. Two indexes involving only two characters had correlation coefficients as large or larger than the index for all characters. The first of these, the index

TABLE XI

POSSIBLE SELECTION INDEXES CONSIDERING FOUR CHARACTERS AND THE CORRELATIONS BETWEEN EACH INDEX AND AGGREGATE BREEDING VALUE

Indexes	r_{AI}
(-0.253)PH[a]	0.50
(0.790)PY	0.40
(0.272)K/H	0.37
(-0.068)V	0.18
(-0.152)PH+(0.689)PY	0.37
(1.131)PH+(0.252)K/H	0.38
(-0.253)PH+(1.081)V	0.50
(20.450)PY-(0.223)K/H	0.39
(0.788)PY-(0.882)V	0.40
(0.272)K/H+(3.010)V	0.35
(-0.151)PH+(0.687)PY-(1.023)V	0.37
(0.947)PH+(17.542)PY-(0.167)K/H	0.40
(1.140)PH+(0.251)K/H-(10.360)V	0.38
(19.761)PY-(0.195)K/H+(144.442)V	0.40
(0.960)PH+(17.603)PY-(0.170)K/H-(17.434)V	0.40

[a] PH, PY, K/H, and V represent plant height, plant yield, kernels per head, and vigor, respectively.

for plant height and vigor, would be the easier of the two to employ because the values for the characters involved are more easily determined than are those in the second index. Both plant yield and kernels per head are relatively difficult to determine. Two indexes involving three characters, had index-aggregate breeding value correlation coefficients equal to the four-character index. However, considering the time and expense involved, either of the indexes involving only two characters would be preferred.

Two breeding procedures were compared to determine whether one procedure would give greater response than the other. One method was the regular pedigree method, i.e., F_2 individuals were selected on the basis of their phenotypic differences and advanced to the next generation. The response due to selection was measured as the mean deviation of the F_3 family means, progeny of the selected F_2 individuals, from the total F_3 population mean for a given character. The other procedure, a topcross, was a progeny test method, i.e., F_2 individuals were selected on the basis of their progenies' performance. The selected F_2 individuals were then advanced to the F_3 and response due to selection measured as stated above. To be as effective as the pedigree method per unit of time the topcross procedure would have to give twice the response of the pedigree since it requires two years per cycle compared to one year per cycle for the pedigree.

Actual responses from selecting the most desirable ten per cent for each character under each breeding procedure are presented in Table XII. The values in this table are in actual units of measure, i.e., centimeters for plant height, head length, peduncle length, flagleaf height, and vegetative height and grams for plant yield, head weight, and weight per kernel. Progress was made under both procedures for all characters in the desired direction. Significant response, five per cent or greater, was realized for all characters under the pedigree procedure except for flower date. For the topcross procedure significant response was not realized for flower date, node number, and vigor. All of the characters except head length exhibited considerable amounts of dominance variance when compared to the magnitudes of the additive variances. However, the actual responses demonstrated that for practically all of the characters additive effects were important.

In no case were responses for any character using the topcross twice as large as for the same character under the pedigree procedure except for fertility. In fact, only plant height, flagleaf height, vegetative height, plant yield, kernels per head, and fertility showed greater responses under the topcross procedure in the deisred direction. Considering the additional time and expense involved, the topcross procedure was not as effective per unit of time in this material as was the pedigree procedure.

Inbreeding depression for each character from the F_2 to the F_3, is presented in Table XIII. Inbreeding

TABLE XII

ACTUAL RESPONSE TO SELECTION UNDER TWO BREEDING PROCEDURES

Characters	Response							
	P[a]	%$\bar{X}$	T	%$\bar{X}$	IP	%$\bar{X}$	IT	%$\bar{X}$
Flower Date	1.85	2.7	2.05	3.0	–	–	–	–
Node Number	1.61	8.7	0.83	4.5	–	–	–	–
Plant Height	42.34	23.7	52.65	29.5	-19.55	-11.0	-35.52	-19.9
Head Length	6.24	30.4	5.56	27.1	–	–	–	–
Peduncle Length	6.01	14.7	4.93	12.0	–	–	–	–
Flagleaf Height	52.45	35.3	57.03	38.3	–	–	–	–
Vegetative Height	45.43	38.8	56.89	48.6	–	–	–	–
Plant Yield	7.85	31.0	9.90	39.0	9.82	38.7	9.90	39.0
Head Weight	10.87	26.7	8.88	21.8	–	–	–	–
Weight Per Kernel	–	–	–	–	–	–	–	–
Kernels Per Head	275.5	28.3	358.4	36.8	357.6	36.7	350.4	36.0
Fertility	5.79	11.2	17.69	34.3	–	–	–	–
Vigor	0.58	15.5	0.16	4.3	0.07	1.9	-0.06	-1.6

[a] P, T, IP, and IT are response due to selection under the pedigree, topcross, selection index in pedigree, and selection index in topcross procedures, respectively.

TABLE XIII

INBREEDING DEPRESSION (I) FROM THE F_2 TO THE F_3

Characters	I
Flower Date	-1.48
Node Number	0.26
Plant Height	15.66
Head Length	1.22
Peduncle Length	1.74
Flagleaf Height	14.06
Vegetative Height	12.95
Plant Yield	-0.43
Head Weight	0.97
Weight Per Kernel	-
Kernels Per Head	-70.89
Fertility	-5.44
Vigor	-0.04

depression was determined by subtracting the total F_3 character means from the corresponding F_2 character means. Negative values indicated that no inbreeding depression from the F_2 to the F_3 occurred, i.e., the F_3 character mean was larger than the F_2 character mean. Both the F_2 and the F_3 populations were grown during the same two years so that year effects should be at a minimum. The positive values indicated that inbreeding depression did occur for those characters exhibiting them.

Differences between expected genetic advance and actual response in the original units of measurements for each character under each breeding procedure are presented in Table XIV. A comparison of differences for each character gives an indication which heritability estimate was more accurate for predictive purposes. The two heritability estimates compared were the regression of F_3 family means on their respective F_2 parents and twice the regression of topcross family means on their respective F_2 parents. Absolute differences were smaller for all characters for the F_3 family mean method of estimation than for topcross method of estimating heritability. This was true probably because the expectation of $Cov(F_2, \bar{F}_3)$ is $\sigma_A^2 + \frac{1}{2}\sigma_D^2$ and one-half the dominance deviations in the F_2 are passed to the F_3. Therefore, the estimate of heritability that includes dominance would more accurately predict the change expected in the means of the progeny from the selected parents. These considerations led to the conclusion that the regression of the

TABLE XIV

DIFFERENCES BETWEEN EXPECTED AND ACTUAL GENETIC ADVANCE FOR TWO BREEDING PROCEDURES

Characters	Advance Determined	
	by using b_1[a]	by using $2b_2$
Flower Date	0.39	0.82
Node Number	0.13	0.87
Plant Height	7.25	24.68
Head Length	-1.19	0.01
Peduncle Length	-0.38	0.63
Flagleaf Height	-2.45	26.21
Vegetative Height	7.95	26.62
Plant Yield	-0.36	-8.83
Head Weight	-0.06	-5.07
Weight Per Kernel	-	-
Kernels Per Head	54.49	-288.16
Fertility	1.71	-10.82
Vigor	-0.38	0.01

[a] b_1 and $2b_2$ Estimates of heritability determined by regression of F_3 family means on F_2 parents and by twice the regression of topcross family means on F_2 parents, respectively.

F_3 family means on their respective F_2 parents was the best estimate of heritability to use for predictive purposes in the F_2.

Application of the method proposed by Mather (47) involving the F_2 and both first backcross generations of the F_1 to the parents would also have allowed a narrow sense estimate of heritability to be made in the F_2. His procedure would require less time and expense than would either of the two above procedures. In addition, all material could be grown the same year. Therefore, environmental differences would be very similar for the F_2 and backcrosses.

The average degree of dominance, h, was calculated by Mather's (47) formula given below. The formula has been applied by various investigators (12, 26, 42, 51). The values for each character are presented in Table XV. The formula used to determine the average degree of dominance, h, is:

$$h = \sqrt{\hat{\sigma}^2_D / \hat{\sigma}^2_A}$$

where

$\hat{\sigma}^2_D$ = estimate of dominance genetic variance.

$\hat{\sigma}^2_A$ = estimate of additive genetic variance.

All characters for which the determination could be made exhibited some degree of dominance except head length. As demonstrated previously, this character is determined almost entirely by additive gene action. The average degree of

TABLE XV

AVERAGE DEGREE OF DOMINANCE (h) OF LOCI CONTRIBUTING TO EACH CHARACTER

Characters	h
Flower Date	U
Node Number	5.58
Plant Height	1.58
Head Length	0.00[a]
Peduncle Length	2.14
Flagleaf Height	1.20
Vegetative Height	1.12
Plant Yield	1.18
Head Weight	0.82
Weight Per Kernel	U[b]
Kernels Per Head	1.65
Fertility	U
Vigor	2.50

[a] Estimate of dominance genetic variance was zero.

[b] U: Undefined mathematical operation, i.e., $\hat{\sigma}_A^2 = 0$.

dominance for flower date, weight per kernel, and fertility could not be calculated because the estimate of additive genetic variance for these characters was zero. The highest average degree of dominance was for node number, followed by vigor and peduncle length, respectively. The values for average degree of dominance agreed with the conclusions drawn when the means of each character were compared in the F_1 and parents. These revealed that for the vegetative characters except head length dominance existed in the direction of and in some cases exceeded the tall parent. For plant yield and the yield components dominance appeared to exist largely in the direction of the lower parent; even exceeding the lower parent in some cases. Dominance was important for all characters considered in the investigation, except head length.

CHAPTER V

SUMMARY AND CONCLUSIONS

Estimates of phenotypic, genotypic, and environmental variance were obtained for thirteen mature plant characters in the F_2 of a cross between two inbred lines. Estimates of environmental variance were relatively small compared to their respective phenotypic variance estimates except for peduncle length, plant yield, head weight, and kernels per head. The estimates of environmental variance for those characters were approximately one-half the magnitude of their respective phenotypic variance estimates. The genotypic variance estimates were relatively high for all characters when compared to their phenotypic variance estimates except for peduncle length, plant yield, head weight, and kernels per head. With the exception of weight per kernel, all characters exhibited sufficient genotypic variance to indicate that progress under selection could be expected if selection were practiced on this population.

Additive, dominance, genetic, environmental, and phenotypic variance estimates were obtained in the F_3. The phenotypic variance estimates of the F_3 followed the trend set by the F_2 except for plant yield, head weight, weight per kernel, and kernels per head. The magnitude of the F_3

phenotypic variance estimate was larger for each character than in the F_2 except for the characters previously mentioned. Due to rounding error and the lack of refinement of the balance used to measure weight per kernel, the estimates of variance for this character in the F_3 were zero. Additive variance was demonstrated for all characters except flower date, weight per kernel, and fertility. Estimates of additive genetic variance for the other characters indicated that considerable progress on an individual plant basis would be expected should selection be practiced for them. Estimates of the dominance genetic variance for head length and weight per kernel were zero. Assuming no epistasis, gene action for head length appeared entirely additive. Estimates of dominance genetic variance exceeded their respective estimates of additive genetic variance for all characters except head weight. However, since additive variance may exist when any degree of dominance is present, progress under selection for those characters would be realized to some extent.

Estimates of genetic variance were obtained by adding the estimates of additive and dominance variance for each character. The most obvious fact was the increase of the estimates of genetic variance in the F_3 for the vegetative characters and vigor as compared to the estimates of genotypic variance for these characters in the F_2. If the major contribution to these characters is additive effects, then these increases would be expected. Another interesting fact was the decrease in magnitude of the estimates of genetic variance for yield, head weight, and kernels per head in the F_3 compared to their magnitudes in the F_2. These decreases would be expected if the major contribution to the genetic differences of each of these characters was due to dominance gene action.

Estimates of heritability were obtained in the F_2 and F_3. In the F_2, heritability was estimated in the broad sense, as the regression of the F_3 family means on their respective F_2 parents, and as twice the regression of the topcross family means on their respective F_2 parents. In the F_3, a narrow sense estimate of heritability on an individual plant basis, and an estimate of heritability determined on the family mean basis were made. All estimates of broad sense heritability in the F_2 were high, indicating rapid progress under selection. However, since these estimates contain all of the genetic variance, little confidence could be placed in them as estimates of additive variance. The estimates of heritability determined by the other two methods in the F_2 corresponded more closely with heritabilities reported for other organisms, especially for characters connected with reproduction. The covariances for the estimates of heritability obtained by regressing F_3 family means on their F_2 parents contained a fraction of the dominance variance and, therefore, were not strictly narrow sense estimates. However, the estimates of heritability obtained by doubling the regression of topcross family means on their

F_2 parents contained no dominance variance and were narrow sense heritability estimates. For this reason, it was concluded that the estimates obtained by this method were the best estimates of heritability in the F_2, and should be used for predictive purposes.

The narrow sense estimates of heritability in the F_3 were relatively low, yet for most of the characters they indicated that some progress under selection would be expected. The estimates for flower date, fertility and weight per kernel were zero while the estimates for vigor and node number were very low. The estimates of heritability on the family mean basis were high compared with either the narrow sense estimates in the F_3 or F_2. They were of approximately the same magnitude as the broad sense estimates in the F_2. Estimates of heritability on the family mean basis contained a fraction of the dominance variance and were not heavily relied upon as indicators of progress to be expected under selection.

Expected progress under selection was determined using each estimate of heritability obtained in the F_2 and F_3. The expected response was reported in the actual units of measurement and as a per cent of the mean. When the broad sense estimate of heritability from the F_2 was used, the values obtained were relatively high. Except for flower date and vigor, expected genetic advance for all characters was greater than ten per cent. Expected genetic advance determined by both regression estimates of heritability in the F_2 was in general lower for each character. Expected advance based on twice the regression of topcross family means on their F_2 parents was lower for all characters, except for plant height, head length, flagleaf height, and vegetative height, than expected advance based on the regression of F_3 family means on their F_2 parents. The characters whose expected advances were greater when determined on the topcross heritabilities than on the other regression estimate of heritability were characters whose ratios of additive to dominance variance estimates were high. A significant fact about the expected advances determined using the topcross heritabilities is that the values for most of the vegetative characters were high but that the values for yield and its components were low.

Expected genetic advance determined in the F_3 from the narrow sense estimates of heritability were lower for the vegetative characters than any of the estimates in the F_2. However, for plant yield, head weight, and kernels per head, the estimates were higher than those of the topcross heritabilities in the F_2. From these estimates, it was concluded that little or no progress could be expected for flower date, node number, peduncle length, weight per kernel, fertility, and vigor. Except for flower date, node number, and vigor expected genetic advances determined on the family mean estimate of heritability were relatively high indicating adequate progress would be expected.

Phenotypic, genetic, and environmental correlation coefficients were determined for each possible pair of five characters. The characters considered were plant height, plant yield, weight per kernel, kernels per head, and vigor. The correlation coefficient estimates in the F_2 were determined on an individual plant basis and in the F_3 on a family mean basis. Phenotypic correlation coefficients in the F_2 were quite variable. Except for two, plant height and vigor and kernels per head and vigor, all estimates were positive. All estimates of F_2 phenotypic correlation coefficient were significant at the 0.01 level of significance except for plant yield and vigor. All F_2 environmental correlation coefficients were significant at the 0.05 level of significance, and most were significant at the 0.01 level. The highest F_2 genetic correlation coefficient was for plant yield and kernels per head. All genetic correlations involving vigor were negative indicating that selection for this character would result in negative responses for the other characters. For plant height, this association would be desirable.

Except for plant height and vigor, the F_3 phenotypic correlation coefficients were of greater magnitude than the respective estimates in the F_2. All F_3 correlation coefficients involving vigor were negative except for the environmental correlation coefficient, weight per kernel and vigor. The F_3 genetic correlation coefficients followed the trend set by the phenotypic correlation coefficients and equaled or exceeded their respective phenotypic correlations except for plant height and vigor. The large magnitudes of the F_3 genetic correlation coefficients indicated that genes affecting one character also are linked to genes influencing other characters or directly exert influence on those other characters through pleiotrophy. Therefore, it was assumed that selection for any one of the five characters would result in some response being exhibited by the other four.

Breeding value correlation coefficients were determined for the same five characters considered for the above correlation coefficients. Those involving weight per kernel could not be determined because the estimate of additive genetic variance was zero. All of the correlations were considered significant. These correlations indicated that genes influencing one character affect others to some extent in the same manner or are linked to genes which do.

Selection indexes were constructed for all possible combinations of plant height, plant yield, kernels per head, and vigor. Correlation coefficients between aggregate breeding value and the index for each combination were determined and their magnitudes compared to determine the most efficient index. Theoretically, the index that considers all characters included in the definition of worth would be the most efficient index. However, an index composed of a subset of those characters may be as efficient as one that considers all characters, especially when time and expense of data collection are considered. It was found that two separate indexes involving only two characters were as efficient as the index composed of all four characters. Those indexes were b_1 plant height + $b_2$vigor and b_1 plant yield + $b_2$kernels per head. When the ease of data collection was considered, the first index would be the more efficient. The indexes for plant height and for plant yield had coefficients as large or larger than the index for all characters. However, it was decided not to rely on them.

Selection was practiced under the pedigree and the topcross breeding methods. The topcross method is a progeny test procedure and takes twice as much time per cycle as the pedigree method. Therefore, to be considered more efficient the topcross method must result in more than twice the actual response of the pedigree method. The response to selection was reported in actual units of measure for each character. Progress was made for all the characters under both breeding procedures. In no case was response for any character under the topcross procedure more than twice as great as the pedigree method except for fertility. Thus, the pedigree method was the more desirable breeding procedure under which selection should be practiced in this material.

For each breeding procedure compared, a different estimate of heritability was used. For the pedigree procedure, the regression of F_3 family means on their respective F_2 parent was used as the estimate; and for the topcross procedure, twice the regression of the topcross family means on their respective F_2 parents was used. Differences between the expected and actual genetic response for each character under each breeding procedure were compared in an effort to determine which estimate of heritability was more accurate for predictive purposes. The absolute differences were smaller for each character under the F_3 family mean method. These results were expected because the expectation of the $Cov(F_2, \bar{F}_3)$ includes in addition to additive variance a fraction of the dominance variance. Both the additive and a fraction of the dominance effects would be transmitted to the F_3. Therefore, it was concluded that this estimate of heritability was the better of the two for predictive purposes. When the time and expense were considered to obtain both estimates of heritability, the additional precision if any gained by the topcross estimate did not appear to be worthwhile from a practical standpoint.

The average degree of dominance was determined for the genes influencing each character by using Mather's (47) formula. Except for head length, all characters exhibited some degree of dominance. The average degree of dominance for flower date, weight per kernel, and fertility could not be determined because their estimates of additive variance were zero. The highest average degree of dominance was for node number followed by vigor and peduncle length. These results agreed with the conclusions reached when the means of each character were compared for the F_1 and parents. A comparison of means revealed that in general the vegetative characters exhibited dominance in the direction of the higher parent while yield and its components exhibited dominance in the direction of the lower parent. Dominance was important for each character except head length.

The estimates of population parameters reported and the conclusions obtained concerning their implications apply strictly to the material used in this investigation and the set of environmental conditions sampled. Caution should be exercised before attempting to apply these results and the conclusions drawn from them to other sorghum material under other environmental conditions.

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APPENDIX

TABLE XVI

CHARACTER MEANS AND MEAN SQUARES FOR THE PARENTS, F_1, F_2

Character	P_1			P_2		F_1		F_2		
	Mean	df	MS	Mean	MS	Mean	MS	Mean	df	MS
Flower Date	71.6			65.9		66.0		67.1		
Yrs		1	4334.0		1899.5		2970.3		1	7452.9
Reps + Reps x Yrs		4	15.4		9.3		19.4		4	4.4
Rows in Reps in Yrs		6	16.3		14.9		21.3		18	27.3
Plts in Rows in Reps in Yrs		132	2.9		4.1		3.1		336	12.5
Node Number	19.4			17.7		18.3		18.2		
Yrs		1	19.5		40.1		0.4		1	4.4
Reps + Reps x Yrs		4	0.9		1.8		3.8		4	0.3
Rows in Reps in Yrs		6	2.2		1.2		0.5		18	4.4
Plts in Rows in Reps in Yrs		132	0.5		0.6		0.5		336	2.9
Plant Height	99.7			224.2		237.2		194.2		
Yrs		1	95.1		491.4		6778.8		1	7802.7
Reps + Reps x Yrs		4	292.9		744.5		1927.5		4	2093.5
Rows in Reps in Yrs		6	15.3		276.0		290.1		18	3235.0
Plts in Rows in Reps in Yrs		132	40.1		143.2		145.9		336	1893.1
Head Length	23.2			15.3		23.9		21.7		
Yrs		1	297.6		41.2		57.5		1	265.2
Reps + Reps x Yrs		4	6.7		8.6		6.1		4	18.6
Rows in Reps in Yrs		6	5.9		1.6		6.5		18	17.0
Plts in Rows in Reps in Yrs		132	3.6		2.0		2.6		336	15.0

TABLE XVI (Continued)

	P_1			P_2		F_1		F_2		
Character	Mean	df	MS	Mean	MS	Mean	MS	Mean	df	MS
Peduncle Length	39.7			39.1		45.1		42.8		
Yrs		1	184.5		383.5		58.8		1	525.6
Reps + Reps x Yrs		4	68.8		41.3		48.3		4	82.5
Rows in Reps in Yrs		6	11.7		36.8		34.5		18	97.9
Plts in Rows in Reps in Yrs		132	14.4		22.6		26.8		336	54.2
Flagleaf Height	72.6			198.3		204.8		162.8		
Yrs		1	0.8		0.0		6958.3		1	4876.7
Reps + Reps x Yrs		4	46.4		1023.8		2282.0		4	2625.3
Rows in Reps in Yrs		6	21.5		343.5		230.1		18	3187.3
Plts in Rows in Reps in Yrs		132	24.9		136.6		152.7		336	1969.4
Vegetative Height	36.4			169.7		167.8		130.0		
Yrs		1	64.0		38.3		6346.8		1	7290.0
Reps + Reps x Yrs		4	49.9		826.5		1884.4		4	2626.9
Rows in Reps in Yrs		6	14.2		307.4		345.2		18	3101.0
Plts in Rows in Reps in Yrs		132	24.3		123.3		193.0		336	1947.3
Plant Yield	44.4			53.3		40.4		24.9		
Yrs		1	4534.9		9220.8		6313.6		1	683.4
Reps + Reps x Yrs		4	119.9		839.1		511.3		4	293.8
Rows in Reps in Yrs		6	228.1		200.5		732.3		18	501.8
Plts in Rows in Reps in Yrs		132	119.4		163.0		417.9		336	542.9
Head Weight	63.7			66.7		60.7		41.7		
Yrs		1	4415.6		17038.9		3906.3		1	210.8
Reps + Reps x Yrs		4	129.1		1101.0		718.2		4	523.3
Rows in Reps in Yrs		6	330.4		265.1		815.2		18	681.4
Plts in Rows in Reps in Yrs		132	181.9		243.6		528.8		336	729.8

TABLE XVI (Continued)

Character	P_1			P_2		F_1		F_2		
	Mean	df	MS	Mean	MS	Mean	MS	Mean	df	MS
Weight Per Kernel	0.0265			0.0253		0.0307		0.0238		
Yrs		1	0.000001		0.000013		0.000434		1	0.000049
Reps + Reps X Yrs		4	0.000014		0.000005		0.000019		4	0.000224
Rows in Reps in Yrs		6	0.000017		0.000014		0.000007		18	0.000070
Plts in Rows in Reps in Yrs		132	0.000008		0.000004		0.000012		336	0.000091
Kernels Per Head	1671.6			2124.3		1283.6		903.6		
Yrs		1	6174835.5		12018534.4		3622621.1		1	449814.0
Reps + Reps X Yrs		4	346498.7		1579452.8		506623.4		4	414199.5
Rows in Reps in Yrs		6	157491.8		343420.3		783722.1		18	692318.8
Plts in Rows in Reps in Yrs		132	135511.5		315245.1		398826.0		336	718995.3
Fertility	68.9			79.6		61.8		46.1		
Yrs		1	1252.2		130.0		6105.6		1	3675.7
Reps + Reps X Yrs		4	177.8		92.2		320.4		4	155.2
Rows in Reps in Yrs		6	17.1		21.7		566.4		18	752.8
Plts in Rows in Reps in Yrs		132	28.3		18.2		274.0		336	806.9
Vigor	3.7			3.7		3.6		3.7		
Yrs		1	6.6		14.4		8.3		1	18.6
Reps + Reps X Yrs		4	0.1		0.1		0.1		4	0.0
Rows in Reps in Yrs		6	0.0		0.1		0.1		18	0.1
Plts in Rows in Reps in Yrs		132	0.0		0.0		0.0		336	0.1

TABLE XVII

CHARACTER MEAN PRODUCTS FOR THE PARENTS, F_1, AND F_2

	P_1		P_2	F_1	F_2	
Character	df	MP	MP	MP	df	MP
PH,PY						
Rows in Reps in Yrs	6	31.3	200.7	-156.4	-	-
Plts in Rows in Reps in Yrs	132	29.3	69.3	-33.7	336	271.5
PH,K/H						
Rows in Reps in Yrs	6	516.5	5938.1	-4188.8	-	-
Plts in Rows in Reps in Yrs	132	716.4	2619.2	-1141.2	336	6246.3
PH,Vig						
Rows in Reps in Yrs	6	-0.1560	-2.5995	1.0133	-	-
Plts in Rows in Reps in Yrs	132	-0.0596	-1.3192	-0.3435	336	-3.6398
PY,K/H						
Rows in Reps in Yrs	6	5314.7	7075.2	23598.3	-	-
Plts in Rows in Reps in Yrs	132	3606.2	6836.1	12826.2	336	19434.8
PY,Vig						
Rows in Reps in Yrs	6	-2.1062	-3.9297	2.8546	-	-
Plts in Rows in Reps in Yrs	132	-0.2085	-1.0242	0.2808	336	-0.5308
K/H,Vig						
Rows in Reps in Yrs	6	-55.7	160.9	125.9	-	-
Plts in Rows in Reps in Yrs	132	0.9	-42.6	11.3	336	-17.8

TABLE XVIII

CHARACTER MEANS AND MEAN SQUARES FOR THE F_3

		F_3	
Character	Mean	df	MS
Flower Date	68.5		
Yrs		1	61918.48
Reps		2	32.55
Fams		48	276.82
Yrs x Fams		48	23.53
Exp Error		194	21.67
Within Fams		3234	8.09
Node Number	18.5		
Yrs		1	0.57
Reps		2	4.92
Fams		48	84.47
Yrs x Fams		48	6.93
Exp Error		194	3.51
Within Fams		3234	2.39
Plant Height	178.6		
Yrs		1	146250.35
Reps		2	13514.95
Fams		48	71496.95
Yrs x Fams		48	2100.91
Exp Error		194	1639.34
Within Fams		3234	1141.82
Head Length	20.5		
Yrs		1	3029.01
Reps		2	24.67
Fams		48	782.36
Yrs x Fams		48	14.29
Exp Error		194	12.79
Within Fams		3234	7.49
Peduncle Length	41.0		
Yrs		1	7202.86
Reps		2	542.44
Fams		48	1240.17
Yrs x Fams		48	184.95
Exp Error		194	59.12
Within Fams		3234	39.67

TABLE XVIII (Continued)

		F_3	
Character	Mean	df	MS
Flagleaf Height	148.7		
Yrs		1	98705.48
Reps		2	12345.58
Fams		48	79646.88
Yrs X Fams		48	1792.03
Exp Error		194	1548.15
Within Fams		3234	1067.61
Vegetative Height	117.1		
Yrs		1	118086.43
Reps		2	12132.71
Fams		48	81097.09
Yrs X Fams		48	1823.84
Exp Error		194	1613.55
Within Fams		3234	1050.16
Plant Yield	25.4		
Yrs		1	1600.43
Reps		2	620.68
Fams		48	8151.47
Yrs X Fams		48	698.67
Exp Error		194	420.17
Within Fams		3234	314.14
Head Weight	40.7		
Yrs		1	18647.48
Reps		2	337.61
Fams		48	11097.74
Yrs X Fams		48	884.79
Exp Error		194	542.75
Within Fams		3234	410.15
Vigor	3.7		
Yrs		1	186.02
Reps		2	0.07
Fams		48	1.71
Yrs X Fams		48	0.17
Exp Error		194	0.07
Within Fams		3234	0.05

TABLE XVIII (Continued)

Character	Mean	F_3 df	MS
Kernels Per Head	974.5		
Yrs		1	6106717.88
Reps		2	2049404.34
Fams		48	12426233.62
Yrs x Fams		48	920820.54
Exp Error		194	612552.14
Within Fams		3234	446465.22
Fertility	51.6		
Yrs		1	7633.00
Reps		2	1061.00
Fams		48	13112.00
Yrs x Fams		48	726.00
Exp Error		194	715.00
Within Fams		3234	467.00

TABLE XIX

CHARACTER MEAN PRODUCTS FOR THE F_3

	F_3	
Characters	df	MP
PH,PY		
Fams	48	9062.03
Yrs x Fams	48	179.19
Exp Error	194	217.04
Within Fams	3234	143.64
PH,K/Hd		
Fams	48	288779.60
Yrs x Fams	48	6846.98
Exp Error	194	8277.32
Within Fams	3234	4458.04
PH,Vigor		
Fams	48	-18.48
Yrs x Fams	48	-5.11
Exp Error	194	-1.53
Within Fams	3234	-1.10
PY,K/Hd		
Fams	48	312954.36
Yrs x Fams	48	24853.53
Exp Error	194	15525.77
Within Fams	3234	11505.69
PY,Vigor		
Fams	48	-24.95
Yrs x Fams	48	-2.01
Exp Error	194	-0.84
Within Fams	3234	-0.50
K/Hd,Vigor		
Fams	48	-795.13
Yrs x Fams	48	-61.41
Exp Error	194	-29.05
Within Fams	3234	-18.37

VITA

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