HERITABILITY ESTIMATES AND GENE EFFECTS FOR SEVERAL AGRONOMIC CHARACTERS IN A SYSTEMATIC SERIES OF GRAIN SORGHUM (SORGHUM BICOLOR (L.) MOENCH) GENOTYPES

by 4589

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INTRODUCTION

Plant breeders with the task of developing superior genotypes in crop plants must deal largely with traits of quantitative inheritance. Most of the economic characters with which they work exhibit continuous variation generally explained by the polygenic inheritance or a modification thereof. Owing to the fact that Mendelian approach is not applicable to the study of polygenic inheritance, many statistical procedures have been developed so as to obtain basic genetic information. For example, knowledge about heritability indicates the relative degree to which a character is transmitted from parent to progeny. The magnitudes of such estimates also suggest the extent to which improvement is possible through selection. Estimation of various types of genetic effects including epistasis is of value to plant geneticists or breeders because it provides information useful in choosing the most advantageous breeding procedures for the improvement of the attribute in question. In sorghum, relatively little data are available relative to these aspects.

Sorghum is remarkable for its wealth of variability in almost all plant characteristics. Much of the research investigations reported earlier deal largely with phenotypic variability and correlations. A knowledge about heritability coupled with gene effects for such agronomic traits will be of great value in the selection concept and choice of selection procedure.

This investigation was designed to determine the magnitude of heritability estimates in the narrow sense for quantitative traits such as grain yield, kernel weight, plant height, and flowering time in 10 genetic groups of grain sorghum derived from a 5 variety diallel. The estimates of

gene effects and relative importance of additive, dominant, and digenic epistasis were also obtained for these attributes.

LITERATURE REVIEW

General Considerations

Prior to the rediscovery of Mendel's laws of inheritance, plant breeding was primarily an art. The most powerful selection tool employed was progeny test. Following the rediscovery of Mendelism, plant breeders were quick to realize the importance of rapidly expanding quantitative genetics to plant improvement.

Fisher (16) studied the nature of gene control of a quantitative trait in 1918. He showed how to separate the genetic variance into three components: that due to additive effects of genes, that due to dominance deviations from the additive scheme, and that due to deviations attributed to interalleic interactions or epistasis. This theoretical basis of quantitative genetic concept was subsequently established by Haldane (21) and Wright (51). Sewall Wright was the pioneer in the field of heritability studies. His concept of separation of genetic and environmental effects has laid a firm basis for development of modern quantitative genetics.

The study of quantitative inheritance in plants started with the works of Johannson (26), Nilsson-Ehle (38), and East (14). Johannson demonstrated that both heritable and nonheritable agencies contributed to somatic variation in segregating population, that the variation in a pure line was exclusively environmental and that selection would be ineffective within a pure line. East and Nilsson-Ehle, while confirming the work of Johannson, showed how quantitative inheritance conformed with Mendelian concept of inheritance.

Subsequent development in the field of quantitative genetics over succeeding years was made by many geneticists, statisticians, and breeders. Notable among these were the works of Fisher (16), Mather (36), Wright (51), Lugh (33), Anderson and Kempthorne (4), Cockerham (10), Comstock and Robinson (11), and Hayman (23, 24, 25).

Heritability Studies

The portion of total variance which is attributable to the additive effects of gene measures the extent of resemblances between the parent and the offspring. Lugh (33) proposed the use of the ratio of the additive genetic components of variance to total variance within a segregating population as a measure of the degree of heritability. Thus, estimation of heritability provides a quantified statement indicating the relative importance of genetic and the environment on the expression of a trait.

Heritability is used in both a "broad sense" and a "narrow sense" (33). In the broad sense, heritability is the ratio of total genetic variance to phenotypic variance; while heritability in the narrow sense is the ratio of additive genetic variance to phenotypic variance. Detailed reviews on heritability, its concepts, definitions, use in plant breeding programs have been reported by Hanson (22), Robinson (42), Sprague (46), Panse (39), and Dudley and Moll (13).

Several methods have been proposed for estimating the degree of heritability in crop plants. Of these, parent-offspring regression method proposed by Lugh (33) is widely used in self-pollinating species. This technique is comparatively straight-forward and involves the regression of the mean value of a characteristic in the progeny upon the value of the same characteristic in the parent. The regression values are converted directly to heritability percentages by multiplying with hundred. In cross pollinated

plants, where both parents are measured, the regression on one parent is doubled to obtain the heritability estimate.

Since parent-offspring regressions for characteristics in crop plants are computed by regressing data collected in one year upon data obtained in the previous year, any environmental factor could change the range of phenotypic variation from year to year which may overestimate heritability and values greater than 100% may be obtained. To avoid such situations, Frey and Horner (17) proposed a method called standard unit or correlation method. Standard unit heritabilities are obtained by computing the regressions on data coded in terms of standard deviation units for each character under study. Such a regression is identical to correlation coefficients on the original data. According to the authors, this method eliminates the environmental effects of different years which increase or decrease the range of the progenies relative to that of the parent by establishing a heritability ceiling of 100%. Thus, the standard unit method eliminates the unrealistic heritability values of over one.

With a view to avoid over estimates of heritability, regardless of the degree of inbreeding or breeding system, Smith and Kinman (45) proposed an adjusted method in self-pollinating plants. According to them, the regression coefficient should be divided by two times the probability that a random gene at a specific locus in one parent (x) is identical by descent to a random gene at the same locus of the other parent (y), then h^2 (heritability) = $b/2r_{xy}$. These adjusted heritabilities are based on the genetic variance of a random breeding population.

Heritabilities are also estimated by variance component method in which the variance components are obtained by equating the mean squares to their expectations. Robinson et al. (43) used this method in corn.

Estimation of additive and non-additive genetic variances requires the use of appropriate mating design. Cockerham (10) classified mating designs as one, two, three, or four factor designs depending upon the number of ancestors per progeny over which control is exercised. Common mating designs such as the diallel cross, design I, II, and III of Comstock and Robinson (11) are usually employed to obtain estimation of genetic variance components.

A method of estimating heritability from the variances of three types of segregating populations the F_2 and the summed backcrosses to each parent was reported by Warner (49). According to him, this method has the advantage of not requiring an estimate of environmental or of total genetic variance but uses only total within-population variance. Thus, this method is an approach to estimate heritability in the narrow sense. However, it is pointed out that nonheritable variances of the F_2 and backcrosses should be approximately similar in magnitude.

Any method developed for the estimation of heritability involves a series of biological assumptions. These vary somewhat with the method, but the more common restrictions are (1) normal diploid behavior at meiosis, (2) no maternal or cytoplasmic effects, (3) no multiple alleles, (4) no selection, (5) no epistasis, and (6) linkage equilibrium (10).

Heritability has value primarily as a method of quantifying the concept of whether progress from selection for a plant character is relatively easy or difficult in a breeding program (22). A high heritability in the narrow sense indicates that reliance may be placed on mass selection and as heritability becomes lower emphasis should be on pedigree method of breeding with progeny tests and selection. Heritability in the narrow sense may be used to estimate expected genetic gain due to selection. Formulas for computing expected response to selection for various breeding schemes are given by Falconer (15),

Sprague (46), Allard (3), and Comstock and Robinson (11).

Sprague (46) in his review on quantitative genetics in plant improvement stated that in animals, the individual is normally the unit of both evaluation and selection, and estimates of heritability for different attributes within a given class of livestock under similar management practices are therefore comparable and provide a general guide to the progress to be expected from selection. However, in plants the individual remains the unit of selection, but the unit of evaluation may be a single plant, a plot, or a group of plots grown under one set of environmental conditions or under two or more environments. Therefore, estimates of heritability may vary under each set of circumstances. Thus, heritability in plant breeding is not a stable population parameter, but differs with the precision with which the environmental variance is estimated. Results of studies by many investigators revealed that heritability estimates depend upon the specific plant material investigated, the character and the environmental conditions, size and stage of segregating population, and the method employed to estimate heritability.

Swarup and Chaugale (47) studied phenotypic variation and its heritable component in some important quantitative characters in a 70-variety experiment comprising both Indian and exotic strains of grain sorghum (Sorghum vulgare Pers.). Broad sense heritability values for panicle emergence (96.69%), plant height (98.36%), stalk diameter (70.91%), leaf number (98.18%), peduncle length (94.29%), peduncle diameter (87.18%), panicle length (98.00%), panicle girth (88.38%), panicle weight (76.23%), grain yield per plant (72.38%), 100 seed weight (85.44%), and HCN content (98.83%) showed that almost all the characters exhibited high heritability value, but a few — like stalk diameter, panicle weight, grain yield, sugar content, and reaction to stem borer — had comparatively lower heritability estimates. Subsequent investigations of Rao

and Rochie (41), in their 12 variety grain sorghum experiment, reported that almost all the characters showed high broad sense heritability values, thus confirming the earlier results.

Chiang and Smith (9) reported heritability estimates for several agronomic traits in a 7X7 diallel cross of grain sorghums. The results showed that except for head length and number of tillers, the heritability estimates were low for other characters such as plant height, head weight, and threshing percentage. Using F_2 variance method, Alikan and Weibel (2) reported heritability estimates for 9 plant and seed characters in their study of the parental, F_1, and F_2 generations of the crosses Redlan x Plainsman (Cross 1) and Combine Kafir 60 x Combine 7078 (Cross 2). Highest heritability estimates were obtained for plant height and those for days to flowering were comparatively high in both crosses. The estimates for head weight and grain yield were higher in Cross 1 than in Cross 2. On Cross 1, the estimate for bushel weight was negative due to a large environmental variance. On the basis of these results, it was concluded that individual plant selection in F_2 population would be effective for plant height and days to flowering, but less effective for head weight, grain yield, head length, threshing percentage, kernel weight, kernels per plant, and bushel weight.

Heritability estimates calculated on the basis of original scale, logarithmic transformation, and variance mean ratio using Warner's (49) method were reported for several agronomic traits in 3 genetic groups of grain sorghums by Liang and Walter (30). The results showed that heritabilities of grain yield and kernel number were of lower magnitude than those of head weight, kernel weight, stalk diameter, and half blooming. Heritability estimates for plant height and germination percentage were of still higher order. The magnitude of heritability varied greatly among crosses for yield, head

weight, and kernel number. In another investigation involving a 6-variety diallel, Liang et al. (28) reported heritable variation for three traits in grain sorghum. The results indicated low heritability values for grain yield (13%), intermediate for protein content (43%), and high for anthesis time (64%). High heritability estimates for anthesis time indicate that a major part of the phenotypic variability in the diallel cross was genetic.

Using three different methods, Liang et al. (32) reported heritability estimates for 12 agronomic traits in two segregating grain sorghum populations and of F_3 and F_4 generations. The results showed that all the three methods in each population provided similar estimates. In population 1, the head number and kernel weight were less heritable than were grain yield, head weight, kernel number, peduncle diameter, germination percentage or threshing percentage. In population 2, head number was less heritable than germination percentage, threshing percentage, protein percentage, grain yield, head weight, kernel weight, kernel number, and peduncle diameter; while half bloom, leaf number, and plant height were most heritable. Half bloom, leaf number, and plant height were highly heritable in both the populations indicating that response to selection would be more effective for these traits than the rest.

Gene Effects

Knowledge of gene effects is basic to a decision as to the kind of breeding program, population improvement, or hybridization. In polygenic inheritance the individual genes cannot be studied because their effects are diminutive. Methods are now available for partition of either means or variance which provide information on the extent of genetic variability and, in addition, provide information on the nature of gene effects involved.

The nature of the gene control of a quantitative character was first approached in a comprehensive way by Fisher (16). He considered the

simultaneous action of several genes on a character and showed how to represent and estimate the average main and dominance effects of these genes, even when the genes were unequal in effect and exhibited incomplete dominance. Many genetic models have been developed (11, 23, 36, 39) for estimation of gene effects. Most of these genetic models assumed some basic requirements and were employed primarily to estimate relative importance of additive and dominance gene effects. Epistatic genes were assumed to be absent or negligible. However, reports (1, 4, 18, 19, 24, 25, 30, 34, 44) showed the presence of epistatic gene effects in sufficient magnitudes and that genetic models assuming negligible epistasis may be biased in certain cases.

A model for partitioning the genotypic value into additive, dominant, and epistatic gene effects was provided by Anderson and Kempthorne (4). This method employs the means of populations obtained from crossing two homozygous lines followed by subsequent selfing. Six parameters, K_2, E, F, G, L, and M, were derived where K_2 represents mean effects, and E and F represent non-epistatic effects. Some of these parameters are difficult to interpret because of pooled gene effects in the parameter. Cockerham (10) and Mather (36) have proposed models for partitioning genetic variances into the above compounds. All these models, however, are primarily based on the factorial statistical experiments.

Hayman described parameters which estimate the additive, dominant, additive x additive, additive x dominant, and dominant x dominant with less difficulty in interpretation. However, where significant epistasis is present, additive and dominant gene effects are difficult to separate and the relative contributions of the types of gene action to various genetic phenomenon cannot be interpreted by the partioning method (24).

Using the means of six populations, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\bar{B}_1(\bar{P}_1 x \bar{F}_1)$, and $\bar{B}_2(\bar{P}_2 x \bar{F}_1)$, Gamble (18) outlined a procedure to estimate 6 parameters, namely mean effects, additive and dominant gene effects, and the three types of digenic epistatic effects. Using the same method he also estimated the 6 parameters. The results showed that dominant gene effects made the major contribution to variation in yield of grain corn in all the 15 crosses studied. In all the crosses, the estimates were positive and highly significant. Epistatic effects were also observed to be important contributors to variation for yield. The magnitude and significance of the estimates for aa, ad, and dd over the 15 crosses indicate that epistatic gene effects are present and important in the basic genetic mechanism of yield inheritance in the corn population. These results are in contrast to the earlier investigations reported by Robinson et al. (43) which indicate that additive gene effects make a greater contribution to the total genetic variation than the estimates obtained by Gamble (18).

Estimates of gene effects calculated by Hayman's method (24) were also reported in pearl millet (1, 34, 44). Results obtained by Singh et al. (44) showed that additive gene effects were highly significant for all the characters except for number of branches. Except days to flower, all the characters were observed to be associated with highly significant dominant gene effects. The additive x dominant type of digenic epistatic effects were found to be less important than other two types of non-allelic interactions. Duplicate epistasis was exhibited by plant height, number of internodes, stem thickness, number of tillers, number of spike-bearing tillers, number of spike-bearing branches, leaf breadth, days to flower, and 250 grain weight and complimentary epistasis was observed for number of branches, leaf length, peduncle length, peduncle thickness, spike length, and spike thickness.

Few investigations regarding gene effects have also been reported in grain sorghum. Whitehead (50) reported that additive gene action governed flowering date, plant height, head length, and head opening in short grain varieties. Investigations of Chiang and Smith (9), in a 7 x 7 diallel cross, showed that additive gene action appeared to be the important type in the inheritance of head length, plant height, head weight, and threshing percentages.

Liang et al. (28) reported information on the general nature of actions of genes controlling the development of grain yield, anthesis time, and protein content in grain sorghum from a 6-variety diallel. It was noted that both general and specific combining ability were important for anthesis time, and that specific combining ability seemed more important for grain yield. Significant interactions were observed between general combining ability and locations for yield, anthesis time, and protein content while significant interaction between specific combining ability and locations was observed for protein content only. With regard to gene effects, overdominance was indicated for grain yield; partial dominance was observed for anthesis time and protein content.

Using the method outlined by Hayman (24) and used by Gamble (18), gene action for seed size in grain sorghum was reported by Voigt et al. (48). The results showed that gene action appeared to be almost entirely additive. Using Gamble's method (18), Liang and Walter (30) obtained gene effects for certain agronomic traits in grain sorghum. The results indicated that dominant gene effects are important to grain yield, head weight, kernel weight, and kernel number. Epistasis, especially "aa" and "dd" type, was found to be important for yield and blooming time in sorghum. The existence of epistasis suggests that the breeding plan should be designed to utilize various types of

gene interactions and that genetic models assuming negligible epistasis could be biased in certain cases.

MATERIALS AND METHODS

The plant material in this study was obtained from 10 genetic groups of grain sorghum derived from a 5 variety diallel. The 5 sorghum varieties chosen as parental material were supplied by Dr. A. J. Casady from his breeding stocks. Contrasting characteristics of these varieties include plant height, flowering time, kernel weight, and grain yield. A brief description of parental varieties is given in Table 1.

In the present study, all possible single crosses (F_1), single crosses selfed (F_2), and backcrosses (P_1xF_1 and P_2xF_1) were used. Thus each genetic group included 6 populations as described below.

Group 1: P_1(Redlan), P_2 (Plainsman), their F_1, F_2, $B_1(F_1xP_1)$, and $B_2(F_1xP_2)$ derivatives

Group 2: P_1(Redlan), P_2 (Martin), their F_1, F_2, B_1, and B_2 derivatives

Group 3: P_1 (Redlan), P_2 (Combine 7078), their F_1, F_2, B_1, and B_2 derivatives

Group 4: P_1 (Redlan), P_2 (Combine Kafir 60), their F_1, F_2, B_1, and B_2 derivatives

Group 5: P_1 (Plainsman), P_2 (Martin), their F_1, F_2, B_1, and B_2 derivatives

Group 6: P_1 (Plainsman), P_2 (Combine 7078), their F_1, F_2, B_1, and B_2 derivatives

Table 1. Brief description of parental sorghum varieties used in the 5 variety diallel

No.	Variety	Chief Characteristics
1	Redlan	Red seeded, large and compact head, large stalks, awnless.
2	Plainsman	Red seeded, seeds large, awned.
3	Martin	Red seeded, seeds heavy and rich in protein content, heads are medium in size, awnless.
4	Combine 7078	Red seeded, heads are small in size, awned.
5	Combine Kafir 60	White seeded, comparatively smaller stalks, leaves relatively narrow, awnless.

Group 7: P_1 (Plainsman), P_2 (Combine Kafir 60), their F_1, F_2, B_1, and B_2 derivatives

Group 8: P_1 (Martin), P_2 (Combine 7078), their F_1, F_2, B_1, and B_2 derivatives

Group 9: P_1 (Martin), P_2 (Combine Kafir 60), their F_1, F_2, B_1, and B_2 derivatives

Group 10: P_1 (Combine 7078), P_2 (Combine Kafir 60), their F_1, F_2, B_1, and B_2 derivatives

All the crosses between parental lines, selfing of F_1 hybrids and backcrosses of F_1 hybrids to their parents were made in the greenhouse at Manhattan, Kansas, in 1966. Five A-lines (male sterile) were used as female parents and crossed to B-lines (fertile non-restorer counterparts of each male sterile) to produce F_1 and backcross hybrids.

The 6 populations of all the genetic groups were grown in June of 1968 and 1969 on 2 Agronomy Farms of the Kansas Agricultural Experiment Station, Manhattan, Kansas. The soil type was dark silt-loam at Manhattan and sandy-loam at Ashland. The crop was grown irrigated at Ashland but not irrigated at Manhattan. All the experimental plots at both the locations were fertilized at the rate of 80 lbs. of nitrogen per acre prior to seeding.

The experimental design was a randomized block with 2 replications at both locations. Each genetic group was considered as a single unit in the process of randomization. The components in each genetic group were also randomized in each replication at each location. The parental lines, F_1, F_2, and backcross progeny of each group was replicated twice.

The seeds for all populations were space planted with a cone planter with a row spacing of 91 cm (36 inches) and plant spacing in the row of 15 cm (6 inches). Three row plots were used, the center row for observations and the outer rows to guard against competition from adjacent plots. Thirty competitive plants from the center row of each plot for each component were chosen to record observations for parental lines, F_1, and backcrosses while 90 plants were measured for F_2. All the characters were measured on an individual plant basis.

Measurement Procedures

The following measurements were recorded for each component of the respective genetic group.

1. Yield: Weight in grams of threshed grain at 10% moisture. The mature panicle were harvested from the plants on the main field. They were subsequently dried and threshed. The weight of the threshed grain in grams was recorded by Avery balance.

2. Kernel weight: Weight of 1,000 seeds in grams at 10% moisture. Based on number of kernels in a 5 gram random sample drawn from the seed of each plant. The number of kernels in the 5 gram sample was obtained by an electronic seed counter and the result was subsequently converted to grams per 1,000 kernels.

3. Flowering time: Number of days elapsed from date of planting to date of the panicle was in bloom.

4. Plant height: Measured in centimeters from ground to base of leaf blade of the flag leaf.

5. Head number: Number of tillers bearing heads.

Statistical Treatment of the Data

Analyses of variance combined over years and locations for yield, kernel weight, flowering time, and plant height were calculated. Mean squares for each component in each genetic group were estimated as shown in Table 2. Error mean square was estimated by the arithmatic mean of two parental lines and their F_1 progeny.

Warner's (49) method of estimating heritability from the variances of three types of segregating populations, the F_2 and the summed backcrosses to each parent, were employed to obtain heritability values in narrow sense for all the 4 attributes. According to him, this method has the advantage of not requiring an estimate of environmental or of total genetic variance but uses only total within population variances.

Assuming that the genes neither interact nor are linked, Mather (36) showed that genetic variance of F_2 plants in self-pollinated species could be partitioned into additive and dominance variances. The phenotypic variance is expressed as follows:

$V_{F_2} = \frac{1}{2}D + \frac{1}{2}H + E$ where D, H, and E represent additive, dominant, and environmental variances respectively.

Similarly, sum of the variances of backcross to parent 1 and 2 may be expressed as follows:

$(V_{B_1} + V_{B_2}) = \frac{1}{2}D + \frac{1}{2}H + 2E$

The difference between twice the variance of F_2 generations and the sum of the two first backcross generations was attributable to additive gene effects. Thus the additive genetic variance in F_2 could be estimated from the expected mean square of F_2 and backcrosses, i.e.,

$\frac{1}{2}D = 2V_{F_2} - (V_{B_1} + V_{B_2})$

Table 2. An example of AARDVARK 3-way analysis removing effects due to locations, years, replications, first order and second order interactions and obtaining variance among plants for flowering time of B_2, genetic population 4

Source of variation	df	MS
Location (L)	1	4524.0
Year (Y)	1	1500.0
Replication (R)	1	24.1
L x Y	1	666.7
L x R	1	1.7
Y x R	1	109.3
L x Y x R	1	312.8
Among plants	232	4.99

Warner's method of estimating heritability would then be expressed as follows:

$$h^2 = \frac{\left[2V_{F_2} - (V_{B_1} + V_{B_2})\right]}{V_{F_2}} \times 100\% \cong \frac{\left[2s^2_{F_2} - (s^2_{F_2} + s^2_{B_2})\right]}{s^2_{F_2}} \times 100\%$$

Information on the nature of gene action involved for the four traits was obtained by the method developed by Anderson and Kempthorne (4), Hayman (24), and modified by Gamble (18). This procedure would be of specific use in situations where the individual genotypes are not identifiable but where average genetic expectations are known. Thus, with the means of only 6 populations, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\bar{B}_1$, $\bar{B}_2$, 6 parameters were estimated as follows:

$$m = \bar{F}_2$$

$$a = \bar{B}_1 - \bar{B}_2$$

$$d = \tfrac{1}{2}\bar{P}_1 - \tfrac{1}{2}\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$aa = -4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$ad = -\tfrac{1}{2}\bar{P}_1 + \tfrac{1}{2}\bar{P}_2 + \bar{B}_1 - \bar{B}_2$$

$$dd = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 + 4\bar{B}_2$$

Where m = the F_2 mean

a = additive gene effects

d = dominance gene effects

aa = additive x additive epistatic gene effects

ad = additive x dominant epistatic gene effects

dd = dominant x dominant epistatic gene effects

Significance of these genetic effects was evaluated by the corresponding standard error obtained from the analyses of variance of the population means.

RESULTS AND DISCUSSION

Means and Variances

The average performance of the parental varieties tested at 2 university farms at Manhattan during 1968 and 1969 is presented in Table 3. For flowering time, Redlan was the latest (70.6 days) followed by Plainsman (68.2 days), Combine 7078 (67.8 days), Combine Kafir 60 (67.4 days), and Martin (65.5 days). Redlan was the tallest in plant height with a mean value of 87.1 cm whereas Plainsman was the shortest with a mean value of 68.4 cm. Among the rest, Combine Kafir 60 was relatively taller (75.2 cm) than Martin and Combine 7078. Greatest yield was observed in Redlan and was closely followed by Combine 7078. Plainsman and Combine Kafir 60 showed intermediate values, while Martin showed lowest mean value. With regards to kernel weight, highest mean performance was obtained in Combine 7078 followed by Redlan, Combine Kafir 60, Martin, and Plainsman.

The mean values obtained for the parental varieties included in the present study were in agreement with the values reported by Liang et al. (30). In general it was noted that the differences among the 5 lines were conspicuous for all the 4 characteristics. Data were also collected for the trait head number, but no significant difference in mean values among the 5 lines was noted. Therefore, the present study was limited to only 4 traits.

Table 4 gives the variances of the characters studied in the F_2, B_1, and B_2 generations of the 10 genetic groups. It was observed that greatest variability was observed for grain yield followed by plant height, kernel weight, and flowering time.

For grain yield, genetic groups 3, 8, and 10 showed relatively higher variability. One, 5, and 6 had intermediate values and 2, 4, 7, and 9 showed

Table 3. The average performance of 5 sorghum varieties for flowering time, plant height, grain yield, kernel weight, and head number at 2 locations in each of 2 years

Character	Variety				
	Redlan	Plainsman	Martin	Combine 7078	Combine Kafir 60
Flowering time (days)	70.6	68.2	65.5	67.8	67.4
Plant height (cm)	87.1	68.4	73.3	72.1	75.2
Grain yield (gr)	68.7	63.1	53.8	68.0	57.7
Kernel weight* (g/1000)	29.79	27.33	28.33	33.93	28.89
Head number	1.00	1.00	1.01	1.02	1.01

*Average from 2 locations in 1969 only.

Table 4. Variances of F_2, B_1, and B_2 for flowering time, plant height, grain yield, and kernel weight of 10 genetic groups

Genetic Group	Generation	Characters			
		Flowering Time	Plant Height	Grain Yield	Kernel Weight
1	F_2	11.47	60.1	475.3	24.1
	B_1	6.10	45.5	430.9	16.8
	B_2	8.29	36.8	347.1	18.0
2	F_2	12.42	65.5	398.1	30.7
	B_1	6.95	38.0	292.0	23.7
	B_2	10.78	35.0	282.7	18.8
3	F_2	15.36	97.7	584.7	40.6
	B_1	10.60	86.3	476.3	27.9
	B_2	11.78	64.6	470.7	26.2
4	F_2	15.78	73.6	349.5	27.5
	B_1	10.14	46.5	220.0	20.3
	B_2	10.00	48.8	212.2	15.9
5	F_2	12.67	62.4	438.1	33.9
	B_1	7.70	33.0	421.9	27.0
	B_2	6.84	43.3	357.0	23.6
6	F_2	20.08	44.4	467.0	44.1
	B_1	20.67	26.0	405.4	19.3
	B_2	7.54	34.5	400.1	39.0
7	F_2	11.77	62.9	329.6	27.1
	B_1	12.04	43.3	254.8	17.4
	B_2	6.57	55.2	326.1	18.4
8	F_2	13.01	74.0	475.3	45.5
	B_1	10.16	74.0	373.9	33.4
	B_2	12.67	42.5	495.5	40.0
9	F_2	13.54	74.7	348.0	26.1
	B_1	9.82	37.1	253.6	22.6
	B_2	8.06	65.3	371.2	10.2
10	F_2	10.55	97.6	506.8	41.6
	B_1	9.27	62.8	378.3	32.3
	B_2	7.55	56.2	364.0	26.9

lower values. In absolute values, grain yield varied from 584.7 to 212.2. For kernel weight, relatively more variability was observed in genetic groups 3, 6, 8, and 10; intermediate values in 2 and 5; and lower values in 4, 7, and 9. For plant height, higher values were recorded in genetic groups 3, 8, and 10; intermediate values in 1, 2, 4, 7, and 9; and lower values in 5 and 6. With regards to flowering time, genetic groups 3, 4, and 6 showed comparatively higher variability; 2, 8, and 9 showed intermediate variability; and 1, 5, 7, and 10 showed relatively lower variability.

In general, the variability occurring among different populations from a cross is dependent upon the genetic differences which exist between parents. As an example, the highest variability in genetic group 3 for grain yield can be attributed to the influence of Redlan and Combine 7078 germplasms. The effect of low yielding parents "Martin" and "Combine Kafir 60" is evident in genetic groups 2 and 4 respectively.

Heritability Estimates

Based on the variances presented in Table 4, heritability estimates (narrow sense) were computed by Warner's method (49) and are given in Table 5.

The magnitude of heritabilities varied among the genetic groups for all the characteristics; it ranged from 24.5% to 85.2% for flowering time, 42.5% to 83.7% for plant height, 38.2% to 68.2% for kernel weight, and 17.11% to 76.3% for grain yield. In general it is noted that heritability estimates for plant height, flowering time, and kernel weight were relatively high while those for grain yield were low except for genetic groups 2, 4, and 10 which showed intermediate values.

The relatively high heritabilities for flowering time and plant height are in agreement with previous reports (2, 28, 30) indicating the importance of additive gene effects in relation to nonadditive gene effects and

Table 5. Heritability estimates (h^2) of flowering time, plant height, grain yield, and kernel weight for 10 genetic groups

Genetic Group	Heritability Estimates* (%)			
	Flowering Time	Plant Height	Grain Yield	Kernel Weight
1	74.5	61.5	36.3	55.7
2	57.2	79.3	55.6	63.1
3	54.3	45.4	38.0	66.9
4	64.3	83.9	76.3	68.2
5	85.2	79.3	22.2	50.7
6	59.5	63.7	27.5	67.8
7	41.9	43.5	26.4	68.1
8	24.5	42.5	17.1	38.2
9	67.9	62.9	20.5	74.0
10	40.6	78.0	53.5	57.6
Average	57.0	62.0	37.3	61.0

*$h^2 = \frac{2V_{F_2} - (V_{B_1} + V_{B_2})}{V_{F_2}} \times 100\%$

environmental influence. However, Chiang and Smith (9) reported lower heritability estimates for blooming time and plant height than the estimates obtained in this study. This apparent discrepancy cannot be explained readily. The parental lines used in their investigations differed with respect to the Ma_1, Ma_2, and Ma_3 loci with regards to flowering time and possessed different height genes. Interactions among the major maturity genes and major height genes may be responsible for the low heritability values obtained in their investigation. In addition to this, the discrepancy can be accounted for in part by the different method they have employed in computing heritability estimates.

The relatively high heritability estimate obtained for kernel weight also stresses the importance of additive gene effects and is in agreement with that reported by Voigt et al. (48) but not with the results reported by Liang and Walter (30) and Ali Khan and Weibel (2). Both of these investigations were based on relatively few genetic populations carried in one season. Moreover, Ali Khan and Weibel employed F_2 variance method for computing heritabilities. Even in the present investigations, kernel weight was not measured in 1968 and computing of heritability for this trait was done on the data collected in 1969 only. This would suggest that the estimates of additive genetic variance may be biased somewhat due to genotype-environment interactions.

In fact, it is common for different workers to obtain contradictory results when studying the same characters. This may be due to genotypic differences of the parental material included (46) or due to invalidity of certain assumptions made. Differential response of genotypes to environments (29) could also be a reason for the discrepancies. Heritability depending so much on these factors must be treated with some caution and the comparisons of

estimates for a particular character by different workers is of doubtful utility (22).

Low heritability estimates obtained for grain yield were in agreement with several reports published (2, 28, 30). The low heritability estimates for grain yield indicate nonadditive and environmental variations constituted the major portion of phenotypic variation.

Heritability estimates were also computed by parent-offspring regression method for the 4 traits under study for the purpose of comparison. The results are presented in Table 6. The estimates were calculated by regressing F_3 data on F_2 means. Each F_3 line was derived from a single, randomly selected F_2 plant, and the data were based on an average of a 30-plant-plot in 2 replications at 2 locations in each of 2 years.

A comparison between the heritability estimates computed by Warner's method and parent-offspring regression method revealed that plant height and flowering time showed high values irrespective of the method employed. Heritabilities for kernel weight and grain yield were variable and low respectively. Thus, it is reasonable to state that kernel weight and grain yield are subject to more environmental influence and non-additive gene effects than flowering time and plant height and fluctuate more in their phenotypic expression.

Theoretically, when heritability is high reliance should be placed mainly on mass selection and as heritability becomes lower emphasis must be on pedigree method of breeding with progeny tests and selection. Assuming that the heritability estimates obtained by Warner's method were reasonably accurate, it can be stated that for improvement of flowering time, plant height, and kernel weight, mass selection would be the appropriate approach by which rapid and effective selection could be made for these traits. However, if the breeding goal is for the improvement of grain yield, progeny tests

Table 6. Heritability estimates obtained by regressing F_3 performance on F_2 means of 10 genetic groups

Character	Heritability estimates (%)
Flowering time	63.4
Plant height	69.0
Grain yield	39.4
Kernel weight	42.5

should be the appropriate approach as genetic effects are masked by environmental effects and the genotypes to be selected cannot be represented by their phenotypes.

It is sometimes difficult to specify heritability in desirable narrow limits. Differences in heritability for the same trait in two or more populations indicate differences between populations and may be traced to the contrast in crosses of the original parents. However, in the present study parental differences did not show any significant relationship with the magnitude of heritability. The "r" value obtained was 0.301 for flowering height, 0.081 for plant height, 0.263 for grain yield, and a negative value of -0.338 for kernel weight. All the correlation coefficients were nonsignificant indicating that the sampled differences between the parents did not show any significant trends to the heritability computed by Warner's method.

Since heritability is a single numerical expression or the ratio of two variances, information may be lost if based on heritability estimates only. It may also provide misleading indication as to the amount of progress which may be made in the population sampled, because, by Mather's approach, the magnitude of genetic variability as compared to environmental variability is not indicated explicitly. Table 7 presents the magnitude of genetic and environmental variances and their ratios.

It is clear that genetic variability does not appear to be great enough as seen by the ratios between genetic variance and environmental variance. For flowering time and plant height genetic variance is only about twice the amount of environmental variance; while the ratio for grain yield and kernel weight were 1.6 and 1.4 respectively. In general, the genetic population to be selected as the basic breeding material should have a high mean performance as compared to other populations and a greater genetic variability within

Table 7. Comparison of the magnitude of genetic and environmental variances

Genetic group	Flowering time (days)			Plant height (cm)			Grain yield (gr)			Kernel weight (g/1000)		
	Variance			Variance			Variance			Variance		
	Genetic*	Environment**	Ratio	Genetic*	Environment**	Ratio	Genetic*	Environment**	Ratio	Genetic*	Environment**	Ratio
1	8.10	3.37	2.4	38.9	21.2	1.8	475.3	255.8	1.9	14.79	9.30	1.6
2	9.03	3.39	2.7	45.3	20.2	2.2	243.2	154.9	1.6	18.93	11.77	1.6
3	10.58	4.78	2.2	76.4	21.3	3.6	429.2	155.5	2.8	27.20	13.44	2.0
4	12.02	3.76	3.2	46.8	26.9	1.7	179.2	170.3	1.1	17.27	10.22	1.7
5	8.10	4.57	1.8	42.5	19.9	2.1	251.5	186.6	1.3	17.30	16.60	1.0
6	14.78	5.30	2.8	22.5	21.9	1.0	288.3	179.7	1.6	17.77	16.31	1.1
7	7.36	4.44	1.7	39.3	23.6	1.7	165.2	164.4	1.0	16.57	10.57	1.6
8	7.99	5.02	1.6	49.9	24.1	2.1	306.4	168.9	1.8	25.28	20.27	1.2
9	7.70	5.84	1.3	43.7	31.0	1.4	206.9	141.1	1.5	14.42	11.63	1.2
10	7.43	3.12	2.4	65.0	32.7	2.0	312.6	194.2	1.6	22.52	19.08	1.2
		Ave.	2.2		Ave.	2.0		Ave.	1.6		Ave.	1.4

*Variance of F_2 - variance of environment

**$\frac{V_{F_1} + V_{P_1} + V_{P_2}}{3}$

population. Progress from selection is realized only when superior genotypes in a population are readily identified. From the data presented in Table 7, it is doubtful that the 10 genetic populations sampled possessed sufficient genetic variability upon which the breeders and geneticists may operate. If this is true for all other genetic populations at the disposal of sorghum breeders, then it would be expected that progress by selection irrespective of selective methods will be difficult to make. To improve the situation, the most important approach appears to be creation of sufficient variability by introduction of exotic germ plasm into the domestic lines. This may be accomplished by using genetic male sterile lines as female parents in crosses with exotic lines as males. Thus, a large number of crosses can be made and in F_2 segregates of male sterile progeny can be further crosses with some exotic parental lines to increase the genetic diversity.

Estimation of Gene Effects

Population Means

Mean performance of the 6 populations in each of the 10 genetic groups is given in Table 8. Relative to the midparent, F_1 performance varied from character to character and from group to group. The F_1 population mean performance was greater than the better performing parent in all the genetic groups for grain yield; in 5, 6, 8, 9, and 10 for plant height; and in 2, 4, 7, and 9 for kernel weight, indicating the presence of heterosis. However, F_1 population mean performance was earlier than mean performance of either parent in genetic groups 1, 5, 6, 7, 8, and 10 for flowering time and in 1, 3, 5, and 8 for kernel weight. The F_1 performance was intermediate in the rest of the genetic groups for all the attributes.

With few exceptions, F_2 means of all the genetic groups fell in between the range of the parents. In most of the genetic groups the

Table 8. Mean performance of the parental, F_1, F_2, and backcrosses for flowering time, plant height, grain yield, and kernel weight in 10 genetic groups of grain sorghum

Genetic group	P_1	P_2	F_1	F_2	B_1	B_2
			Grain yield (gr/plant)			
1	71.5	65.1	72.9	65.6	73.6	65.5
2	67.4	57.3	78.4	67.3	70.1	61.9
3	70.2	72.7	80.7	64.1	64.5	63.3
4	65.8	60.9	65.5	60.6	57.3	51.0
5	62.8	51.5	63.4	60.0	65.3	65.1
6	62.8	65.5	66.9	58.4	59.0	66.6
7	61.5	54.5	70.0	57.6	66.8	54.7
8	55.0	67.3	72.7	51.6	62.3	64.4
9	51.2	60.8	61.1	57.5	59.6	50.8
10	66.4	54.9	70.4	57.2	62.6	62.2
			Kernel weight (g/1000)			
1	28.88	27.06	26.16	27.68	32.65	25.94
2	26.65	27.25	32.98	29.54	30.28	32.98
3	29.22	32.94	28.14	27.50	28.84	27.98
4	28.17	28.78	36.05	29.59	34.43	34.21
5	27.30	27.33	24.10	25.77	26.05	28.67
6	27.63	35.06	28.09	27.13	25.73	27.80
7	27.32	27.45	30.04	28.85	26.96	33.67
8	30.63	35.41	26.66	28.18	30.36	28.57
9	28.10	27.23	33.25	29.84	32.28	34.75
10	32.31	26.67	30.86	28.91	32.79	30.93

Table 8 (cont.). Mean performance of the parental, F_1, F_2, and backcross generations for agronomic traits in grain sorghum

			Flowering time (days)			
1	70.7	67.5	68.5	69.1	70.8	68.0
2	71.0	65.2	67.5	67.5	70.4	69.6
3	70.1	67.6	68.5	69.4	70.7	67.7
4	70.8	68.1	69.4	68.1	71.8	71.7
5	67.7	65.1	64.6	65.9	67.0	65.9
6	68.7	68.7	63.5	66.9	68.2	64.4
7	68.9	66.3	65.6	67.5	65.1	66.7
8	66.2	67.0	64.2	67.5	65.9	65.8
9	65.3	67.5	66.2	62.7	67.7	69.1
10	67.9	67.5	63.2	66.6	66.3	67.6
			Plant height (cm)			
1	87.0	68.8	78.8	78.4	84.9	70.4
2	87.2	72.9	83.2	81.6	86.8	79.5
3	86.5	70.2	81.6	82.5	85.2	76.1
4	87.6	77.2	84.2	82.0	85.7	82.2
5	67.5	73.5	75.1	73.7	72.3	76.7
6	69.3	65.7	74.7	68.9	69.4	72.9
7	68.0	75.3	72.8	73.2	71.1	75.8
8	73.7	70.3	75.5	73.6	78.2	71.8
9	72.9	75.7	78.4	76.7	77.8	79.4
10	73.0	72.6	77.5	78.0	74.1	79.8

performance of a backcross population was related with its recurrent parent. That is, the backcross to the better performing parent was generally the better performing of the 2 backcross populations for any one cross. The degree of association of the backcross with its recurrent parent varied somewhat among attributes.

The estimates of the 6 gene effects of the 10 genetic groups for the 4 attributes were obtained using the procedure outlined by Hayman (24) and modified by Gamble (18). The results are presented in Tables 9, 10, 11, and 12.

Additive Gene Effects

Additive gene effects were significant in 9 of the 10 genetic groups for plant height and in 8 of the 10 groups for kernel weight. Significant gene effects were also obtained for the other 2 attributes in certain genetic groups only. For flowering time, genetic groups 1, 3, and 8 exhibited significant additive gene effects, while genetic groups 2, 4, 6, 7, and 9 showed similar results for grain yield.

The relative magnitudes of parameter "a" to parameter "m" suggest that the additive gene effects made only a minor contribution to the inheritance of flowering time and grain yield. Material used in this study was derived from single crosses. It may be that, as materials used become more selected in genetic background, additive gene effects are reduced (18). However, additive gene effects appeared to be more important for plant height as more genetic groups showed significant additive gene effects with relatively large magnitudes. This corresponds to the results reported in sorghum (30) and in other cereal crops (1, 19, 34, 44) which indicate that additive genetic variation is greater in the traits which are assumed to have a less complex inheritance. Amount of additive variation seems to be sufficient for further improvement of

Table 9. Mean estimates of the 6 gene effects for the 10 genetic groups for flowering time.

Genetic group	Gene effects					
	m	a	d	aa	ad	dd
1	69.0	2.8**	-4.9	12.8	1.2*	-5.4
2	67.5	0.8	3.3	3.7	-2.0	-11.9*
3	68.8	3.0*	1.3	0.9	0.7	-1.3
4	69.7	0.1	8.2*	8.3**	-1.2	-17.4**
5	66.2	1.1	-0.9	0.9	-0.1	-4.7
6	66.9	3.9	-7.6*	-2.3	3.9*	1.4
7	66.9	-1.6*	-6.1*	-7.1	-2.9**	7.0*
8	67.9	0.1	-10.4*	-6.4*	-0.2	6.3
9	67.2	1.3	4.2	4.9	-0.3	-13.1*
10	65.7	-0.9	0.5	5.0**	-1.4	-10.9

* significant at 5% level

** significant at 1% level

Table 10. Mean estimates of the 6 gene effects for the 10 genetic groups for plant height.

Genetic group	Gene effects					
	m	a	d	aa	ad	dd
1	79.3	14.5**	-5.4	-6.5**	5.5**	19.9*
2	81.6	7.3**	10.4**	6.3*	0.21	-8.6*
3	83.1	9.1**	-4.0	-9.7**	0.98	4.7**
4	82.0	3.5**	9.7**	7.9	-2.9**	-10.7**
5	75.1	-4.4**	7.9	-2.5	1.3	-9.9
6	68.9	-3.5*	2.8	9.1	-0.8	-18.3*
7	73.2	-4.5*	2.2	0.9	-0.9	-5.7
8	73.6	6.4**	9.1*	5.5	4.7*	-10.5
9	76.7	-1.6	11.5*	7.5	-1.2	-16.6*
10	78.0	-5.7*	0.5	4.2**	-5.9*	2.9

* significant at 5% level

** significant at 1% level

Table 11. Mean estimates of the 6 gene effects for the 10 genetic groups for grain yield.

Genetic group	Gene effects					
	m	a	d	aa	ad	dd
1	65.6	8.1	20.4**	15.9	5.6	-11.8
2	67.3	8.2*	11.0	4.9	3.1	26.5**
3	64.1	1.3	7.2	1.0	2.2	49.8*
4	60.6	6.3*	-23.8**	25.9*	3.8	66.9**
5	60.0	0.2	27.4*	20.7	5.5	-49.4**
6	58.4	-7.6*	20.5*	17.7	6.2	-6.8
7	57.6	11.9**	24.3	21.1	8.4*	24.3
8	51.6	-2.1	58.5**	46.9**	4.1	-32.5
9	57.5	8.9*	-4.4	-9.5	13.3**	2.3
10	57.2	0.1	30.6	20.9	5.3	-8.5

* significant at 5% level

** significant at 1% level

Table 12. Mean estimates of the 6 gene effects for the 10 genetic groups for kernel weight.

Genetic group	Gene effects					
	m	a	d	aa	ad	dd
1	27.68	6.7**	4.6**	6.5**	5.0**	-15.4**
2	29.54	-2.7*	14.4**	8.4**	-2.4	-15.1**
3	27.50	1.3*	-0.4	2.8	3.1*	2.2
4	29.59	-0.3	25.5**	17.9**	0.1	-25.2**
5	25.77	-2.6*	3.1	6.3	-2.6	-12.9**
6	27.13	-2.1*	-4.7	1.4	1.6*	13.2*
7	28.85	-6.7**	8.5*	5.9	6.7**	-12.3*
8	28.19	1.8*	-1.2	5.1	4.2*	-3.6
9	29.84	-2.5*	20.3*	14.7	-2.9	-26.9*
10	28.91	1.9	13.2	11.8	-1.0	-18.5*

* Significant at the 5% level

** Significant at the 1% level

this character through selection. Although, kernel weight appeared to be largely influenced by additive gene effects which were significant in 8 of the 10 genetic groups, the relatively low magnitude of their estimates suggests that interpretation of this attribute exclusively on the basis of additive gene effects must be treated with some caution. However, heritability estimates reported in the previous section do indicate that considerable progress could be made for these attributes by selection.

It should be noted that the sign of parameters "a" and "ad" depends upon the parents being considered as P_1 and P_2. For example in genetic group 1 for plant height, if Redlan is considered as P_1 and Plainsman as P_2, the estimate of parameter "a" is positive. However, if Plainsman is considered as P_1 and Redlan as P_2, the estimate of parameter "a" becomes negative. The sign of "ad" would change correspondingly in most cases but the sign of the other parameters would be unaffected. If the better performing parent had been used as P_1 in each genetic group, most of the estimates of "a" and "ad" would have been positive.

Dominant Gene Effects

In the inheritance of grain yield and flowering time, dominant gene effects seem to have made a major contribution. For grain yield, significant dominant gene effects were obtained in genetic groups 1, 4, 5, 6, and 8 while similar results were noted in genetic groups 4, 6, 7, and 8 for flowering time. For kernel weight, although only 5 genetic groups showed significant dominant gene effects compared to additive genetic effects which were significant in 8 genetic groups, the relative magnitude of estimates suggest that this attribute was also being influenced by dominant gene effects.

The importance of dominant gene effects was indicated not only by its significance and relative magnitude, but also by its sign. Positive dominant

gene effects suggest an enhancing effect on the performance of different traits. For flowering time, dominant gene effects had negative sign in genetic groups 1, 5, 6, 7, and 8 indicating that dominance was in the direction of early blooming. Negative sign for 1 and 3 genetic groups with respect to plant height indicates that dominance was in the direction of short stature. For grain yield, negative sign in genetic groups 4 and 9 showed that dominance for these populations was in the direction of low yields.

Although dominant gene effects were observed in certain genetic groups for all the attributes, their contribution for grain yield was more pronounced than the other traits. Similar results with regards to dominance level for grain yield were reported (18, 30, 44). This indicates that as the inheritance of a quantitative character becomes more complex, the contribution of dominant gene effects to the inheritance of the attributes becomes greater. The complexity of grain yield can also be related to its low heritability, which was reported and discussed in the previous section.

Epistatic Gene Effects

Consideration of the "aa," "ad," and "dd" estimates indicates that epistatic gene effects, although of minor importance in certain genetic groups for any one attribute, are important in general in the inheritance of the 4 attributes. Ignoring the sign, the relative magnitudes of epistatic gene effects were considerably larger for grain yield, plant height, and kernel weight than flowering time. Of the individual types of digenic epistasis it appears that the dominant x dominant and additive x additive were relatively more important than additive x dominant type.

Significant dominant x dominant type of epistasis was observed in 4 genetic groups for flowering time, 4 in grain yield, 6 in plant height, and 8 in kernel weight. However, considering the relative magnitudes, the "dd" type

of gene effects appeared to be more important for grain yield and kernel weight than plant height and flowering time. Most of the "dd" gene effects that were significant were negative. The negative estimates of these gene effects will have a diminishing effect (18) and might be inferred that "dd" type of gene effects are undesirable forms of epistasis.

Significant additive x additive type of gene effects were observed in 2 genetic groups for grain yield, in 5 for kernel weight, in 3 for flowering time, and in 4 for plant height. The data clearly indicated that"aa" epistasis was of least importance in the inheritance of grain yield while plant height and kernel weight appeared to be largely influenced by this kind of digenic epistasis.

Additive x dominant type of epistasis was observed in 2 genetic groups for grain yield, 5 in kernel weight, 3 in flowering time, and 4 in plant height. Although "ad" gene effects were comparable with "aa" type of epistasis in the level of significance, their relative magnitudes showed that "aa" type was more important than "ad" type. In general, it appeared that "ad" gene effects were of minor importance except for kernel weight.

The relative magnitudes of dominant x dominant gene effects, and additive x additive gene effects were comparable to that of dominant and additive gene effects respectively. This indicates that these forms of epistasis were also of larger magnitude. Without specifying the type of epistasis, Quinby (40) also indicated the importance of complimentary action of non-allelic genes for a number of attributes. The presence of epistatic gene effects obtained in the present study are in agreement with the results reported by Liang and Walter (30). The magnitudes of epistasis could be biased by the presence of linkage, especially "aa" and "ad" types of gene action (27), however the effect of epistasis which is a basic genetic

mechanism perhaps cannot be considered as negligible. Genetic models assuming negligible epistasis may be somewhat biased.

On the basis of materials and methods and number of attributes used in this study, additive, dominant, and epistatic gene effects contributed significantly to the inheritance of quantitative characters. In the 4 attributes studied, it appeared that grain yield was largely influenced by dominant and dominant x dominant type of gene effects in its inheritance. For plant height, additive and additive x additive type of gene effects were larger than other types of epistasis. The contribution of additive, dominant, as well as digenic epistasis of "ad" and "dd" type, were observed to be responsible for the inheritance of kernel weight. For flowering time, it appeared that all the 5 types of gene effects contributed equally in magnitude in its inheritance, although no one type in particular exercised greater control than others.

The 6 genetic parameters estimated provide a test for different types of gene action and are useful in supplying information for improvement of these traits with an appropriate breeding procedure. However, these genetic effects cannot be interpreted relative to genetic variances. Also, estimates obtained fron each cross may be unique in varying degrees and may not be applicable to its parental populations (46).

SUMMARY

The experimental material constituting 10 genetic groups derived from a 5 variety diallel: Redlan x Plainsman, Redlan x Martin, Redlan x Combine 7078, Redlan x Combine Kafir 60, Plainsman x Martin, Plainsman x Combine 7078, Plainsman x Combine Kafir 60, Martin x Combine 7078, Martin x Combine Kafir 60, and Combine 7078 x Combine Kafir 60 were grown at two locations in each of two years, 1968 and 1969. Each genetic group was considered as a unit in the investigation and included 6 components: P_1, P_2, F_1, F_2, B_1, and B_2.

Studies were made on heritability and gene effects for flowering time, plant height, grain yield, and kernel weight. Variances of 3 types of segregating populations, the F_2 and the summed backcrosses to each parent, were calculated and heritability estimates for the 4 traits were obtained. Heritability estimates for these traits were also computed by parent-offspring regression method for the purpose of comparison. Magnitudes of genetic and environmental variances and their ratios were also obtained for each trait to determine the extent of genetic divergence. Additive, dominant, and digenic epistatic gene effects expressed in terms of parent, first and second filial, and backcross population means were estimated.

The magnitude of heritability estimates varied among genetic groups for all the traits under study. Heritability estimates showed that flowering time, plant height, kernel weight were highly heritable while heritability value for grain yield was of low magnitude. A comparison between the heritability estimates computed by Warner's procedure and parent-offspring regression method revealed that plant height and flowering time showed high values regardless of method of calculation, indicating selection for these characters would be relatively easy. Heritability estimate for the grain

yield was low and variable for kernel weight.

The magnitude of genetic and environmental variances and their ratios showed there was a lack of adequate genetic variability in the breeding material used in the study. To obviate the situation introduction of exotic germ plasm into the domestic lines was suggested.

Information on the nature of gene action revealed that dominant gene effects and dominant x dominant epistasis appeared to have a major role in the inheritance of grain yield while additive, dominant, and additive x dominant epistasis were largely responsible for the inheritance of kernel weight, indicating that these two are complex characteristics. The significant contribution of additive gene effects was quite evident in the inheritance of plant height. On the other hand, no single type of gene effect contributed exclusively in the inheritance of flowering time.

In general, among the 3 types of digenic epistasis dominant x dominant, additive x additive were relatively more important than dominant x additive type. Most of the dominant x dominant estimates which were significant were negative, suggesting a diminishing effect due to this type of gene action. On the basis of significant occurrence of epistasis, it was suggested that a suitable breeding program in sorghum should be developed to utilize all types of gene effects and that genetic models assuming negligible epistasis would be somewhat biased.

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APPENDIXES

A-1. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 1

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	1320.7	473.2	2870.4	2338.17	2856.6	2035.8
		2	751.9	434.7	3836.0	1273.6	3326.4	438.7
		3	4454.8	13832.0	976.1	12600.5	20739.0	21812.3
		4	230.1	1170.8	22.1	326.2	795.3	125.1
Y	1	1	2375.1	1012.7	3110.4	2508.8	4100.3	4343.5
		2	7.6	266.7	1563.1	4849.1	91.9	1309.0
		3	19656.6	34129.4	3681.7	14368.5	28188.3	94168.7
		4	---	---	---	---	---	---
R	1	1	80.5	36.0	41.7	11.7	58.0	30.1
		2	5.5	80.5	151.2	311.4	134.3	141.8
		3	17616.3	2306.4	4541.4	47.7	1237.6	3511.3
		4	494.2	39.5	135.1	74.7	36.0	187.6
LY	1	1	495.9	218.5	91.3	385.3	46.8	519.2
		2	434.2	1530.1	261.4	1647.9	79.9	2223.5
		3	104.0	3226.7	2898.1	4.5	916.5	12936.0
		4	---	---	---	---	---	---
LR	1	1	165.0	214.7	290.4	165.3	60.0	75.9
		2	197.7	52.3	0.0	237.9	177.7	122.5
		3	936.1	558.1	1490.0	10975.5	656.7	13740.0
		4	1.3	87.4	0.0	7.9	98.3	27.7
YR	1	1	670.0	42.5	360.1	254.4	528.1	434.7
		2	421.8	56.1	2.5	67.5	11.9	1.1
		3	481.7	2470.4	70.4	8131.7	1301.9	29.4
		4	---	---	---	---	---	---
LYR	1	1	21.0	113.4	138.0	100.3	163.3	279.5
		2	173.7	102.7	126.9	485.1	49.9	43.8
		3	322.0	1126.7	336.1	2891.2	44.2	552.1
		4	---	---	---	---	---	---
Among plants	232	1	3.37	3.16	3.58	11.47	6.10	8.29
		2	24.8	21.2	21.6	60.1	45.5	36.8
		3	237.6	219.5	299.5	475.3	430.9	347.1
		4	14.4	15.0	9.3	24.1	16.8	18.0

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-2. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 2

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	3534.3	3074.5	1744.2	2342.1	2287.8	3736.6
		2	1991.8	244.0	3781.0	2038.7	3248.7	706.9
		3	710.7	31.5	9126.7	8991.5	4995.9	1995.3
		4	200.8	1224.6	54.2	75.7	326.0	40.9
Y	1	1	3367.5	152.0	1088.0	1593.1	2178.0	2451.2
		2	879.3	9437.6	2479.4	2957.5	589.1	2974.4
		3	2740.5	6070.2	53401.6	3352.5	21187.6	3969.1
		4	---	---	---	---	---	---
R	1	1	65.1	21.0	0.1	137.8	7.7	16.5
		2	1.4	10.0	11.9	118.3	52.3	42.4
		3	121.8	3382.5	2666.7	127.6	10101.0	212.8
		4	263.7	1.1	6.7	109.1	5.5	70.6
LY	1	1	175.1	36.0	397.8	141.1	980.1	11.7
		2	378.5	570.4	3163.9	346.8	1411.3	189.2
		3	924.3	1219.5	15328.0	110.7	40.8	421.3
		4	---	---	---	---	---	---
LR	1	1	82.8	5.7	24.7	155.4	0.7	14.5
		2	179.2	3.7	61.4	0.1	190.8	108.1
		3	1228.5	555.1	150.4	6375.7	5.7	209.1
		4	0.9	191.2	28.7	114.9	18.7	12.8
YR	1	1	23.4	5.1	1.5	13.1	4.0	1.5
		2	172.4	158.4	5.2	556.6	34.5	6.0
		3	4158.3	3784.2	756.1	478.8	972.0	589.1
		4	---	---	---	---	---	---
LYR	1	1	13.5	37.6	2.2	135.5	5.7	9.2
		2	61.4	58.0	24.4	0.1	5.7	4.8
		3	3017.5	1255.8	1685.4	6880.1	745.5	66.1
		4	---	---	---	---	---	---
Among plants	232	1	3.39	3.20	3.58	12.4	6.94	10.78
		2	23.1	20.9	16.6	65.5	38.0	35.0
		3	168.8	154.8	160.5	398.1	292.0	282.7
		4	12.8	9.4	12.9	30.7	23.7	18.8

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-3. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 3

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	1606.8	839.9	721.1	2913.9	573.5	1722.7
		2	2954.7	3390.0	585.9	2905.1	136.5	313.9
		3	7740.7	16925.5	10023.3	11228.2	1109.4	2400.3
		4	50.9	1271.5	373.2	438.8	128.9	30.2
Y	1	1	670.0	1627.6	273.1	1237.7	2754.0	877.8
		2	92.6	7763.4	749.1	5587.3	329.0	10766.9
		3	7831.8	15275.0	10101.0	27701.4	16368.0	27456.2
		4	---	---	---	---	---	---
R	1	1	507.5	49.5	470.4	211.2	113.4	100.1
		2	166.8	15.0	9.6	250.1	2.4	12.4
		3	357.7	282.7	5143.0	2163.2	539.9	690.2
		4	1.6	1.6	75.6	17.9	0.1	51.2
LY	1	1	1.5	254.2	653.4	93.7	37.6	196.2
		2	683.8	513.3	2106.3	2580.7	2933.0	556.6
		3	87.6	1312.9	4655.2	2635.8	1050.0	338.4
		4	---	---	---	---	---	---
LR	1	1	16.5	10.8	9.6	28.5	113.4	121.8
		2	1590.8	6.7	13.5	41.7	19.3	69.9
		3	5752.6	2227.3	292.6	1545.9	1264.6	90.0
		4	176.0	143.3	49.9	86.5	0.0	32.7
YR	1	1	310.5	45.9	355.3	12.8	15.5	210.9
		2	377.3	275.2	25.3	27.3	35.3	241.0
		3	1575.9	0.3	7537.6	2872.0	1135.3	262.5
		4	---	---	---	---	---	---
LYR	1	1	155.2	49.5	106.7	147.9	283.8	254.2
		2	44.1	8.4	39.2	16.0	390.1	60.5
		3	2082.7	1932.1	97.5	2205.5	2318.8	1535.2
		4	---	---	---	---	---	---
Among plants	232	1	3.25	5.82	4.78	15.36	10.60	11.78
		2	21.2	18.4	24.3	97.65	86.3	64.6
		3	155.5	186.7	124.3	584.7	476.3	470.7
		4	15.9	14.1	9.9	40.6	27.9	26.1

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-4. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 4

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	1306.7	2232.6	1586.2	2448.3	1399.5	4524.0
		2	1299.7	2863.5	1244.4	944.3	137.4	440.1
		3	3270.8	2626.8	35.3	20258.4	2733.7	721.1
		4	11.4	19.8	701.3	44.8	56.9	570.5
Y	1	1	4166.7	91.3	3944.7	4258.3	3234.0	1500.0
		2	1389.6	710.7	719.3	7679.9	300.6	1139.7
		3	21394.8	6510.4	35235.2	19062.3	42400.4	38304.2
		4	---	---	---	---	---	---
R	1	1	5.4	74.8	49.5	141.3	5.7	24.0
		2	167.5	6.7	9.4	144.4	140.5	0.6
		3	3270.8	1664.2	453.7	230.1	799.3	1892.8
		4	93.1	17.3	1.1	25.0	0.5	7.9
LY	1	1	742.0	240.0	357.7	174.8	788.4	666.7
		2	140.3	855.0	40.4	1035.1	1119.7	5.7
		3	101.4	26.7	240.0	11.7	1826.0	10401.7
		4	---	---	---	---	---	---
LR	1	1	2.8	43.3	22.2	39.6	116.2	1.7
		2	84.6	355.3	94.4	209.7	58.6	180.3
		3	1325.4	4018.0	6805.3	26.0	2788.0	2196.1
		4	93.1	142.5	1.4	81.3	250.7	319.0
YR	1	1	8.8	558.1	185.5	203.7	121.8	109.3
		2	170.8	52.3	213.7	29.0	1.6	380.1
		3	481.7	390.1	2269.3	484.5	799.3	350.4
		4	---	---	---	---	---	---
LYR	1	1	45.1	476.0	14.5	305.1	27.3	312.8
		2	0.2	4.3	11.1	120.6	99.6	14.0
		3	1430.8	960.0	1632.8	171.7	3450.4	98.8
		4	---	---	---	---	---	---
Among plants	232	1	3.21	5.82	2.25	7.89	5.70	4.99
		2	27.1	30.5	23.1	73.6	46.5	48.8
		3	171.2	168.6	170.3	349.5	220.0	212.2
		4	10.3	15.9	4.5	27.5	20.3	15.9

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-5. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 5

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	1334.8	976.1	992.3	1158.5	2444.8	1131.0
		2	488.8	250.7	1980.9	517.4	231.1	327.8
		3	22814.9	3427.7	2574.1	10216.1	44064.5	8906.0
		4	845.2	45.7	202.6	0.8	23.6	63.8
Y	1	1	212.8	365.0	448.3	1191.7	1470.1	604.8
		2	282.7	4239.5	578.1	245.0	48.1	1980.9
		3	26966.4	15184.5	10454.4	13851.2	22854.0	11537.0
		4	---	---	---	---	---	---
R	1	1	16.0	0.8	74.8	2.3	3.7	9.2
		2	83.4	58.7	368.8	508.8	414.7	428.0
		3	1550.4	972.0	6303.7	7081.3	3904.3	1224.0
		4	30.8	10.9	73.9	90.2	116.7	77.5
LY	1	1	18.1	25.3	56.1	568.0	194.4	473.2
		2	302.6	1238.9	1031.3	344.7	3056.6	506.1
		3	4611.3	2275.5	1760.4	5651.9	12673.1	9052.8
		4	---	---	---	---	---	---
LR	1	1	33.7	209.1	163.3	56.3	0.3	185.5
		2	96.9	41.1	761.5	676.5	27.7	25.7
		3	30.8	262.5	944.0	2302.5	1372.8	8166.7
		4	60.7	36.0	42.8	107.5	50.7	579.7
YR	1	1	70.4	576.6	104.0	39.3	426.7	617.6
		2	229.1	31.3	143.4	1.0	930.2	27.0
		3	7194.1	51.3	799.3	3158.4	1540.3	498.8
		4	---	---	---	---	---	---
LYR	1	1	66.1	0.1	1.3	60.8	390.1	19.8
		2	16.3	1405.0	165.8	63.0	394.0	596.9
		3	2244.8	3204.7	3.3	2184.3	742.0	29.4
		4	---	---	---	---	---	---
Among plants	232	1	4.69	4.44	4.58	12.67	7.70	6.84
		2	21.5	18.3	19.9	62.4	33.0	43.3
		3	178.9	175.8	205.1	438.1	421.9	357.0
		4	15.7	17.7	16.4	33.9	27.0	23.6

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-6. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 6

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	2318.8	370.0	1066.8	1255.8	3808.1	595.3
		2	988.2	759.3	226.2	801.4	992.3	824.0
		3	8027.3	7571.3	7106.8	5649.6	7706.7	34728.2
		4	348.8	1577.1	19.2	36.8	29.4	273.6
Y	1	1	385.1	350.4	26.7	1344.1	4166.7	1.3
		2	112.1	1842.0	17992.0	8642.3	3197.4	4440.2
		3	40507.9	51626.6	21622.0	27330.7	55085.4	27541.8
		4	---	---	---	---	---	---
R	1	1	897.1	1170.4	212.8	10.7	370.0	70.4
		2	246.0	76.9	7992.6	1252.2	1591.3	291.9
		3	9375.0	91.3	7437.1	1462.0	564.3	1228.5
		4	16.5	144.7	640.7	3.4	4.5	96.6
LY	1	1	21.6	194.4	91.3	611.1	141.1	32.3
		2	1118.0	246.2	742.0	1074.6	731.5	715.2
		3	777.6	4699.3	5358.1	4652.5	28.0	124.7
		4	---	---	---	---	---	---
LR	1	1	355.3	448.3	70.4	44.6	62.0	64.1
		2	18.7	264.4	39.2	1059.7	55.1	723.5
		3	1938.0	0.8	1092.3	1018.6	1016.8	900.9
		4	40.5	2.0	453.7	338.5	8.3	13.8
YR	1	1	132.0	232.1	24.1	8.8	260.4	29.4
		2	317.4	201.5	2587.3	1086.5	885.5	1579.5
		3	38.4	2788.0	1837.1	2784.8	132.0	127.6
		4	---	---	---	---	---	---
LYR	1	1	1152.8	742.0	187.3	106.3	170.0	88.8
		2	442.8	13.0	1749.6	634.4	96.3	131.6
		3	686.8	81.7	6489.6	950.5	194.4	3519.0
		4	---	---	---	---	---	---
Among plants	232	1	5.90	5.84	4.16	20.08	20.67	7.54
		2	20.9	24.0	20.8	75.0	54.5	47.8
		3	179.7	194.7	154.7	467.0	405.4	400.1
		4	15.3	17.0	16.6	44.1	19.3	39.0

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-7. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 7

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	510.4	445.5	56.1	2899.5	881.7	803.3
		2	0.1	838.1	242.0	164.5	878.2	1.3
		3	9250.4	5674.5	14430.5	16884.1	3621.5	21527.2
		4	818.2	201.1	42.5	450.3	2.2	40.9
Y	1	1	874.0	246.0	851.3	167.4	260.4	51.3
		2	1552.9	2157.0	1050.0	11075.6	4488.5	153.6
		3	44444.8	33867.5	64320.9	16683.3	35745.9	77220.9
		4	---	---	---	---	---	---
R	1	1	232.1	61.0	150.4	121.0	1.7	90.3
		2	191.7	16.8	464.8	379.7	25.4	2.8
		3	2587.3	940.1	656.7	670.0	13305.7	5616.3
		4	16.5	78.6	96.9	30.0	98.4	70.6
LY	1	1	64.1	2325.0	326.7	451.4	7.3	429.3
		2	29.7	2631.7	1.5	670.4	107.9	185.5
		3	6365.4	175.1	28842.3	2835.9	4.5	158.4
		4	---	---	---	---	---	---
LR	1	1	2.0	2.2	43.3	388.9	8.1	33.0
		2	30.4	471.8	168.3	412.9	40.7	45.9
		3	70.4	3488.4	4550.1	8062.0	12921.3	6355.1
		4	31.1	95.1	43.2	8.4	5.9	12.8
YR	1	1	104.0	6.3	6.0	11.2	3.7	372.5
		2	11.1	6.2	60.0	418.4	17.1	192.6
		3	183.7	579.7	392.7	1495.0	0.0	13.4
		4	---	---	---	---	---	---
LYR	1	1	41.7	49.5	183.7	244.8	1.3	55.1
		2	83.4	520.7	30.1	204.5	87.7	48.6
		3	0.3	242.0	0.9	14.5	2489.7	683.4
		4	---	---	---	---	---	---
Among plants	232	1	5.20	5.79	2.33	11.8	12.03	6.57
		2	23.6	20.6	26.6	62.9	43.3	55.19
		3	201.7	164.4	148.5	329.5	254.8	326.1
		4	13.4	11.6	6.7	27.1	17.4	18.4

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-8. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 8

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	58.0	799.3	585.9	3686.3	2926.0	3518.9
		2	391.4	2610.3	212.8	516.7	2589.9	287.3
		3	26145.9	14014.8	31327.3	8754.3	21527.2	6468.8
		4	257.8	1483.3	0.9	0.0	195.0	0.9
Y	1	1	58.0	1224.0	37.6	278.8	286.0	196.2
		2	5362.9	4510.3	6784.1	35925.6	7537.6	15720.5
		3	7425.9	41764.8	16500.4	16.2	19421.9	47498.0
		4	---	---	---	---	---	---
R	1	1	9.6	322.0	142.6	118.4	18.1	27.3
		2	79.9	1002.5	1320.7	1809.7	15.0	414.5
		3	10600.1	3168.3	564.3	2254.3	10.0	680.1
		4	776.5	60.7	17.5	117.3	71.3	305.3
LY	1	1	21.6	4.8	9.2	352.9	426.7	1265.0
		2	1018.9	1073.1	1430.7	1933.9	2666.7	3027.4
		3	440.1	5358.1	350.4	1969.7	5405.7	228.1
		4	---	---	---	---	---	---
LR	1	1	36.8	144.1	67.2	314.3	11.3	175.1
		2	159.3	90.7	893.2	256.0	21.0	104.8
		3	100.1	153.6	240.0	2734.7	5772.2	3792.1
		4	199.3	46.9	19.7	159.2	139.0	465.9
YR	1	1	984.1	0.4	136.5	0.1	1.7	168.3
		2	0.5	65.6	152.0	564.4	688.2	17.9
		3	59.0	56.1	481.7	27676.8	724.5	11.3
		4	---	---	---	---	---	---
LYR	1	1	19.3	98.8	82.8	352.9	79.3	28.7
		2	204.4	42.1	10.8	216.3	34.8	523.3
		3	124.7	735.0	2356.3	3453.4	258.3	150.4
		4	---	---	---	---	---	---
Among plants	232	1	6.47	4.73	3.86	13.01	10.16	12.67
		2	27.3	20.9	24.1	74.0	74.0	42.5
		3	168.9	169.2	16.85	475.3	373.9	495.5
		4	20.3	17.4	22.9	45.5	33.4	39.9

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-9. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 9

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	250.1	1288.1	749.1	1193.9	1643.3	1749.6
		2	0.1	46.4	105.3	3441.9	1537.7	4.8
		3	7106.8	7304.1	5443.5	8287.9	7889.1	19260.4
		4	48.9	26.1	89.7	717.9	48.3	91.9
Y	1	1	7.7	70.4	312.8	1349.5	2053.3	866.3
		2	3304.1	2217.4	3480.8	5077.4	2957.5	756.1
		3	18480.1	11206.7	47292.3	20055.5	64484.8	32853.6
		4	---	---	---	---	---	---
R	1	1	161.7	220.4	248.1	0.5	74.8	481.7
		2	121.1	70.9	421.3	145.8	455.1	21.0
		3	2432.1	504.6	67.2	0.3	2982.1	5626.0
		4	495.4	45.3	160.5	198.9	5.7	63.9
LY	1	1	145.7	721.1	68.3	517.7	7.3	1.1
		2	1394.4	165.8	579.7	1380.4	1823.3	614.4
		3	653.4	498.8	2541.5	3455.5	2406.7	1706.7
		4	---	---	---	---	---	---
LR	1	1	102.7	64.1	138.0	82.5	252.1	38.4
		2	96.9	125.4	6.3	88.8	356.5	49.5
		3	1870.4	7774.8	810.3	2541.1	9126.7	2870.4
		4	115.9	622.3	22.9	1133.0	173.9	49.0
YR	1	1	67.2	10.4	81.7	0.3	5.4	135.0
		2	346.8	98.2	459.3	3.1	55.6	27.3
		3	4593.7	3480.8	24.7	15015.1	1050.0	6040.1
		4	---	---	---	---	---	---
LYR	1	1	175.1	481.7	498.8	92.1	17.1	45.1
		2	645.2	59.5	196.2	356.7	42.9	4.5
		3	160.1	1401.7	3088.8	2238.5	224.3	5377.1
		4	---	---	---	---	---	---
Among plants	232	1	5.63	6.79	5.10	13.54	9.82	8.06
		2	31.6	34.0	27.4	74.7	37.1	65.3
		3	162.2	141.1	120.9	348.0	253.6	371.2
		4	21.7	18.8	11.6	26.1	22.6	10.2

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

A-10. 3-way analysis of variance for flowering time, plant height, grain yield, and kernel weight of genetic group 10

Source of variation	df	Character[a]	Mean squares					
			P_1	P_2	F_1	F_2[b]	B_1	B_2
L	1	1	2801.7	3572.8	1406.5	3070.3	2640.1	3619.3
		2	8120.1	110.0	164.2	377.8	167.5	172.5
		3	6976.8	5529.6	17767.6	8464.9	23088.8	4446.2
		4	478.3	37.8	684.6	93.8	184.6	106.9
Y	1	1	1058.4	28.0	525.1	0.6	601.7	660.0
		2	15136.8	284.9	13930.9	18327.5	4246.2	4810.6
		3	58844.0	546.0	47573.5	27763.4	62726.7	23740.7
		4	---	---	---	---	---	---
R	1	1	493.1	35.3	59.0	58.4	294.8	93.7
		2	467.6	102.0	17.3	2.6	229.1	200.7
		3	2666.7	8425.3	2515.5	599.5	365.1	6171.2
		4	225.4	141.3	577.0	514.6	124.3	249.4
LY	1	1	10.4	1260.4	21.0	69.0	135.0	3.7
		2	1118.0	1133.2	651.7	1634.1	488.8	272.0
		3	2706.8	1540.3	12862.7	1732.1	2996.3	4463.4
		4	---	---	---	---	---	---
LR	1	1	98.8	29.4	357.7	316.3	16.0	6.0
		2	234.0	9.8	31.9	148.3	906.8	4.1
		3	308.3	194.4	1733.4	346.1	1520.1	996.3
		4	451.8	0.1	50.1	364.7	1463.0	150.8
YR	1	1	50.4	180.3	495.9	19.7	2.0	38.4
		2	226.2	52.7	85.8	54.2	872.1	388.9
		3	273.1	6594.0	1887.2	4565.2	370.1	847.5
		4	---	---	---	---	---	---
LYR	1	1	5.4	17.1	382.5	156.2	421.3	224.3
		2	87.6	2.5	177.7	183.0	4.7	26.3
		3	8.1	1008.6	2250.9	331.1	4018.0	14030.1
		4	---	---	---	---	---	---
Among plants	232	1	4.61	3.90	3.12	10.55	9.27	7.56
		2	34.0	32.7	35.5	97.56	62.8	56.2
		3	194.2	236.9	147.7	506.8	378.3	364.0
		4	19.1	22.3	15.8	41.6	32.3	17.0

a: 1 - flowering time; 2 - plant height; 3 - grain yield; 4 - kernel weight

b: df for F_2 was 712

HERITABILITY ESTIMATES AND GENE EFFECTS FOR SEVERAL AGRONOMIC CHARACTERS IN A SYSTEMATIC SERIES OF GRAIN SORGHUM (*SORGHUM BICOLOR* (L.) MOENCH) GENOTYPES

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Improvement of quantitative traits such as yield in sorghum, needs adequate genetic information. For example, knowledge about heritability coupled with gene effects is of great value in the selection concept and choice of selection procedure. Owing to the fact that Mendelian approach is not applicable to the study of polygenic inheritance, many biometrical procedures have been developed to obtain information useful to a breeding program.

This investigation was designed to obtain heritability estimates and gene effects for flowering time, plant height, grain yield, and kernel weight. Variances of the 3 types of segregating populations, i.e. the F_2 and the backcrosses of F_1 to each parent, were calculated. Heritability estimates were then computed. Magnitudes of genetic and environmental variances and their ratios were obtained to determine the extent of genetic variability for each trait. Additive, dominant, and digenic epistatic gene effects expressed in terms of parent, first and second filial, and backcross population means were estimated.

The experimental material constituting 10 genetic groups derived from a 5 variety diallel: Redlan x Plainsman, Redlan x Martin, Redlan x Combine 7078, Redlan x Combine Kafir 60, Plainsman x Martin, Plainsman x Combine 7078, Plainsman x Combine Kafir 60, Martin x Combine 7078, Martin x Combine Kafir 60, and Combine 7078 x Combine Kafir 60 were grown at two locations at the agronomy farms of Manhattan, Kansas, in each of two years (1968 and 1969). Each genetic group was considered as a unit in the investigation and included 6 components: P_1, P_2, F_1, F_2, B_1, and B_2.

The magnitude of heritability estimates varied among genetic groups for all the traits under study. Heritability estimates showed that flowering time, plant height, kernel weight were highly heritable while heritability

value for grain yield was of low magnitude. A comparison between the heritability estimates computed by using backcrosses and F_2 technique and parent-offspring regression method revealed that plant height and flowering time showed high values regardless of the method of calculation, indicating selection for these characters would be relatively easy. Heritability estimate for the grain yield was low, and variable for kernel weight.

The magnitude of genetic and environmental variances and their ratios showed there was a lack of adequate genetic variability in the breeding material used in the study. To obviate the situation, introduction of exotic germ plasm into the domestic lines was suggested.

Information on the nature of gene action revealed that dominant gene effects and dominant x dominant epistasis appeared to have a major role in the inheritance of grain yield while additive, dominant, and additive x dominant epistasis were largely responsible for the inheritance of kernel weight, indicating that these two are complex characteristics. The significant contribution of additive genetic effects was quite evident in the inheritance of plant height. On the other hand, no single type of genetic effect contributed exclusively in the inheritance of flowering time.

In general, among the 3 types of digenic epistasis dominant x dominant, additive x additive were relatively more important than additive x dominant type. Most of the dominant x dominant estimates which were significant were negative, suggesting a diminishing effect due to this type of gene action. On the basis of significant occurrence of epistasis, it was suggested a suitable breeding program in sorghum should be developed to utilize all the types of genetic effects and that genetic models assuming negligible epistasis would be somewhat biased.