INHERITANCE OF HEAD SHAPE AND

SEED SIZE IN SORGHUM

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CHAPTER I

INTRODUCTION

A knowledge of the inheritance of specific traits is required as a basis of more efficient breeding programs in sorghum. Most breeding programs tend to develop a genetically variable base population, if it does not exist, then select within that population for desirable characteristics. The progress under selection depends on the recognition of individuals, or selection units in general, with desirable characteristics and the extent to which these characteristics could be transmitted to the following generations.

In general, traits could be classified according to the mode of their expression into qualitative and quantitative traits. A qualitative trait has distinct expressions by which individuals could be classified into different groups. Such traits are simply inherited and are controlled by a relatively few number of genes. On the other hand, for a quantitative trait, differences among individuals are considered in terms of the degree, rather than the kind of the expression of the trait. Most quantitative traits are controlled by a large number of genes and their expressions are affected by the genetic and by the environmental conditions as well. The progress of breeding for such traits is primarily conditioned by the magnitude, nature, and interrelations of genetic and environmental variations in the population.

Two schools of thought exist in theoretical quantitative genetics
(57). These are the Mather school and the Lush school. Mather's
approach to quantitative genetics was primarily concerned with gene
action and linkage without considering a random breeding population
to which the results may be applied. On the other hand, the Lush
school has been primarily concerned with random breeding populations,
with the descriptions of the relationships between different individ-
uals in the population and with the prediction of the response of the
population to short-term selection.

Many studies of the inheritance of quantitative characters in
sorghum have been done. However, few investigations on the inheritance
of head shape and seed size have been reported. Such information is
needed for the development of varieties or hybrids with desirable
characteristics.

The main objective of this research was to investigate the genetic
parameters of head shape and seed size in six crosses of sorghum.
Subject matter is grouped into three topics: (a) phenotypic, genetic,
and environmental variation, (b) heritability, genetic advance, and
gene number, and (c) phenotypic, genetic, and environmental correlations.
Each topic is presented in a separate chapter in the form and style
required by scientific journals in the author's field.

CHAPTER II

MATERIALS AND METHODS

The following six populations of sorghum crosses were studied in
the F_2 and F_3 generations.

Population 1:   Woodward Big Head x Chicken Maize

Population 2:   4 Dwarf x Chicken Maize

Population 3:   Red Kafir x Chicken Maize

Population 4:   Dwarf Broomcorn x Chicken Maize

Population 5:   4 Dwarf x Woodward Big Head

Population 6:   OK8 x Woodward Big Head

'Woodward Big Head' is a selection from a cross involving 'Cyto #1',
a male sterile plant of milo origin, and 'Kaura', a direct introduction
from Nigeria. 'Chicken Maize' is probably a selection from an intro-
duction from India. It is a durra type which implies a small compact
head, crooked neck, and the plants are tall. '4 Dwarf', or 'B OK 24',
is a selection from cross 'B Redlan^4' x 'SA 3002-1-El', where 'SA 3002-
1' is 'Day' x 'Sooner', source of 4-dwarf. 'Red Kafir C I 34' is a
direct introduction from South Africa. 'Dwarf Broomcorn' is a selec-
tion from the cross Early White-Aksorben x Tan-2-5-6-2-1 where Early
White was probably a derivative from a cross with Broomcorn Kaoliang,
and Tan was a derivative from a Leoti cross from which it received tan
plant and leaf disease resistance. 'OK8' is from the cross between
Dwarf Kafir, a Kafir derivative for dwarfness, and 'Sudan Red Kafir'

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which is early maturing with bright grain.

All parents involved in the populations studied were considered to be homozygous diploid for the characters studied. The general characteristics, with respect to head shape and seed size, of the parents are shown in Table I. Head shape was measured in terms of head length, head width, and seed-branch length, in millimeters, and node number per head. The weight of one hundred seeds, in decigrams, was taken to be a measure of seed size. Head width and seed weight for Broomcorn were not measured since the heads consisted of typical broomcorn brush and the seeds were covered by glumes.

The F_2 populations and the parents were grown in 1967 at two locations, Perkins and Woodward, Oklahoma, in a randomized complete block design with six blocks at each location. All heads obtained were measured for head length, head width, seed-branch length, node number per head, and 100-seed weight. In the same year 97 and 99 F_3 families of population 1 and 4, respectively, were grown at Woodward, and 91 and 97 F_3 families of population 2 and 3, respectively, were grown at Perkins. Each family was grown in one row. Five heads, taken at random from each F_3 family, were measured for head shape and seed size.

In 1968 the only available location was at Perkins. Fifty F_3 families of each of the six populations were grown in a randomized complete block design with two blocks. The seeds, used to produce the fifty families, were taken from the F_2 generation, grown at Perkins, in the following manner. All F_2 plants of a particular population were grouped, according to head length, into ten classes, and five plants were taken at random from each class to supply the seed source

TABLE I

PARENT MEANS FOR FIVE CHARACTERS BASED
ON TWO LOCATIONS

Character	WBH[a]	CM	4D	RK	BC	OK8
Head Length (mm)	462.87	89.30	204.02	275.61	455.11	250.65
Head Width (mm)	47.86	48.93	42.19	33.09	-------	43.57
Seed-Branch Length (mm)	105.28	28.97	65.58	71.02	407.68	73.85
Node Number	17.34	9.07	7.66	12.07	5.90	8.84
100-Seed Weight (dg)	36.09	15.52	25.17	17.68	-------	23.16

[a]WBH = Woodward Big Head
CM = Chicken Maize
4D = 4 Dwarf
RK = Red Kafir
BC = Dwarf Broomcorn

of the F_3 families. This procedure was applied on each population to obtain a representative sample of fifty families, each five families coming from each group. Each F_3 family was grown in a row in each of the two blocks. To obtain estimates of the between and the within row environmental variations, three rows of each of the two parents involved in each population were grown together with the F_3 population. Five plants were taken at random from each row and measurements were recorded for head shape and seed size.

The frequency distributions of the F_2 populations and their parents were made for the five characters studied. In general, the different populations showed similar distributions, which approached the normal distribution for the different characters. The frequency distributions of population 1, for the different characters, were typical of the other populations. Those frequency distributions are shown in the appendix.

Estimates of the phenotypic, environmental, and genetic variabilities for each character in each population were obtained from the F_2 generation and the parents since the F_1 populations were not available, based on two locations and one year, by the analysis of variance technique. The model assumed for each of the parents and the F_2 populations was as follows:

$$Y_{ijk} = \mu + a_i + b_{ij} + c_{ijk}$$

where Y_{ijk} = the observation from the ith location, the jth block, and the kth plant for a given character.

μ = effect due to the overall mean.

a_i = effect due to the ith location, i = 1, 2, ..., L.

b_{ij} = effect due to the jth block in the ith location, j = 1,

2, ..., R,

c_{ijk} = effect due to the kth plant in the jth block and the ith location, $k = 1, 2, ..., n_{ij}$.

The form of the analysis of variance is shown in Table II. K_o, K_1, and K_2 in the last column are constants depending on the number of plants in the ith location and the jth block. Since the locations were fixed, it should be noted that σ_a^2 stands for the sum of the squares of the true location effects divided by the corresponding degrees of freedom. The assumptions associated with the model and the deriviation of the expected mean squares are discussed in detail by Graybill (25). Plants in blocks in locations mean square is an unbiased estimate of σ_c^2 which is composed of the genetic and the environmental variances in case of an F_2 generation analysis, and the environmental variance only in case of a parent analysis, assuming that genotype-environment interaction is not present.

The estimate of the environmental variance for each character in the six populations was calculated from the data of the parents only since the F_1 generation was not available, in three different manners: (a) the pooled variance, (b) the geometric, and (c) the arithmetic means of the estimates of the variances of the two parents involved in the given population. The difference between the F_2 variance and the environmental variance was taken to be an estimate of the total genetic variance which is composed of the additive, the dominance, and the epistatic variance estimates.

It was possible to obtain estimates of the additive and the dominance variances from the F_3 generation. However, the following assumptions have to be drawn: (a) regular diploid meiosis, (b) no

TABLE II

ANALYSIS OF VARIANCE TABLE FOR AN F_2 POPULATION OR FOR A PARENT

Source	d.f.	MS	EMS
Total	$\sum_{ij} n_{ij} - 1$		
Loc.	L-1	MS3	$\sigma_c^2 + K_1 \sigma_b^2 + K_2 \sigma_a^2$
Blk. in Loc.	L(R-1)	MS2	$\sigma_c^2 + K_o \sigma_b^2$
Plants in Blk. in Loc.	$\sum_{ij}(n_{ij} - 1)$	MS1	σ_c^2

linkage, or equilibrium with respect to linkage relations, (c) no epistasis, (d) gene frequency of one-half, and (e) no genotype-environment interaction. The following model was assumed for the analysis of any F_3 population.

$$Y_{ijk} = \mu + r_i + b_j + e_{ij} + w_{ijk}$$

where Y_{ijk} = the observation from the ith block, the jth family, and the kth plant for a given character.

μ = effect due to the overall mean.

r_i = effect due to the ith block, i = 1, 2, ..., R.

b_j = effect due to the jth family, j = 1, 2, ..., F.

e_{ij} = error associated with the jth family in the ith block.

w_{ijk} = effect due to the kth plant in the jth family, and in the ith block, k = 1, 2, ..., S.

The analysis of variance for the above model was of the form shown in Table III. The assumptions associated with the model and with the derivation of the expected mean squares are discussed by Graybill (25). The mean squares in the above analysis were equated to their corresponding expectations and the resulting set of four equations were solved for the four unknowns $\hat{\sigma}_w^2$, $\hat{\sigma}_e^2$, $\hat{\sigma}_b^2$, and $\hat{\sigma}_r^2$. It should be pointed out that $\hat{\sigma}_w^2$ is an estimate of the within families genetic variance in addition to plant-to-plant environmental variance. Similarly, $\hat{\sigma}_b^2$ is an estimate of the between families genetic variance plus row-to-row variance. To obtain estimates of the within and the between rows environmental variances, the data of each of the two parents were analyzed separately in a similar manner as the F_3 generation except the between and the within families became the between and the within rows in this case. Two estimates for each of the within and the

TABLE III

ANALYSIS OF VARIANCE TABLE FOR AN F_3 POPULATION

Source	d.f.	MS	EMS
Total	RFS-1		
Blocks	R-1	MS4	$\sigma_w^2 + S\sigma_e^2 + FS\sigma_r^2$
Between Families	F-1	MS3	$\sigma_w^2 + S\sigma_e^2 + RS\sigma_b^2$
Experimental Error	(R-1)(F-1)	MS2	$\sigma_w^2 + S\sigma_e^2$
Within Families	RF(S-1)	MS1	σ_w^2

between rows environmental variation were calculated. The first esti-
mate was the arithmetic mean of the estimates of the variances of the
two parents which is the same as the pooled variance estimate since
the number of observations in the two parents was equal. The second
estimate was the geometric mean of the estimates of the variances of
the two parents. Two estimates for each of the within and the between
F_3 families genetic variances were calculated as the difference between
the F_3 generation variances and each of the two environmental variances
obtained from the two parents.

The genetic variance components of the within and the between
family genetic variance are as follows:

$$(\hat{\sigma}^2_{wF_3} - \hat{\sigma}^2_{wP}) = \frac{1}{2} \hat{\sigma}^2_A + \frac{1}{2} \hat{\sigma}^2_D + \frac{1}{4} \hat{\sigma}^2_{AA} + \frac{1}{4} \hat{\sigma}^2_{AD} + \frac{1}{4} \hat{\sigma}^2_{DD} + \dots$$

$$(\hat{\sigma}^2_{bF_3} - \hat{\sigma}^2_{bP}) = \hat{\sigma}^2_A + \frac{1}{4} \hat{\sigma}^2_D + \hat{\sigma}^2_{AA} + \frac{1}{4} \hat{\sigma}^2_{AD} + \frac{1}{16} \hat{\sigma}^2_{DD} + \dots$$

In the above two expressions $\hat{\sigma}^2_{wF_3}$, $\hat{\sigma}^2_{wP}$, $\hat{\sigma}^2_{bF_3}$, and $\hat{\sigma}^2_{bP}$ stand for the
estimates of the within F_3 families, the within rows environmental,
the between F_3 families, and the between row environmental variance,
respectively. $\hat{\sigma}^2_A$ and $\hat{\sigma}^2_D$ are the estimates of the additive and the
dominance respectively. $\hat{\sigma}^2_{AA}$, $\hat{\sigma}^2_{AD}$, and $\hat{\sigma}^2_{DD}$ are the estimates of the
epistatic variances: additive by additive, additive by dominance,
and dominance by dominance variance, respectively. It was assumed
that epistatic variances are absent, consequently the above two equa-
tions would be reduced to the following:

$$(\hat{\sigma}^2_{wF_3} - \hat{\sigma}^2_{wP}) = \frac{1}{2} \hat{\sigma}^2_A + \frac{1}{2} \hat{\sigma}^2_D$$

$$(\hat{\sigma}^2_{bF_3} - \hat{\sigma}^2_{bP}) = \hat{\sigma}^2_A + \frac{1}{4} \hat{\sigma}^2_D$$

These two equations are the same as those given by Mather (49), where
$\hat{\sigma}^2_A$ and $\hat{\sigma}^2_D$ are the estimates of the additive and dominance variance of

the F_2 generation. By solving the two equations, estimates of the

additive and dominance genetic variances were obtained. The estimate

of total environmental variance, $\hat{\sigma}^2_E$, was calculated by the following

equation:

$$\hat{\sigma}^2_E = \hat{\sigma}^2_{wP} + \hat{\sigma}^2_{bP} + \hat{\sigma}^2_{eF_3} + \hat{\sigma}^2_{rF_3}$$

where $\hat{\sigma}^2_{wP}$ and $\hat{\sigma}^2_{bP}$ are as defined before and $\hat{\sigma}^2_{eF_3}$ and $\hat{\sigma}^2_{rF_3}$ are the

estimates of the error and block variance, respectively, for the F_3

generation analysis. The estimates of the total genetic and the total

phenotypic variances were calculated as follows:

$$\hat{\sigma}^2_G = \hat{\sigma}^2_A + \hat{\sigma}^2_D$$

$$\hat{\sigma}^2_P = \hat{\sigma}^2_G + \hat{\sigma}^2_E$$

Heritability estimates were essentially obtained by four methods:

(a) parent-offspring regression, (b) standard unit method, (c) approx-

imation of the environmental variance to estimate the total genetic

variance in the F_2 generation, and (d) variance component method from

the analysis of variance of the F_3 generation. The environmental

variance in the third method was estimated in three different manners:

(a) the pooled variance, (b) the geometric, and (c) the arithmetic

means of the estimates of the variances of the two parents involved

in a given F_2 population. Three estimates of heritability were calcu-

lated by the variance component method for the F_3 generation. The

first was based on the F_3 family means. The other two estimates were

heritability in the narrow sense and in the broad sense.

Genetic advance, G. A., was calculated by the following formula:

$$\text{G. A.} = i \, \hat{\sigma}_p \, \hat{h}^2 = \frac{z}{p} \, \hat{\sigma}_p \, \hat{h}^2$$

where i = the intensity of selection, $i = \frac{z}{p}$.

z = the height of the ordinate at the point of truncation

assuming normal distribution.

p = the proportion selected.

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

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

The number of genes controlling the different traits studied for each of the six populations was estimated by the following formula:

$$n = \frac{(\bar{P}_2 - \bar{P}_1)^2}{8(\hat{\sigma}_{F_2}^2 - \hat{\sigma}_E^2)}$$

where $\bar{P}_2$ and $\bar{P}_1$ are the means of the parents involved in the given population, $\hat{\sigma}_{F_2}^2$ is the estimate of the phenotypic variance based on the F_2 generation, and $\hat{\sigma}_E^2$ is the estimate of the environmental variance. Two estimates of the environmental variance were applied: (a) the pooled variance and (b) the geometric mean of the estimates of the variances of the two parents involved. The assumptions associated with the estimation of gene number, by the above formula, are several (72). Some of these assumptions are not met which would result in downward biased estimates of gene number.

Phenotypic, genetic, and environmental correlations between different characters were calculated for the F_2 and the F_3 generations. Phenotypic correlations for the F_2 generation were calculated by the following formula:

$$r_p = \frac{\hat{Cov}_{F_2}(X, Y)}{\sqrt{\hat{\sigma}_{F_2X}^2 \, \hat{\sigma}_{F_2Y}^2}}$$

where $\hat{Cov}_{F_2}(X, Y)$ = the estimate of the phenotypic covariance of character X and character Y in the F_2 generation.

$\hat{\sigma}^2_{F_2X}$ and $\hat{\sigma}^2_{F_2Y}$ = the estimates of the phenotypic variances for character

X and character Y, respectively, in the F_2 generation.

Covariance estimates were obtained by the analysis of covariance which

is similar to the analysis of variance. Environmental correlations

were calculated in a similar manner as the phenotypic correlations

except that the phenotypic variances and covariances were replaced

by the environmental ones. Environmental variances and covariances

were estimated from the informations obtained from the two parents

involved in a particular population in two different manners: (a)

the pooled variance and covariance and (b) the geometric means of the

variances and covariances. Genetic correlations were calculated by

using the genetic variances and covariances which were obtained by

subtracting the environmental variances and covariances from the

corresponding phenotypic variances and covariances.

Phenotypic, genetic, and environmental correlations for the F_3

generation were based on family means. The analysis of variance of

family means was made according to the following model:

$$Y_{ij} = \mu + r_i + b_j + e_{ij}$$

where Y_{ij} = the mean of jth family from the ith block.

μ = the effect due to the overall mean.

r_i = the effect due to the ith block, i = 1, 2, ..., R.

b_j = the effect due to the jth family, j = 1, 2, ..., F.

e_{ij} = error associated with j^{th} family in the ith block.

The analysis of covariance for each two characters was similar to the

analysis of variance. The mean product of families for traits X and Y,

obtained from the analysis of covariances, was considered to be an

estimate of the phenotypic covariance of the two traits. MS2 obtained

from the analysis of variance tables for each of trait X and trait Y

were taken as estimates of the phenotypic variances. Phenotypic

correlation between traits X and Y was then obtained by the following

formula:

$$r_p = \frac{MP\ 2\ (X,\ Y)}{\sqrt{MS2\ (X)\ MS2\ (Y)}}$$

where MP2 (X, Y) = family mean product for traits X and Y.

MS2 (X) and MS2 (Y) = family mean square for trait X and for trait Y,

respectively.

Environmental and genetic correlations for traits X and Y, based on

the F_3 family means, were calculated in a similar manner using formulas

given by Anand and Torrie (2). The formulas are as follows:

$$r_E = \frac{MP1(X,\ Y)}{\sqrt{MS1\ (X)\ MS1(Y)}}$$

$$r_G = \frac{\hat{Cov}_b\ (X,\ Y)}{\sqrt{\hat{\sigma}^2_{bX}\ \hat{\sigma}^2_{bY}}}$$

where

$$\hat{Cov}_b(X,\ Y) = [MP2\ (X,\ Y) - MP1\ (X,\ Y)]/R$$

$$\hat{\sigma}^2_{bX} = [MS2(X) - MS1(X)]/R$$

$$\hat{\sigma}^2_{bY} = [MS2(Y) - MS1\ (Y)]/R$$

The analysis of variance of F_3 family means was of the form shown

in Table IV.

TABLE IV

ANALYSIS OF VARIANCE TABLE FOR FAMILY MEANS OF AN
F_3 POPULATION

Source	d.f.	MS	EMS
Total	RF-1		
Blocks	R-1	MS3	$\sigma_e^2 + F\sigma_r^2$
Families	F-1	MS2	$\sigma_e^2 + R\sigma_b^2$
Experimental Error	(R-1)(F-1)	MS1	σ_e^2

CHAPTER III

PHENOTYPIC, GENETIC, AND ENVIRONMENTAL VARIATION

Quantitative traits are controlled by both genetic and environmental effects. The genetic effects are due to breeding value, dominance, and epastatic deviations. The breeding value of an individual for a given trait is 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 (21). Dominance deviation, or the intra-allelic interaction, is the interaction between alleles at the same locus while epistatic deviation, or the inter-allelic interaction, is the interaction between alleles at different loci.

Selection in a given population is based on the phenotype of individuals while only a portion of the phenotypic value is transmitted to the following generation. Hence, it is of primary importance to know the relative magnitudes of the different components of the phenotypic value. Two approaches have been used in this respect, first and second order statistics. First order statistic is used to estimate the different effects of the phenotypic expression. Anderson and Kempthorne (3) presented a model based on the factorial model to estimate genetic effects. Hayman's (29, 30) analysis is also used to separate epistatic and dominance variation in generation means. Anderson and Kempthorne (3) and Hayman (30) have pointed out that no accurate estimate of the additive, or breeding, effects could be

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obtained if epistasis is present in a great magnitude. Some authors
(20, 41, 47, 48, and 65) applied the Hayman analysis, using generation
means, to investigate gene action.

Second order statistics, in terms of variances and covariances
among relatives, is more commonly used to estimate genetic and environ-
mental variance components. To estimate genetic variances, relatives
are developed by some mating system and they are grown under a set
of environmental conditions. An analysis of variance for a given
design is conducted to obtain estimates of variance and covariance
components which are interpreted genetically and environmentally.
Cockerham (15) has represented the analysis of variation for various
mating designs together with the genetic interpretation of the variance
components. Cockerham (14) discussed the implication of genetic
variance components with respect to some general aspects of various
selection and breeding procedures in a hybrid breeding program. Horner
and Weber (32) derived the expected values of sample covariances and
variance components in terms of genetic variances and covariances for
populations produced from crossing two homozygous lines and subsequent
self-fertilization. Application of their derivations was made to
maturity data of a soybean experiment. Brim and Cockerham (8) applied
Horner and Weber method in their studies on soybeans.

The development of relatives is not necessary to estimate genetic
and environmental variations. However, it is not possible to break
down the genetic variance into its components in such cases. Genetic
variance of families, lines, or clones could be obtained free of the
genotype-environmental interactions by using appropriate environmental
designs. Comstock and Robinson (17) presented the form of the analysis

of variance for data on families compared in replicated trials at two or more years and at different locations. Hanson et al. (27) used this approach on Korean lespedeza families, in the F_3 and F_4 generations, to estimate genetic and environmental variances. Johnson and Frey (34) studied the behavior of genetic variance of 27 oat cultivars under varying levels of environmental stress. Gandhi et al. (24) made an estimate of the genetic variance using 90 varieties of wheat to provide genetically variable material. Swarup and Chaugale (62) applied the same approach on 70 varieties of sorghum. Estimates of genetic and environmental variances were obtained for some traits in soybeans by Johnson et al. (35), in corn by Lindsey et al. (42), in barley by Rasmusson and Glass (55) and in oats by Wallace et al. (66).

Mather (49) suggested the use of two pure parental lines together with their cross, F_1, F_2, and the first two back-crosses as a procedure for estimating genetic variance components. Since then, Mather's method has been used widely, particularly in self-pollinated crops. Some examples in wheat and sorghum will follow. Weibel (70) estimated the genetic variance components for some quantitative traits in wheat. Sharma and Knott (60) used the same procedure in wheat. In sorghum, Hadley (26) and Watkins (68) analyzed plant height and Jowett (37) analyzed glume size and awn length using Mather's method. In a cross of two varieties of sorghum, 'Big Seed' and 'Norghum', Voigt et al. (65) found that dominance variance for seed size was a small negative quantity and, hence, it was assumed to be zero. They concluded that genes controlling seed size, in the sorghum population studied, act largely in an additive manner. Seed weight was one of the characters

investigated by Beil and Atkins (7) in two crosses of sorghum, Reliance

x North Dakota Mandan Sorghum No. 158, and Redlan x North Dakota Mandan

Sorghum No. 158. They found that the genetic variation for seed weight

was low. Seed weight in sorghum was also one of the characters studied

by Liang and Walter (41). They reported that additive gene effects

seemed to make a minor contribution to the inheritance of seed size

in the crosses investigated, 'Redlan' x 'Martin', 'Redlan' x 'Combine

7078', and 'Plainsman' x 'KS7'. It was concluded that genetic models

assuming negligible epistases may be somewhat biased.

Sib analysis and diallel crosses have proved useful in estimating

genetic variance components. Sib analysis was discussed by Falconer

(21), Horner (31), and Lowry (44). It is more widely used in open-

pollinated crops. For example sib analysis was applied to corn popu-

lations by Comstock and Robinson (16), Da Silva (19), and Williams

et al. (71). Diallel analysis was used to estimate genetic variance

components in sorghum by Chiang and Smith (12, 13) and Liang (38).

Chiang and Smith (13) found highly significant additive variance but

non-significant dominance component for head length in a 7-variety

diallel cross of sorghum, Liang (38) studied the variances for general

and specific combining abilities for some quantitative characters in

a 6-variety diallel cross in sorghum.

Comstock and Robinson (17) have pointed out that the variance

resulting from genotype-environment interaction is frequently a source

of upward bias in estimates of genetic variances. Allard and Bradshaw

(1) discussed the different types of genotype-environment interaction

and their implications in plant breeding programs. The implication

of genotype-environment interaction to sorghum breeding programs has

been investigated by Liang and Walter (40).

Results and Discussion

Phenotypic, genetic, and environmental variance estimates for
head length, head width, seed-branch length, node number per head, and
100-seed weight, based on the F_2 generation are shown in Tables V,
VI, VII, VIII, and IX, respectively. Three estimates of the environ-
mental variance were obtained, depending on the method of calculation
from the variances of the two parents involved in a particular popu-
lation. In general, the environmental variance based on the geometric
mean was less than those based on the pooled variance and on the
arithmetic mean except for head width in populations 3 and 4. The
pooled environmental variance was only 0.17 less than the one based
on the geometric mean in the case of head width in population 3. The
three estimates of the environmental variance for head width were the
same in population 4 because head width of only one parent, 'Chicken
Maize', was considered. The two environmental variance estimates,
based on the pooled variance and on the arithmetic mean, were about
the same since the difference in the number of plants obtained from
the two parents involved in all populations was small.

Genetic variance estimates were obtained by subtracting the
estimates of environmental variances from the corresponding estimates
of phenotypic variances. This procedure resulted in some negative
estimates of the genetic variances, for which a value of zero was
considered to be more reasonable. This situation arose in the case
of branch length for populations 1 and 4 and in the case of seed
weight for populations 1 and 3 when the pooled environmental variance

TABLE V

ESTIMATES OF THE VARIANCE COMPONENTS FOR
HEAD LENGTH BASED ON THE F_2 GENERATION AND THE PARENTS

		Basis of Estimating the Environmental Variance					
		Pooled		Arithmetic Mean		Geometric Mean	
Population	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
1	2,317.30	951.43	1,365.87	934.82	1,382.48	1,635.11	682.19
2	764.93	450.34	314.59	453.31	311.62	482.46	282.47
3	1,449.69	689.71	759.98	618.94	830.75	933.24	516.45
4	2,577.79	753.36	1,824.43	677.50	1,900.29	1,770.42	807.37
5	3,852.62	2,377.59	1,475.03	2,338.57	1,514.05	2,782.29	1,070.33
6	3,229.03	1,625.06	1,603.97	1,710.57	1,518.46	2,148.11	1,080.92

TABLE VI

ESTIMATES OF THE VARIANCE COMPONENTS FOR
HEAD WIDTH BASED ON THE F_2 GENERATION AND THE PARENTS

| | | Basis of Estimating the Environmental Variance | | | | | | |
| | | Pooled | | Arithmetic Mean | | Geometric Mean | | |
Population	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
1	146.24	91.36	54.88	91.06	55.18	95.46	50.78
2	198.39	161.07	37.32	161.15	37.24	161.33	37.06
3	117.95	78.45	39.50	77.73	40.22	78.28	39.67
4	120.80	87.21	33.59	87.21	33.59	87.21	33.59
5	148.29	90.12	58.17	89.47	58.82	92.27	56.02
6	146.15	76.39	69.76	77.00	69.15	77.42	68.73

TABLE VII

ESTIMATES OF THE VARIANCE COMPONENTS FOR
SEED-BRANCH LENGTH BASED ON THE F_2 GENERATION AND THE PARENTS

| | | Basis of Estimating the Environmental Variance | | | | | |
| | | Pooled | | Arithmetic Mean | | Geometric Mean | |
Population	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
1	246.64	000.00	362.08	000.00	366.43	59.07	187.57
2	235.13	105.33	129.80	107.06	128.07	132.36	102.77
3	268.08	105.44	162.64	91.89	176.19	143.45	124.63
4	1,420.78	000.00	1,788.47	000.00	1,868.59	984.48	436.30
5	904.17	470.01	434.16	461.32	442.85	530.94	373.23
6	606.82	135.85	470.97	154.17	452.65	216.12	390.70

TABLE VIII

ESTIMATES OF THE VARIANCE COMPONENTS FOR
NODE NUMBER PER HEAD BASED ON THE F_2 GENERATION AND THE PARENTS

		Basis of Estimating the Environmental Variance					
		Pooled		Arithmetic Mean		Geometric Mean	
Population	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
1	3.27	0.59	2.68	0.56	2.71	1.30	1.97
2	2.26	0.92	1.34	0.93	1.33	1.02	1.24
3	3.93	1.95	1.98	1.81	2.12	2.23	1.70
4	4.45	3.74	0.71	3.75	0.70	3.77	0.68
5	4.88	1.75	3.13	1.69	3.19	2.01	2.87
6	4.86	1.43	3.43	1.52	3.34	1.76	3.10

TABLE IX

ESTIMATES OF THE VARIANCE COMPONENTS FOR
SEED WEIGHT BASED ON THE F_2 GENERATION AND THE PARENTS

		Basis of Estimating the Environmental Variance					
		Pooled		Arithmetic Mean		Geometric Mean	
Population	$\hat{\sigma}^2_P$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$
1	22.50	0.00	27.77	0.00	28.10	7.67	14.83
2	14.59	2.19	12.40	2.37	12.22	5.34	9.25
3	9.46	0.00	10.25	0.00	10.98	0.80	8.66
4	-----	-----	-----	-----	-----	-----	-----
5	62.84	27.33	35.51	26.75	36.09	30.43	32.41
6	59.86	24.75	35.11	26.22	33.64	31.65	28.21

estimate and the one based on the arithmetic mean were used. Since

it was impossible for the environmental variance to exceed the pheno-

typic variance, if the assumptions were met, it was thought that the

pooled estimate of the environmental variance and the one based on

the arithmetic mean were unreliable estimates of the environmental

variance, at least for the situation discussed above.

The estimates of the variances of the two parents involved in

a particular population should estimate the same thing, namely the

environmental variance of that particular population, since the

individual plants of each parent were genetically identical. Hence,

the difference between the two estimates should be small. However,

in some cases the difference was very large which resulted in large

estimates of the environmental variances, and small or negative esti-

mates of the genetic variances, when the estimates of the two variances

of the parents were pooled or when their arithmetic average was taken.

On the other hand, the geometric mean yielded smaller estimates of

the environmental variances and hence resulted in more reasonable

estimates of the genetic variances. For this reason, it was thought

that the estimates based on the geometric mean were more reliable

and, hence, they will be considered throughout the text.

Phenotypic variance estimates, obtained from the F_2 generation,

varied very widely for different characters. Head length showed the

highest phenotypic variance estimates, and node number showed the

lowest for all populations. This was in close agreement with the

genetic and the environmental variance estimates, based on the geo-

metric mean in particular, except for population 3 for which the

estimate of the genetic variance of seed weight was less than that

of the node number. The descending order of the characters in all
populations with respect to the phenotypic variance estimates was:
head length, branch length, head width, seed weight, then node number.
The order was the same for the environmental, but not for the genetic
variance estimates based on the geometric mean. Branch length and
head width in population 1 and in population 2, and seed weight and
node number in population 3 interchanged their order with respect
to the genetic variance estimates. However, the difference between
the interchanged estimates was not large which might imply that the
corresponding variances were not significantly different.

The relative magnitude of the genetic variance to the environmental
variance is of primary importance to the breeder since only the genetic
variance, or at least part of it, passes from one generation to the
next. Meanwhile, selection is based on phenotypic variability in
most breeding programs. Based on the estimates obtained by the
geometric mean, it was noticed that the genetic variance estimates
were about twice the environmental variance estimates, or more, for
most populations for head length. Branch length did not show any
regular pattern in that respect. The genetic variance estimate was
about one-third of the environmental variance estimate for population 1,
and it was about one-half of the environmental variance estimate for
population 6. One the other hand, genetic variance estimates were
larger than the environmental for branch length in populations 2, 3,
4, and 5. For head width, all populations had larger genetic variance
estimates. The genetic and environmental estimates were about the
same for seed weight in populations 5 and 6 and for node number in
populations 1, 2, and 5. Populations 1, 2, and 3 for seed weight,

and population 6 for node number showed smaller genetic variance
estimates. Genetic variance estimates were larger for node number
in populations 3 and 4.

It was pointed out earlier that not all of the genetic variability
is transmitted from one generation to the next. The success of most
breeding programs depends on the proportion transmitted which in turn
depends on the various components of the genetic variance. These are the
additive variance, the dominance variance, and the epistatic variance.
However, it was assumed that the epistatic variance was zero or
negligible for the characters studied, in order to obtain estimates
for the additive and dominance variances.

Additive and dominance variance estimates together with genetic,
environmental, and phenotypic variance estimates obtained from the F_3
generation for head length, head width, branch length, node number,
and seed weight are shown in Tables X, XI, XII, XIII, and XIV,
respectively. As previously described, variance estimates of the
between and within rows from the parents' analysis were subtracted
from the between and within F_3 families variance estimates to obtain
estimates free of the row-to-row and the plant-to-plant variations.
For each population, two estimates were obtained for each of the
between and the within row variances, from the two parents. The
two estimates for a given variance were combined in two different
manners: (a) pooled, which was the same as the arithmetic mean since
the number of observations was the same for the two parents in this
case, and (b) their geometric mean was used as the other estimate.
This resulted in two sets of estimates of genetic and environmental
variabilities.

TABLE X

ESTIMATES OF THE VARIANCE COMPONENTS FOR
HEAD LENGTH BASED ON THE F_3 GENERATION AND THE PARENTS

Population	Basis	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$
1	Pooled	1,941.68	0.00	1,941.68	1,490.13	3,431.81
	Geometric Mean	1,941.68	0.00	1,941.68	1,057.55	2,999.23
2	Pooled	366.97	4.31	371.28	221.28	592.56
	Geometric Mean	372.17	0.00	372.17	217.38	589.55
3	Pooled	1,042.22	0.00	1,042.22	297.61	1,339.83
	Geometric Mean	982.73	0.00	982.73	202.37	1,185.10
4	Pooled	1,777.29	0.00	1,777.29	1,246.52	3,023.81
	Geometric Mean	1,280.44	457.88	1,738.32	501.25	2,239.57
5	Pooled	0.00	2,149.41	2,149.41	1,765.93	3,915.34
	Geometric Mean	1,029.48	1,329.92	2,359.40	750.03	3,109.43
6	Pooled	1,030.01	0.00	1,030.01	1,541.03	2,571.04
	Geometric Mean	677.31	826.11	1,503.42	966.09	2,469.51

TABLE XI

ESTIMATES OF THE VARIANCE COMPONENTS FOR
HEAD WIDTH BASED ON THE F_3 GENERATION AND THE PARENTS

Population	Basis	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$
1	Pooled	0.00	128.52	128.52	36.39	164.91
	Geometric Mean	0.00	141.24	141.24	31.59	172.83
2	Pooled	0.00	156.75	156.75	25.70	182.45
	Geometric Mean	0.00	157.92	157.92	25.26	183.18
3	Pooled	0.00	60.96	60.96	156.53	217.49
	Geometric Mean	0.00	54.29	54.29	50.31	104.60
4	Pooled	0.00	793.93	793.93	181.97	975.90
	Geometric Mean	0.00	813.96	813.96	174.46	988.42
5	Pooled	0.00	75.08	75.08	75.17	150.25
	Geometric Mean	0.00	81.59	81.59	72.73	154.32
6	Pooled	0.00	42.77	42.77	52.98	95.75
	Geometric Mean	0.00	64.39	64.39	38.98	103.37

TABLE XII

ESTIMATES OF THE VARIANCE COMPONENTS FOR
SEED-BRANCH LENGTH BASED ON THE F_3 GENERATION AND THE PARENTS

Population	Basis	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$
1	Pooled	100.57	0.00	100.57	345.14	445.71
	Geometric Mean	47.60	111.32	158.92	63.70	222.62
2	Pooled	28.64	63.80	92.44	52.85	145.29
	Geometric Mean	21.61	105.67	127.28	31.99	159.27
3	Pooled	0.00	2.85	2.85	435.69	438.54
	Geometric Mean	90.49	41.63	132.12	70.27	202.39
4	Pooled	1,124.67	0.00	1,124.67	1,799.55	2,924.22
	Geometric Mean	828.01	61.97	889.98	295.93	1,185.91
5	Pooled	0.00	516.24	516.24	383.40	899.64
	Geometric Mean	54.84	430.16	485.00	235.68	720.68
6	Pooled	90.93	0.00	90.93	386.40	477.33
	Geometric Mean	75.45	20.71	96.16	294.76	390.92

TABLE XIII

ESTIMATES OF THE VARIANCE COMPONENTS FOR
NODE NUMBER PER HEAD BASED ON THE F_3 GENERATION AND THE PARENTS

Population	Basis	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$
1	Pooled	0.87	1.21	2.08	2.56	4.64
	Geometric Mean	0.70	2.48	3.18	1.86	5.04
2	Pooled	0.00	4.71	4.71	2.82	7.53
	Geometric Mean	0.00	4.65	4.65	2.75	7.40
3	Pooled	0.00	4.48	4.48	4.72	9.20
	Geometric Mean	0.32	3.24	3.56	1.98	5.54
4	Pooled	0.65	3.95	4.60	2.11	6.71
	Geometric Mean	0.72	4.12	4.84	1.88	6.72
5	Pooled	2.52	0.24	2.76	2.68	5.44
	Geometric Mean	2.03	2.23	4.26	1.92	6.18
6	Pooled	0.60	2.28	2.88	3.59	6.47
	Geometric Mean	0.11	4.71	4.82	2.50	7.32

TABLE XIV

ESTIMATES OF THE VARIANCE COMPONENTS FOR
SEED WEIGHT BASED ON THE F_3 GENERATION AND THE PARENTS

Population	Basis	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_E$	$\hat{\sigma}^2_P$
1	Pooled	0.00	0.00	0.00	49.73	49.73
	Geometric Mean	6.15	0.17	6.32	4.84	11.16
2	Pooled	2.99	0.07	3.06	3.35	6.41
	Geometric Mean	2.69	1.91	4.60	2.42	7.02
3	Pooled	0.00	2.85	2.85	37.61	40.46
	Geometric Mean	4.05	0.75	4.80	2.81	7.61
4	Pooled	----	----	----	----	----
	Geometric Mean	----	----	----	----	----
5	Pooled	8.93	0.00	8.93	32.84	41.77
	Geometric Mean	6.31	3.01	9.32	24.00	33.32
6	Pooled	4.85	0.00	4.85	24.04	28.89
	Geometric Mean	7.46	0.00	7.46	22.04	29.50

Negative estimates for the genetic variabilities were obtained for;
(a) the within families for head length in population 1, seed-branch
length in populations 1, 4, and 6, and seed weight for populations 1
and 5, and (b) the between families for seed weight in 1 and 3, head
width, seed-branch length, and node number in population 3, when the
pooled variances were used. On the other hand, the geometric mean
procedure resulted in only one negative estimate. This was the esti-
mate of the within genetic variance for head length in population 1.
For this reason the set of estimates based on the geometric mean was
thought to be more reliable. However, the other set of estimates,
based on the pooled information, is represented in the different tables.

Phenotypic variance estimates were the highest for head length
and the lowest for node number in all F_3 populations which was in full
agreement with the information obtained from the F_2 generation. The
order of the different characters, with respect to the magnitude of
the phenotypic variance estimates was the same as in the F_2 generation
except for population 2 for which branch length and head width, and
seed weight and node number interchanged their order. However, the
phenotypic variance estimates for branch length and head width as
well as those for seed weight and node number were of comparable
magnitude in population 2. This was the case for branch length and
head width but not for seed weight and node number for the F_2 gener-
ation. In the F_2 generation, the phenotypic variance estimate for
seed weight was more than six times the estimate for node number. It
was thought that this different behavior might be due to the geno-
type-environment interaction.

The estimates of environmental variances based on the geometric

mean, exhibited the same order as in the F_2 generation for the different characters except in population 2 in which node number and seed weight interchanged their order, but they were about the same magnitude. This was not the case in the F_2 generation, perhaps such a different behavior is due to the genotype-environment interaction. The order of the different characters based on the magnitude of the genetic variance estimates was the same exactly as the one based on the phenotypic variance estimates.

All, or at least most, of the additive variance is transmitted from one generation to the next. On the other hand, in self-pollinated crops only one-half of the dominance variance is transmitted. Hence, it is important to know the magnitude of the additive variance with respect to the other variances making up the phenotypic variance. In general, if head width is excluded, head length had the highest additive variance estimate and node number had the lowest, based on the geometric mean. The estimates of the additive variances for head width in all populations were all zeros, regardless of the method of estimation. Two possible reasons could be suggested for these results. First, head width is completely controlled by environmental factors and those dominance variance estimates, shown in Table XI, are not of practical significance. However, this is not reasonable since the dominance variance estimates were all greater than the environmental variance estimates, at least for those based on the geometric mean. The second reason, which is more plausible, is that the two homozygous individuals, say BB and bb, for a given locus are identical, but heterozygous individuals, Bb, are different. No matter how many loci controlled the head width, at least for all populations studied, the

above statement should hold. This situation can be discussed further as follows:

Suppose that (B, b) was one of the pairs of alleles controlling head width and consider the following general diagram.

```
bb                Bb                                      BB
+-----------------+-----+-------------------------------+
-a                d     0                               a
```
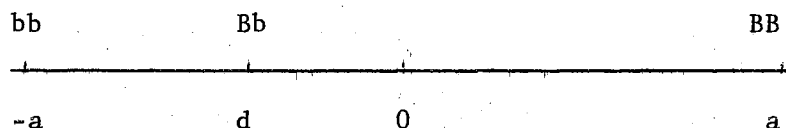
In the above diagram 'a' represents one-half of the difference, say in head width, between the two homozygotes BB and bb, and 'd' represents the deviation of the heterozyote Bb from the mid-point. In other words '-a', 'd', and 'a' are the values of the individuals bb, Bb, and BB, respectively. Let gene frequency, with respect to this locus, be 'q'. The additive and dominance variances are given as follows:

$$\sigma_A^2 = 2q(1 - q)[a + d(1 - 2q)]^2, \text{ and}$$

$$\sigma_D^2 = 4q^2(1 - q)^2 d^2.$$

It was assumed that gene frequency was one-half for the populations studied. This implies that the above expressions are reduced to the following:

$$\sigma_A^2 = \frac{1}{2} a^2, \text{ and}$$

$$\sigma_D^2 = \frac{1}{4} d^2.$$

For more than one locus, say 'n'

$$\sigma_A^2 = \frac{1}{2} \sum_{i=1}^{n} a_i^2 \text{ and}$$

$$\sigma_D^2 = \frac{1}{4} \sum_{i=1}^{n} d_i^2 .$$

In order to have a zero value for σ_A^2 all of the a_i's should be zero.

Since a_i represents one-half of the range between the homozygotes, BB
and bb, for the ith locus and since a_i must be zero, the range between
the two homozygotes should be zero for the ith locus. Consequently,
the two homozygotes should have the same value, or in other words,
they should be identical. This should hold true for all loci control-
ling head width, at least for the populations studied, as was suggested
earlier.

Dominance variance estimates were relatively large for head width
(Table XI), which implied that dominance was present for that character;
i.e., $d \neq 0$ at least for one locus. As it was shown earlier, the
value of 'a' was zero for loci controlling head width in the populations
studied. If gene frequency was not one-half for that character, then
some value, other than zero, should be detected. However, all additive
variance estimates were zeros. This implies that gene frequency should
be one-half, or very close to one-half which justified the assumption
suggested about gene frequency.

Gene action for head length was entirely additive for populations
1, 2, and 3 (Table X). The additive variance estimate was about three
times larger than the dominance variance estimate in population 4, but
it was somewhat smaller than dominance variance estimate in populations
5 and 6. Taking into consideration the magnitude of the non-additive
variance estimates, it was suggested that selection for head length
in early generations should be more effective in populations 3 and 2
than in populations 1 and 4. Much progress from selection in early
generations should not be expected for head length in populations 5
and 6. However, selection might be effective for head length in those
two populations, in later generations since in self-pollinated crops

dominance variance is halved every generation.

Head width (Table XI) did not seem to be a good character on which selection could be practiced. The additive effect for this character was completely lacking in all populations. Although dominance effect was present and was greater than the environmental effects in all cases it would degenerate very rapidly in a few generations.

No regular pattern, with respect to the estimates of genetic and environmental variance components, was observed for seed-branch length (Table XII) in the different populations. Genetic variance estimates were greater than the environmental estimates for all populations except population 6. The additive variance estimates were less than the dominance estimates in populations 1, 2, and 5, but not in the other populations. Population 4 had the highest additive variance estimate relative to the dominance and environmental estimates and, hence, rapid progress could be expected from early generation selection for seed-branch length in this population.

Estimates of the additive variance were less than the estimates of the dominance variance and estimates of the environmental variance were less than the estimates of genetic variance for node number (Table XIII) in all populations. Except for population 5, the additive variance estimates were less than the environmental estimates in all populations. It was suggested that much progress could not be expected from early generation selection for node number in all populations.

Gene action seemed to act almost in an additive manner in the case of seed weight (Table XIV) at least in populations 1, 3, and 6. Additive variance estimates were about twice as much as the dominance variance estimates for populations 2 and 5. In most populations stud-

ied, reasonable progress could be expected from early generation selection for seed weight.

Summary and Conclusions

Genetic and environmental variance components were estimated from the F_2 generation for head length, head width, seed-branch length, node number per head, and 100-seed weight in six populations of sorghum. It was possible to break down the genetic variance estimates, using the data from the F_3 generation, to the additive and dominance variance estimates by assuming that the epistatic effect was absent. Estimates of the environmental variances were obtained from the variance estimates of the two parents by pooling, the arithmetic mean, and the geometric mean of the estimates of the two variances. The geometric mean gave the most relaible estimates of the environmental variances.

Gene action was mostly additive for head length and seed weight for most populations. Additive gene action was completely lacking for head width in all populations. Estimates of the additive variances were less than those of dominance variances for node number, in all populations, and for seed-branch length in some.

It was concluded that rapid progress could be expected from early generation selection for head length in most populations, and for seed-branch length in a few populations. Reasonable progress should be expected from early generation selection for seed weight but not for node number.

Head width did not seem to be a good character on which selection could be practiced. Regardless of the number of loci controlling head width, it was demonstrated that the two homozygotes for each

locus had the same value which was different from the heterozygote value. It was verified that gene frequency for each locus, if more than one, was one-half in all populations studied for that character.

CHAPTER IV

HERITABILITY, GENETIC ADVANCE, AND GENE NUMBER

Progress under selection breeding programs depends on the magnitude of heritability for the trait being selected for. In general, heritability is defined as the ratio of the amount of genetic variation to the total phenotypic variance that passes from one generation to the next. Heritability is recognized in both a broad and a narrow sense. Heritability in the broad sense is the proportion of the total genetic variance to the total phenotypic variance. In the narrow sense, heritability is the proportion of the additive variance to the total phenotypic variance. Several discussions on the concept of heritability and its implications in plant breeding have been reported (10, 21, 28, 50, and 67).

Warner (67) grouped the techniques for estimating heritability into three groups: (a) parent-offspring regression, (b) variance component from an analysis of variance, and (c) approximation of nonheritable variance from genetically uniform populations to estimate total genetic variance. Warner considered that none of these techniques are completely satisfactory to detect the effectiveness of selection in the F_2 generation. He used the difference between the variance of F_2 and the total variance of the two backcrosses as an estimate of the additive variance which is divided by the variance of F_2 to obtain an estimate of heritability. He pointed out that the advantage

of this method is that the estimate is made entirely on the basis of F_2 and the back cross of F_1 to each inbred parent and that the estimation of nonheritable variance is unnecessary. However, the assumptions necessary are: (a) genetic effects are additive among loci, (b) environmental variances must be independent of the genotype, and (c) non-heritable components of variance of F_2 and the backcrosses are of comparable magnitude.

Warner's method has been applied very widely for estimating heritability: a few examples will follow. Culp (18) estimated heritability for plant height to be 40 to 50 percent and for capsule length to be 50 to 70 percent in sesame. Heritabilities for some characters in sorghum were estimated by Liang and Walter (41). They found that heritabilities of grain yield and kernel number were of lower magnitude than those of head weight, kernel weight, stalk diameter, half-blooming, plant height and germination percentage. The magnitude of heritability estimates varied greatly among crosses for some traits. Heritabilities for 1000-kernel weight were 24 percent for 'Redlan' x 'Martin' and 'Redlan' x Combine 7078', and 33 percent for 'Plainsman' x 'KS7' using the original scale. Heritability for seed size in a cross of two varieties, 'Big seed' and 'Norghum', of sorghum was estimated by Voigt et al. (65) to be 60 percent. They concluded that considerable progress could be made in shifting mean seed size by selecting and recombining large-seeded F_2 plants. Warner's method was also used to estimate heritabilities of some quantitative traits in wheat crosses by Sharma and Knott (60), Watkins (68), and Weibel (70).

The regression of the offspring on parent is considered to be

one of the common methods for estimating heritability. Smith and

Kinman (61) reported that this method is frequently misused in self-

pollinated populations due to the failure to consider the previous

inbreeding of the parent which will cause an upward bias of heritability

estimates. They proposed an adjustment of the regression coefficient

to provide an unbiased estimate of heritability. This can be done by

dividing the regression coefficient by twice the degree of genetic

relationship between the parent and its offspring.

Another problem associated with the use of regression for

estimating heritability is the effect of environmental conditions

since in most cases data on offspring are obtained in a different

year from those obtained on parents. To overcome this problem, Frey

and Horner (23) suggested the use of heritability in standard units

rather than the conventional regression method. The data must be

coded in terms of standard deviation units and then the regression

coefficient is calculated to obtain an estimate of standard unit

heritability which is identical to the correlation coefficient on

the original data. The advantages of this method as stated by Frey

and Horner (23) are: (a) it eliminates the unrealistic values of

over 100 percent and (b) the standard unit heritability values come

closer to predicting the actual gain obtained from selection at least

in the case of heading date in oats. They concluded that performance

factors which are most probably affected by the same type of environ-

mental scaling factors, those that cause expansion or contraction of

the phenotypic variability, as heading date in oats, should be well

adapted to standard unit method.

Many authors have used the conventional regression method and/or

the standard unit method for estimating heritabilities. These methods are applied to wheat by Lofgren et al. (43), Reddi et al. (56) Sharma and Knott (60) and Weibel (70). In barley, oats, soybean, flax, and corn estimates of heritabilities, by either or both methods, for some qualitative traits were obtained by Baker et al. (5), Murphy and Frey (52), Anand and Torrie (2), Bartley and Weber (6), Omran et al. (53), and Robinson et al (58), respectively. Heritabilities of plant height in some sorghum crosses were found by Watkins (68).

The variance component method proposed by Comstock and Robinson (16, 17), has been used extensively in estimating heritabilities. The method could be applied to either genetically different varieties or families from a given generation. The method was applied to corn by Robinson et al. (58), to Korean lespedeza by Hanson et al. (27), to flax by Omran et al. (53), to soybean by Anand and Torrie (2) and Johnson et al. (35), to barley by Rasmasson and Glass (55), and to wheat by Gandhi et al. (24) and Weibel (70). Using 70 varieties of sorghum, Swarup and Chaugale (62) reported 85.44 percent for the heritability of 100-seed weight using the variance component method.

The difference between the variances of segregating populations and nonsegregating populations is taken to be an estimate of genetic variance which is divided by the variance of the segregating population to give rise to heritability estimates. Burton (9) has taken the F_1 generation, from a cross of two Pearl millet varieties, to be the nonsegregating population. His method was applied to oil content in a soybean cross by Weber and Moorthy (69) and to plant height in sorghum by Watkins (68). Beil and Atkins (7) and Caviness (11) estimated the variance of nonsegregating population by the average of the

variance of both parents and the F_1 generation. The square root of
the product of the variance of the two parents could be taken as an
estimate of the variance of nonsegregating population as suggested by
Mahmud and Kramer (45). Their method was used by Petr and Frey (54)
to estimate the heritability of some quantitative characters in oats.

Heritabilities could be estimated from the analyses of diallel
crosses or in terms of realized heritability. Liang et al. (39)
estimated the heritabilities of anthesis time, grain yield and protein
content in a 6-variety diallel cross in sorghum. The heritability
of head length in sorghum was one of the characters studied by Chiang
and Smith (13) in a 7-variety diallel cross. The heritability value
for head length was 62 percent and they concluded that rapid and
effective selection could be made for this trait. Frey (22) worked
out the realized heritabilities for some quantitative traits in two
oat crosses.

Whenever heritability is estimated for some quantitative trait
in a population, a question is raised as to what progress would be
expected under selection in that population. The estimate of such
progress is called the genetic advance. Gentic advance is defined
by Falconer (21) to be the product of the intensity of selection, the
estimate of phenotypic standard deviation, and the heritability estimate.
The intensity of selection depends only on the proportion of the popu-
lation included in the selected group, provided the distribution of
phenotypic values is normal. Selection intensity can be calculated
by dividing the height of the normal curve at the point of truncation
by the proportion selected from the population. Genetic advance was
estimated by most authors who investigated heritability of quantitative

traits.

Estimation of the number of genes or blocks of genes is a common device practiced by plant breeders. Mather (49) and Wright (72) gave some formulas which could be used to estimate the number of genes in different situations. However, most formulas are based on several assumptions, some of which are not satisfied and would give rise to biased estimates. Most of those are biased downward. The minimum number of genes controlling some quantitative traits were estimated in Pearl millet by Burton (9), in sesame by Culp (18), in wheat by Sharma and Knott (60), and in rice by Mohamed and Hanna (51). Hadley (26) and Watkins (68) estimated the number of loci controlling height in sorghum. Voigt et al. (65) found that a minimum of 3 or 4 genes or blocks of genes control seed size in sorghum in the cross 'Big Seed' x 'Norghum'. Chiang and Smith (13) reported that at least two factors and one major factor control seed weight and head length, respectively, in a 7-variety diallel cross in sorghum. The number of genes controlling anthesis time, grain yield, and protein content in a 6-variety diallel cross in sorghum were estimated by Liang et al. (39). Robson (59) suggested the use of the fourth degree statistics for estimating gene number controlling the inheritance of a quantiative character under the additive model with dominance.

Results and Discussion

Estimates of heritability percentages for head length, head width, seed-branch length, node number per head, and 100-seed weight are shown on Tables XV, XVI, XVII, XVIII, and XIX, respectively. Several estimates of heritability percentages were obtained from the F_2

TABLE XV

ESTIMATES OF HERITABILITY PERCENTAGE
FOR HEAD LENGTH

Methods and Basis of Estimation	Population					
	1	2	3	4	5	6
I. From the F_2 Generation and Parents						
A. Pooled	41	59	48	29	62	50
B. Arithmetic Mean	40	59	43	26	61	53
C. Geometric Mean	71	63	64	69	72	67
II. From the F_3 Generation						
On Family Mean Basis	94	90	94	91	88	86
III. From the F_3 Generation and Parents						
A. Pooled						
1. Narrow Sense	57	62	78	59	00	40
2. Broad Sense	57	63	78	59	55	40
B. Geometric Mean						
1. Narrow Sense	65	63	83	57	33	27
2. Broad Sense	65	63	83	78	76	61
IV. Regression of F_3 Means on F_2 Values						
A. From 1968 and 1967 Data	74	57	59	67	36	24
B. From 1967 and 1966 or 1965 Data	72	56	77	67	--	--
V. Standard Unit Heritability						
A. From 1968 and 1967 Data	92	72	79	83	56	49
B. From 1967 and 1966 or 1965 Data	77	55	71	68	--	--

TABLE XVI

ESTIMATES OF HERITABILITY PERCENTAGE
FOR HEAD WIDTH

			Population				
Methods and Basis of Estimation		1	2	3	4	5	6
I. From the F_2 Generation and Parents							
A. Pooled		62	81	67	72	61	52
B. Arithmetic Mean		62	81	66	72	60	53
C. Geometric Mean		65	81	66	72	62	53
II. From the F_3 Generation							
On Family Mean Basis		71	66	83	47	39	38
III. From the F_3 Generation and Parents							
A. Pooled							
1. Narrow Sense		00	00	00	00	00	00
2. Broad Sense		78	86	28	81	50	45
B. Geometric Mean							
1. Narrow Sense		00	00	00	00	00	00
2. Broad Sense		82	86	52	82	53	62
IV. Regression of F_3 Means on F_2 Values							
A. From 1968 and 1967 Data		15	20	27	00	6	1
B. From 1967 and 1966 or 1965 Data		00	20	14	--	--	--
V. Standard Unit Heritability							
A. From 1968 and 1967 Data		28	40	48	00	12	4
B. From 1967 and 1966 or 1965 Data		00	24	20	--	--	--

TABLE XVII

ESTIMATES OF HERITABILITY PERCENTAGE
FOR SEED-BRANCH LENGTH

Methods and Basis of Estimation	Population					
	1	2	3	4	5	6
I. From the F_2 Generation and Parents						
A. Pooled	00	45	39	00	52	22
B. Arithmetic Mean	00	46	34	00	51	25
C. Geometric Mean	24	56	54	69	59	36
II. From the F_3 Generation						
On Family Mean Basis	84	82	91	91	77	66
III. From the F_3 Generation and Parents						
A. Pooled						
1. Narrow Sense	23	20	00	38	00	19
2. Broad Sense	23	64	1	38	57	19
B. Geometric Mean						
1. Narrow Sense	21	14	45	70	8	19
2. Broad Sense	71	80	65	75	67	25
IV. Regression of F_3 Means on F_2 Values						
A. From 1968 and 1967 Data	44	35	58	62	22	6
B. From 1967 and 1966 or 1965 Data	45	29	61	67	--	--
V. Standard Unit Heritability						
A. From 1968 and 1967 Data	65	59	80	63	54	18
B. From 1967 and 1966 or 1965 Data	41	32	61	64	--	--

TABLE XVIII

ESTIMATES OF HERITABILITY PERCENTAGE
FOR NODE NUMBER PER HEAD

Methods and Basis of Estimation	Population					
	1	2	3	4	5	6
I. From the F_2 Generation and Parents						
A. Pooled	18	41	50	84	36	29
B. Arithmetic Mean	17	41	46	84	35	31
C. Geometric Mean	40	45	57	85	41	36
II. From the F_3 Generation						
On Family Mean Basis	71	44	68	79	83	69
III. From the F_3 Generation and Parents						
A. Pooled						
1. Narrow Sense	19	00	00	10	46	9
2. Broad Sense	45	63	49	69	51	45
B. Geometric Mean						
1. Narrow Sense	14	00	6	11	33	2
2. Broad Sense	63	63	64	72	69	66
IV. Regression of F_3 Means on F_2 Values						
A. From 1968 and 1967 Data	36	19	36	42	30	13
B. From 1967 and 1966 or 1965 Data	17	9	15	19	--	--
V. Standard Unit Heritability						
A. From 1968 and 1967 Data	40	21	56	57	38	25
B. From 1967 and 1966 or 1965 Data	31	19	29	35	--	--

TABLE XIX

ESTIMATES OF HERITABILITY PERCENTAGE
FOR SEED WEIGHT

Methods and Basis of Estimation	Population					
	1	2	3	4	5	6
I. From the F_2 Generation and Parents						
A. Pooled	00	15	00	--	43	41
B. Arithmetic Mean	00	16	00	--	43	44
C. Geometric Mean	34	37	8	--	48	53
II. From the F_3 Generation						
On Family Mean Basis	87	83	86	--	81	66
III. From the F_3 Generation and Parents						
A. Pooled						
1. Narrow Sense	00	47	00	--	21	17
2. Broad Sense	00	48	7	--	21	17
B. Geometric Mean						
1. Narrow Sense	55	38	53	--	19	25
2. Broad Sense	57	66	63	--	28	25
IV. Regression of F_3 Means on F_2 Values						
A. From 1968 and 1967 Data	22	34	47	--	19	13
B. From 1967 and 1966 or 1965 Data	36	26	19	--	--	--
V. Standard Unit Heritability						
A. From 1968 and 1967 Data	31	61	55	--	39	32
B. From 1967 and 1966 or 1965 Data	38	28	19	--	--	--

generation, the F_3 generation, and the combined information from both
generations. Genetic variance estimates, required for estimating
heritability percentages, were obtained as the difference between
the phenotypic variance estimates and the corresponding environmental
variance estimates. The two variance estimates of the parents were
pooled, their arithmetic mean was calculated, or their geometric mean
was taken, to supply three different estimates of the environmental
variance. In several cases the environmental variance estimates, based
on the pooled variance and on the arithmetic mean, were larger than
the phenotypic variance estimates, which was not reasonable. Hence,
it was thought that heritability estimates obtained by using the
environmental variance estimates based on the geometric mean were
more reliable. The estimates based on pooled variance and the arith-
metic mean will be excluded from the discussion. However, these esti-
mates are reported in Tables XV, XVI, XVII, XVIII, and XIX.

Heritability estimates, obtained from the F_2 generation and the
parents, were broad sense heritabilities. A regular pattern was not
observed for those estimates for the different characters in the six
populations, although generally the descending order of estimates was
head width, head length, node number, seed-branch length, and finally
seed weight. The highest estimate, 84 percent, was observed for node
number in population 4 (Table XVIII). Seed weight in population 3
(Table XIX) showed the lowest heritability estimate, 8 percent.
Estimates for broad sense heritabilities obtained from the F_3 generation
were generally larger than those obtained from the F_2 generation. This
irregular behavior was probably due to the presence of the genotype-
environment interaction, or due to estimating the environmental vari-

ances from a fewer number of individuals, or both.

In general, the narrow sense heritability estimates were smaller or equal to the broad sense estimates obtained from the F_3 generation. Head length (Table XV) showed relatively high estimates and node number (Table XVIII) showed low estimates. Estimates obtained for head width (Table XVI) were all zeros since the additive gene action was completely lacking. Excluding head width, estimates of heritability percentages based on F_3 family mean basis were higher than both narrow and broad sense heritability estimates. This was true for head width only in population 3, which had the lowest broad sense heritability for that character. It was suggested that high estimates of heritability on family mean basis were obtained because the row-to-row and plant-to-plant environmental variabilities were not considered in calculating those estimates. However, this method has been used widely by plant breeders, and is known as the variance component method.

Estimates of heritability were also obtained by the regression of the F_3 family means on their F_2 values. Two sets of estimates were obtained, by this method for all populations, except for populations 5 and 6. The first set of estimates were obtained from the means of the F_3 generation grown in 1968 and their F_2 parents grown in 1967. The second set was obtained by using the means of the F_3 generation grown in 1967, which was available only for populations 1, 2, 3, and 4, and their F_2 parents grown in 1966 for populations 1 and 4, and in 1965 for populations 2 and 3. Head width was not recorded for some plants in population 4, since those plants had typical broomcorn brush, and hence the heritability estimate was not found for that character in the second set. The two regression estimates were compar-

able in many cases. In general, head length had the highest estimates and head width had the lowest in most populations.

Standard unit heritability estimates were a little higher than the corresponding regression estimates in most cases. A possible explanation for this situation is as follows: The standard unit heritability was calculated as the correlation coefficient between F_3 means and the F_2 values. The correlation coefficient for this situation is given as follows:

$$r = \frac{\hat{Cov}\ (\overline{F}_3,\ F_2)}{\sqrt{\hat{\sigma}^2_{\overline{F}_3}\ \hat{\sigma}^2_{F_2}}}$$

where $\hat{Cov}\ (\overline{F}_3,\ F_2)$ = estimate of the covariance between the F_3 means and the F_2 values.

$\hat{\sigma}^2_{\overline{F}_3}$ = estimate of the variance of the F_3 means.

$\hat{\sigma}^2_{F_2}$ = estimate of the variance of the F_2 values.

Using the same notations heritability estimate based on regression is given by the following expression:

$$b = \frac{\hat{Cov}\ (\overline{F}_3,\ F_2)}{\hat{\sigma}^2_{F_2}}$$

Since the standard unit estimates of heritability were higher than the corresponding regression estimates, in most cases, the estimate of the variance of the F_3 means should be less than the estimate of the variance of the F_2 values. This was reasonable since the genetic and environmental components of those two estimates assuming no epistasis, were given by Mather (49), with some modification in notation as

follows:

$$\hat{\sigma}^2_{\overline{F}_3} = \hat{\sigma}^2_A + \frac{1}{4} \hat{\sigma}^2_D + \hat{\sigma}^2_{\overline{E}_3} \text{ , and}$$

$$\hat{\sigma}^2_{F_2} = \hat{\sigma}^2_A + \hat{\sigma}^2_D + \hat{\sigma}^2_{E_2}$$

where $\hat{\sigma}^2_{\overline{F}_3}$ and $\hat{\sigma}^2_{F_2}$ are as defined above.

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

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

$\hat{\sigma}^2_{\overline{E}_3}$ = the estimate of the environmental variance associated with F_3 family means.

$\hat{\sigma}^2_{E_2}$ = the estimate of the environmental variance associated with the F_2 plants.

This would indicate that the estimate of the variance of the F_3 family means should be less than the estimate of the variance of the F_2 plants if dominance is present and if $\hat{\sigma}^2_{\overline{E}_3}$ and $\hat{\sigma}^2_{E_2}$ are of comparable magnitude.

The heritability parameter for a certain character is different in the different generations. Hence, if selection is to be practiced in the F_2 generation, estimates of heritability should be obtained from the F_2 generation and the parents, from the regression of F_3 means on F_2 values, or from the correlation between F_3 means and F_2 values. Estimates obtained from the F_2 generation and the parents are broad sense heritabilities. Such estimates should be used with caution becuase they account for all of the dominance variance where only one-half of that variance is transmitted to the F_3 generation.

The two other estimates based on the regression and the standard unit methods are considered to be better estimates for that situation. The advantages and disadvantages of these two methods were discussed by Frey and Horner (23).

In many cases selection is practiced among the F_3 families. For this situation estimates of heritability, to be considered, should be based on the F_3 family means. This method of estimation was reported by Comstock and Robinson (17) as the variance components method. If selection is to be practiced in the F_3 generation on an individual plant basis, then estimates of heritability in the narrow sense should give better prediction than the broad sense heritabilities.

It is of some interest to know the precision of the estimates of heritability although precise estimates may or may not be unbiased. The standard deviation of the estimate is considered to be one of the measurements of precision. Heritability estimates based on the regression of F_3 means on F_2 values for the characters studied in the different populations are shown again, together with their standard deviations in Table XX. In general, most of the standard deviations were relatively small. Since heritability estimates based on regression are normally distributed with mean equal to the heritability parameter and variance equal to the variance of the estimate, confidence intervals and tests of hypotheses about the heritability parameter, could be constructed by using the t-distribution.

The progress under selection depends on the heritability parameter, the magnitude of the phenotypic variance in the population, and on the proportion selected. Consequently, high heritability estimates do not imply pronounced progress from selection if the phenotypic variance

TABLE XX

ESTIMATES OF HERITABILITY PERCENTAGE BASED ON THE
REGRESSION OF F_3 MEANS ON F_2 VALUES AND THEIR
STANDARD DEVIATIONS FOR FIVE CHARACTERS
IN THE DIFFERENT POPULATIONS

Character	Estimate[a]	Population 1 $\hat{h}^2$[b]	SD[c]	Population 2 $\hat{h}^2$	SD	Population 3 $\hat{h}^2$	SD	Population 4 $\hat{h}^2$	SD	Population 5 $\hat{h}^2$	SD	Population 6 $\hat{h}^2$	SD
Head Length	A	74	05	57	08	59	06	67	07	36	08	24	06
	B	72	06	56	09	77	08	67	07	--	--	--	--
Head Width	A	15	07	20	07	27	07	00	18	06	07	01	05
	B	00	07	20	09	14	07	--	--	--	--	--	--
Seed-Branch Length	A	44	07	35	07	58	06	62	11	22	05	06	05
	B	45	10	29	09	61	08	67	08	--	--	--	--
Node Number	A	36	12	19	13	36	08	42	09	30	10	13	07
	B	17	05	09	05	15	05	19	05	--	--	--	--
Seed Weight	A	22	10	34	06	47	10	--	--	19	06	13	06
	B	36	09	26	09	19	10	--	--	--	--	--	--

a:A = Heritability estimates obtained from regression of F_3 (1968) means on F_2 (1967) values.
B = Heritability estimates obtained from regression of F_3 (1967) means on F_2 (1966) or F_2 (1965) values.
b:$\hat{h}^2$= Heritability estimates.   c:SD=Estimate of the standard deviation of the heritability estimate.

is small. In order to determine the validity of selection, expected
genetic advance should be obtained. Expected genetic advance, and its
percent of the mean, based on selecting the best 10 percent for head
length, head width, seed-branch length, node number per head, and seed
weight for the six populations studied are shown in Table XXI. Three
different bases, A, B, and C, were used for calculating the genetic ad-
vance, depending on which heritability estimate was used. These were:
(a) based on heritability estimates obtained from the F_2 generation by
the geometric mean procedure, basis A, (b) based on heritability
estimates obtained from the F_3 family means, basis B, and (c) based
on heritability estimates obtained by the regression method from 1968
and 1967 data, basis C. The expected genetic advance in percent of
the mean, for bases A, B, and C, was calculated by using the F_2 gener-
ation means, the F_3 generation means, and the means of F_2 parents of
the F_3 families, respectively.

Regardless of the method of estimation, the expected genetic
advance in percent of the mean for head length was higher in populations
1, 2, 3, and 4 than populations 5 and 6, except for population 2 when
method A was used. It was concluded that pronounced progress should
be expected from selection for head length in early generations
particularly in populations 1, 2, 3, and 4.

Head width showed lower expected genetic advance by using methods
B and C than those obtained by using method A. This was not unexpected
since this character was completely lacking of additive gene action.
Genetic advance based on method B was higher than the one based on
method C for all populations. This was in close agreement with the
heritability estimates of head width. Progress under selection should

TABLE XXI

EXPECTED GENETIC ADVANCE (GA) AND ITS PERCENT OF THE MEAN
BASED ON THREE ESTIMATES OF HERITABILITY

Population	Basis[a]	Head Length		Head Width		Branch Length		Node Number		Seed Weight	
		GA	%	GA	%	GA	%	GA	%	GA	%
1	A	59.78	31	13.89	24	6.62	12	1.27	12	2.85	12
	B	65.02	36	7.33	12	14.01	28	1.70	16	4.09	16
	C	63.49	34	2.92	5	10.80	20	0.95	9	1.46	6
2	A	30.70	22	20.16	36	15.19	33	1.19	15	2.46	11
	B	33.25	23	6.19	11	11.08	24	0.90	10	2.86	13
	C	26.70	19	3.75	7	7.99	18	0.42	5	2.08	9
3	A	43.14	27	12.69	25	15.42	32	1.98	19	0.46	2
	B	51.57	33	7.94	15	19.32	42	1.55	15	3.36	18
	C	43.10	26	4.56	9	16.84	34	1.28	13	2.16	12
4	A	61.37	33	13.96	23	45.97	56	3.15	35	-----	--
	B	62.77	33	10.77	15	48.84	58	2.21	24	-----	--
	C	57.02	30	00.00	00	33.93	42	1.59	18	-----	--
5	A	78.89	23	13.34	26	31.08	34	1.60	14	6.76	22
	B	63.34	20	3.51	6	19.66	23	2.66	27	5.43	18
	C	39.91	12	1.10	2	13.92	15	1.23	12	2.63	8
6	A	66.53	20	11.27	23	15.44	17	1.40	12	7.20	22
	B	51.52	16	2.41	4	12.85	15	1.66	15	3.43	12
	C	28.45	9	0.25	1	3.57	4	0.61	5	1.66	5

[a]A = Heritability estimates obtained from the F_2 generation by the geometric mean procedure.
B = Heritability estimates obtained from the F_3 family means.
C = Heritability estimates obtained from the regression of F_3 (1968) means on F_2 (1967) values.

not be expected for this character.

The behavior of seed-branch length, with respect to genetic advance in percent of the mean, was very closely related to head length. Populations 1, 2, 3, and 4 showed higher genetic advance than populations 5 and 6 with respect to methods B and C. Population 4 showed very high values of the expected genetic advance. It was concluded that rapid progress could be expected from early generation selection for seed-branch length at least in populations 1, 2, 3, 4, and 5.

The expected genetic advance was relatively low for node number and seed weight in all populations. Much progress should not be expected from early generation selection for these two characters. However, selection for these two characters in later generations might be more effective.

Estimates of the number of genes or blocks of genes, rounded to the closest integer, are shown in Table XXII. Two estimates of the environmental variance, the pooled and the geometric estimates, were used to calculate the estimate of gene number. The pooled and the geometric estimates of gene number were about the same in most populations. In three cases, the gene number estimate based on the pooled environmental estimate was undefined, denoted by u in Table XXII. The reason for this situation was that the environmental variance estimate was greater than the phenotypic variance estimate which resulted in a negative estimate, considered to zero, for the genetic variance. The estimates of gene number based on the geometric environmental variance estimate were thought to be more reliable than those based on the pooled one. Hence, the later estimate will be excluded from the following discussion.

TABLE XXII

ESTIMATES OF GENE NUMBER FOR FIVE CHARACTERS IN SIX
POPULATIONS OF SORGHUM BASED ON THE POOLED AND THE
GEOMETRIC ENVIRONMENTAL VARIANCE ESTIMATES

Population	Basis	Character				
		Head Length	Head Width	Branch Length	Node Number	Seed Weight
1	Pooled	19	1	u^a	15	u
	Geometric	11	1	13	7	7
2	Pooled	4	1	2	1	6
	Geometric	4	1	2	1	3
3	Pooled	7	1	3	1	u
	Geometric	5	1	2	1	1
4	Pooled	23	1[†]	u	1	-
	Geometric	10	1[†]	19	1	-
5	Pooled	4	1	1	7	1
	Geometric	4	1	1	6	1
6	Pooled	4	1	1	7	1
	Geometric	3	1	1	6	1

[†]Parent means were taken from 1968 data since head width of 'Dwarf Broomcorn' was measured in that year.
[a] = Undefined estimate of the gene number.

The range of the estimates of gene number was from 3, in population 6, to 11, in population 2, for head length. Head width was found to be controlled by only one gene in all populations. This was in close agreement with the distinct behavior observed for that character with respect to the heritability and the variance component extimates. Branch length showed a wide range of gene number. The highest gene number for branch length was found in population 4. Node number was found to be controlled by the same gene number in populations 2, 3, and 4, and in populations 5 and 6. Seed weight seemed to be controlled by one gene in populations 3, 5, and 6 and by 7 and 3 genes in populations 1 and 2, respectively.

The assumptions associated with the formula of gene number are several (72). Many of these assumptions do not hold in most cases which result in a downward bias in the gene number estimate. Consequently, estimates of gene number, or blocks of genes, for a given character should be taken as a lower boundary of the actual gene number.

Summary and Conclusions

Estimates of heritability were obtained from the F_2 generation, the F_3 generation, and from the combined information of both generations for five characters in six populations of sorghum. Three estimates were obtained from the F_2 generation depending on the method of estimation of the environmental variance. Heritability was estimated on a family mean basis and on an individual basis from the F_3 generation. Two estimates were obtained for each of the narrow and the broad sense heritabilities, on the individual basis, by using the pooled variance

estimate of the two parents or their geometric mean. Heritability estimates based on the regression of the F_3 means on the F_2 values, and the correlation between them; i.e., standard unit heritability, were also obtained. Expected genetic advance and estimates of the minimum number of loci were calculated.

Heritability estimates were in general in close agreement with the expected genetic advance for the different characters in most populations. In general, high heritability estimates were observed for head length and seed-branch length in most populations. The expected genetic advance in percent of the mean was also high in magnitude. It was concluded that rapid progress from early generation selection should be expected for these two characters in most populations. Head length was found to be controlled by at least 3 to 11 genes in the different populations studied. A wide range of gene number was observed for branch length, 1 to 19.

Low heritability estimates were obtained for head width in all populations. The narrow sense estimates were all zeros for the different populations which implied that the additive gene action was completely lacking. It was concluded that any progress from selection for this character should not be expected. It was also found that head width was controlled by only one gene.

Seed weight and node number showed relatively small heritability estimates and expected genetic advance in percent of the mean. Much progress from early generation selection should not be expected for these two characters at least in the populations investigated. The number of genes ranged between 1 and 7 for seed weight and node number in the different populations.

CHAPTER V

PHENOTYPIC, GENETIC, AND ENVIRONMENTAL CORRELATIONS

The genetic relationship among quantitative traits is of consider-
able interest to the breeder. Three reasons for that interest were
given by Falconer (21): (a) in connection with the genetic causes
of correlation through the pleiotropic action of genes, (b) in con-
nection with the changes brought about in a given trait when selection
is practiced on another trait, and (c) in connection with natural
selection since the relationship between a metric trait and fitness
is the primary agent that determines the genetic properties of that
trait in a natural population. The phenotypic correlation is a linear
combination of genetic and environmental correlations. However, the
proportion with which genetic and environmental correlations make up
the phenotypic correlations is variable depending on the magnitude
of the heritabilities of both traits.

The correlations between some quantitative traits in sorghum
have been estimated. Beil and Atkins (7) calculated phenotypic,
genetic, and environmental correlations between all possible pairs
of the characters: mid-bloom, plant height, tiller number, 100-seed
weight, and grain yield, in two crosses of sorghum, 'Reliance' x
'North Dakota Mandan Sorghum No. 158' and 'Redlan' x 'North Dakota
Mandan Sorghum No. 158'. The phenotypic correlations of 100-seed
weight with the other characters were significant except for seed

weight with number of tillers in the second cross. Environmental

correlations of seed weight with each of mid-bloom and plant height,

in the first cross, and with plant height and grain yield, in the

second cross, were significant. Liang (38) found that the correlation

between kernel weight and grain yield, both phenotypically and geno-

typically, was low in a 6-variety, randomly selected, diallel cross

of sorghum. Swarup and Chaugale (63), using 70 varieties of sorghum,

concluded that seed weight did not seem to have any genetic correla-

tion with grain yield, but they were positively correlated environ-

mentally. This was also found by Liang (38) using a 6-variety diallel

cross. Malm (46) found positive correlation between kernel weight

and protein content in some crosses of sorghum. The correlations

between different characters in sorghum were also determined by

Ayyangar et al. (4), Ireland (33), and Venkataramanan and Subramanyam

(64). The implications of genetic correlations in selection in soybeans

were reported by Johnson et al. (36).

Results and Discussion

Estimates of the phenotypic, genetic, and environmental correlation

coefficients for five characters in six populations of sorghum are

shown in Tables XXIII, XXIV, XXV, XXVI, XXVII, and XXVIII. The corre-

lation coefficients were estimated from the F_2 generation, on an

individual plant basis, and from the F_3 generation, on a family mean

basis. The environmental and the genetic correlation coefficients

were estimated from the F_2 generation by two methods, depending on

whether the estimates obtained from the two parents were pooled or

their geometric mean was taken. The pooled method resulted in some

TABLE XXIII

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2
GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR
POPULATION 1

| Correlation of | Based on the F_2 Generation and the Parents | | | | | Based on the F_3 Family Means | | |
| | Pooled | | | Geometric Mean | | | | |
	P^a	G	E^b	G	E	P^c	G	E^c
Head Length and								
Head Width	-0.07	-0.04	0.28**	-0.26	0.32	-0.10	-0.16	0.21
Seed-Branch Length	0.75**	u^d	0.46**	1.19	0.54	0.87**	0.92	0.47**
Node Number	0.20**	0.36	0.15**	0.21	0.22	0.28*	0.32	-0.09
Seed Weight	0.09	u	0.04	0.12	0.07	0.12	0.15	-0.12
Head Width and								
Seed-Branch Length	0.18**	u	0.31**	0.19	0.19	0.17	0.09	0.45**
Node Number	-0.06	-0.16	0.00	i^e	i	0.01	0.03	-0.03
Seed Weight	0.09	u	0.05	0.14	0.04	0.15	0.12	0.29*
Seed-Branch Length and								
Node Number	0.06	u	-0.12**	i	i	0.08	0.15	-0.18
Seed Weight	0.07	u	-0.08*	i	i	-0.02	-0.06	0.22
Node Number and								
Seed Weight	0.04	u	-0.01	i	i	0.16	0.22	-0.04

*Significant at the 0.01 level.
**Significant at the 0.05 level.
a: Significant values are 0.105 and 0.137 for the 0.05 and the 0.01 levels, respectively, for 356 degrees of freedom.
b: Significant values are 0.076 and 0.100 for the 0.05 and the 0.01 levels, respectively, for 723 degrees of freedom.
c: Significant values are 0.279 and 0.361 for the 0.05 and the 0.01 levels, respectively for 48 degrees of freedom.
d:u = Undefined estimate of the correlation coefficient.
e:i = complex number estimate of the correlation coefficient.

TABLE XXIV

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2
GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR
POPULATION 2

| Correlation of | Based on the F_2 Generation and the Parents | | | | | Based on the F_3 Family Means | | |
| | Pooled | | | Geometric Means | | | | |
	P^a	G	E^b	G	E	P^c	G	E^c
Head Length and								
Head Width	0.05	-0.08	0.39**	0.07	0.39	0.29*	0.26	0.49**
Seed-Branch Length	0.64**	0.75	0.53**	0.68	0.57	0.87**	0.91	0.65**
Node Number	0.23**	0.33	0.15**	0.32	0.15	-0.14	-0.24	0.07
Seed Weight	-0.12*	-0.62	0.12**	-0.38	0.14	-0.13	-0.13	-0.08
Head Width and								
Seed-Branch Length	0.11*	0.02	0.31**	0.08	0.20	0.42**	0.42	0.46**
Node Number	-0.05	-0.06	-0.05	i^d	i	-0.03	-0.09	0.05
Seed Weight	0.08	0.10	0.12**	0.07	0.13	0.14	0.13	0.18
Seed-Branch Length and								
Node Number	0.08	0.18	0.01	i	i	-0.29*	-0.35	-0.25
Seed Weight	-0.01	-0.28	0.09*	-0.16	0.11	-0.15	-0.21	0.14
Node Number and								
Seed Weight	-0.08	-0.60	0.10**	-0.32	0.09	0.03	0.13	-0.15

*Significant at the 0.05 level.
**Significant at the 0.01 level.
a: Significant values are 0.102 and 0.133 for the 0.05 and the 0.01 levels, respectively, for 373 degrees of freedom.
b: Significant values are 0.075 and 0.098 for the 0.05 and the 0.01 levels, respectively, for 750 degrees of freedom.
c: Significant values are 0.279 and 0.361 for the 0.05 and the 0.01 levels, respectively, for 48 degrees of freedom.
d:i = Complex number estimate of the correlation coefficient.

TABLE XXV

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2
GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR
POPULATION 3

| | Based on the F_2 Generation and the Parents | | | | | Based on the F_3 Family Means | | |
| | Pooled | | | Geometric Mean | | | | |
Correlation of	P^a	G	E^b	G	E	P^c	G	E^e
Head Length and								
Head Width	0.19**	0.00	0.45**	0.05	0.45	-0.20	-0.24	0.24
Seed-Branch Length	0.66**	0.83	0.54**	0.72	0.59	0.92**	0.95	0.59**
Node Number	0.30**	0.47	0.14**	0.38	0.18	0.36*	0.44	-0.03
Seed Weight	0.01	u	0.08*	-0.20	0.10	-0.54**	-0.59	-0.17
Head Width and								
Seed-Branch Length	0.34**	0.26	0.45**	0.39	0.26	-0.09	-0.17	0.47**
Node Number	-0.09	-0.16	0.01	i^e	i	-0.02	-0.07	0.17
Seed Weight	0.23**	u^d	0.15**	0.62	0.15	0.45**	0.52	0.07
Seed-Branch Length and								
Node Number	0.14**	0.42	-0.08*	i	i	0.19	0.26	-0.12
Seed Weight	0.00	u	0.09*	-0.35	0.12	-0.57**	-0.62	-0.17
Node Number and								
Seed Weight	-0.03	u	0.08*	-0.37	0.08	0.06	0.13	-0.18

*Significant at the 0.05 level.
**Significant at the 0.01 level.
a: Significant values are 0.103 and 0.135 at the 0.05 and the 0.01 levels, respectively, for 364 degrees of freedom.
b: Significant values are 0.080 and 0.104 at the 0.05 and the 0.01 levels, respectively, for 661 degrees of freedom.
c: Significant values are 0.279 and 0.361 at the 0.05 and the 0.01 levels, respectively, for 48 degrees of freedom.
d:u = Undefined estimate of the correlation coefficient.
e:i = Complex number estimate of the correlation coefficient.

TABLE XXVI

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2
GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR
POPULATION 4

Correlation of	Based on the F_2 Generation and the Parents					Based on the F_3 Family Means		
	Pooled			Geometric Mean		P^c	G	E^c
	P^a	G	E^b	G	E			
Head Length and								
Head Width	0.11*	0.13	0.12**	0.08	0.18	0.42**	0.49	0.45**
Seed-Branch Length	0.79**	u^d	0.98**	0.79	0.81	0.85**	0.85	0.78**
Node Number	-0.07	-0.06	-0.12**	i^e	i	-0.15	-0.17	-0.01
Seed Weight	-----	-----	-----	----	----	-----	-----	-----
Head Width and								
Seed-Branch Length	0.09	u	0.02	0.12	0.04	0.37**	0.47	0.27
Node Number	0.05	0.02	0.18**	0.02	0.19	0.15	0.14	0.19
Seed Weight	-----	-----	-----	----	----	-----	-----	-----
Seed-Branch Length and								
Node Number	-0.26**	u	-0.19**	i	i	-0.51**	-0.61	0.03
Seed Weight	-----	-----	-----	----	----	-----	-----	-----
Node Number and								
Seed Weight	-----	-----	-----	----	----	-----	-----	-----

*Significant at the 0.05 level.
**Significant at the 0.01 level.
a: Significant values are 0.109 and 0.143 for the 0.05 and the 0.01 levels, respectively, based on 326 degrees of freedom.
b: Significant values are 0.077 and 0.101 for the 0.05 and the 0.01 levels, respectively, based on 702 degrees of freedom.
c: Significant values are 0.279 and 0.361 for the 0.05 and the 0.01 levels, respectively, based on 48 degrees of freedom.
d:u = Undefined estimate of the correlation coefficient.
e:i = Complex number estimate of the correlation coefficient.

TABLE XXVII

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2
GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR
POPULATION 5

Correlation of	Based on the F_2 Generation and the Parents					Based on the F_3 Family Means		
	Pooled			Geometric Mean				
	P^a	G	E^b	G	E	P^c	G	E^c
Head Length and								
Head Width	0.37**	0.42	0.30**	0.39	0.34	-0.15	-0.44	0.41**
Seed-Branch Length	0.65**	0.80	0.45**	0.75	0.47	0.55**	0.58	0.35*
Node Number	0.22**	0.36	0.11**	0.35	0.08	0.46**	0.52	0.13
Seed Weight	0.09	0.15	0.02	0.13	0.03	0.18	0.16	0.32*
Head Width and								
Seed-Branch Length	0.41**	0.43	0.38**	0.42	0.39	0.24	0.05	0.55**
Node Number	-0.04	0.02	-0.09*	0.01	-0.10	-0.34*	-0.34	-0.43**
Seed Weight	-0.09	-0.19	0.02	-0.17	0.02	-0.49**	-0.97	0.15
Seed-Branch Length and								
Node Number	0.01	0.19	-0.13**	0.12	-0.10	-0.19	-0.15	-0.33*
Seed Weight	-0.04	-0.02	-0.06	i^d	i	-0.11	-0.20	0.26
Node Number and								
Seed Weight	0.08	0.16	0.02	i	i	0.23	0.24	0.22

*Significant at the 0.05 level.
**Significant at the 0.01 level.
a: Significant values are 0.098 and 0.128 for the 0.05 and the 0.01 levels, respectively, based on 401 degrees of freedom.
b: Significant values are 0.076 and 0.099 for the 0.05 and the 0.01 levels, respectively, based on 740 degrees of freedom.
c: Significant values are 0.279 and 0.361 for the 0.05 and the 0.01 levels, respectively, based on 48 degrees of freedom.
d:i = Complex number estimate of the correlation coefficient.

TABLE XXVIII

PHENOTYPIC (P), GENETIC (G), AND ENVIRONMENTAL (E) CORRELATIONS BASED ON THE F_2 GENERATION AND THE PARENTS AND ON THE F_3 FAMILY MEANS FOR POPULATION 6

| Correlation of | Based on the F_2 Generation and the Parents | | | | | Based on the F_3 Family Means | | |
| | Pooled | | | Geometric Mean | | | | |
	P^a	G	E^b	G	E	P^c	G	E^c
Head Length and								
Head Width	0.35**	0.43	0.25**	0.41	0.25	0.07	-0.02	0.32*
Seed-Branch Length	0.60**	1.03	0.41**	0.90	0.36	0.53**	0.55	0.56**
Node Number	0.27**	0.53	0.12**	0.46	0.10	0.55**	0.73	-0.13
Seed Weight	0.14**	0.31	0.00	i^d	i	0.46**	0.59	0.04
Head Width and								
Seed-Branch Length	0.39**	0.59	0.31**	0.55	0.28	0.27	0.09	0.49**
Node Number	0.00	0.08	-0.05	0.07	-0.05	-0.12	-0.21	-0.03
Seed Weight	-0.11*	-0.26	0.03	-0.22	0.02	-0.05	-0.39	0.34*
Seed-Branch Length and								
Node Number	0.04	0.52	-0.12**	0.23	-0.06	0.18	0.35	-0.16
Seed Weight	-0.04	0.07	-0.09*	0.00	-0.07	0.19	0.19	0.18
Node Number and								
Seed Weight	0.08	0.17	0.02	i	i	0.41**	0.61	-0.01

*Significant at the 0.05 level.
**Significant at the 0.01 level.
a: Significant values are 0.105 and 0.138 for the 0.05 and the 0.01 levels, respectively, based on 352 degrees of freedom.
b: Significant values are 0.080 and 0.104 for the 0.05 and the 0.01 levels, respectively, based on 660 degrees of freedom.
c: Significant values are 0.279 and 0.361 for the 0.05 and the 0.01 levels, respectively, based on 48 degrees of freedom.
d: i = Complex number estimate of the correlation coefficient.

negative estimates of the genetic variance in some cases. The negative estimates were considered to be zero and, hence, the correlation coefficients based on those estimates were undefined. These are denoted by u in the different tables. The geometric mean of two covariance estimates was a complex number when only one of the estimates involved was negative. Hence, the estimates of the correlation coefficients in such cases were complex numbers. These are denoted by i in the tables. The geometric mean of two negative covariance estimates was considered to be negative.

Tests of significance for the correlation coefficients were accomplished for the phenotypic and the environmental correlations based on the pooled information in the F_2 generation, and for the phenotypic and environmental correlations in the F_3 generation. The degrees of freedom required for testing the non-existence of the phenotypic correlation in the F_2 generation were found by subtracting one, to account for the covariable, from the degrees of freedom of the plants in blocks in locations entry. The pooled degrees of freedom of plants in blocks in locations of two parents involved in a particular population, minus one was used for testing the significance of the environmental correlation in the F_2 generation. In the F_3 generation, the degrees of freedom were determined, for testing the phenotypic and the environmental correlations, by subtracting one from each of the families and the experimental error degrees of freedom, respectively. The degrees of freedom of those two entries were the same since the number of blocks was two in this case. Tests of significance of the genetic correlation have not been developed. The distribution of the estimate of the correlation coefficient based on

the geometric mean of each of the covariance and the two variances involved is not known yet. Consequently, the environmental correlation coefficient estimates, based on the geometric mean, were not tested.

Estimates of the phenotypic and the environmental correlation coefficients in each of the F_2 and the F_3 generation were, in general, of the same sign and significance. The environmental correlations in the F_2 generation based on the pooled and the geometric mean method, when both existed, were similar in all situations. This association was true for the genetic correlation estimates in the F_2 generation. However, the magnitude of the estimates of the genetic correlation coefficients based on the pooled information was slightly larger. The estimates of the phenotypic and environmental correlation coefficients in the F_2 and the F_3 generations were not comparable in several cases. This response might have been expected since the two generations were not grown in the same environment. The genetic correlation coefficient estimates were different in some cases in the two generations. This could be expected since those estimates were calculated on an individual plant basis for the F_2 generation and on a family mean basis for the F_3 generation grown in different years.

Head length and seed-branch length showed the highest positive estimates of the genetic correlation for both generations in all populations except population 6 in which the correlation of head length and node number, node number and seed weight, and head length and seed weight were higher in the F_3 generation. Population 3 showed the highest estimate, 0.95, and population 6 showed the lowest, 0.55, in the F_3 generation. In the F_2 generation, the highest positive

genetic correlation between head length and branch length was shown
by population 1 and the lowest by population 2. Since the genetic
correlation between head length and seed-branch length was positive
and generally high in magnitude, it was concluded that selection for
either character would result in good progress in the other character.

The genetic correlation estimates of head width with the other
characters did not show any consistent pattern in the different popu-
lations. However, in many cases those estimates were small in magni-
tude and sometimes they were negative. It was found earlier that head
width was completely lacking of the additive gene action and controlled
by one gene. This would imply that in very few generations most of
the variation of head width will be environmental in nature. Conse-
quently, the covariance of head width and any of the other characters
will decrease which would result in a decrease in the genetic corre-
lation in the successive generations. It was suggested that selection
should not be practiced on head width to improve any other character,
or on any other character to improve head width.

In general, higher estimates of the genetic correlations were
obtained in the case of head length and node number than in the case
of seed-branch length and node number. The genetic correlation coef-
ficients for head length and node number were positive and large in
all populations except populations 2 and 4. This was reasonable since
the genetic factors affecting node number could result in some changes
in head length in the same direction. Although negative genetic
correlation estimates were found in populations 2 and 4, their magni-
tude was small and might not be significant. It was concluded that
selection could be practiced on head length in populations 1, 3, 5,

and 6 in order to obtain a desirable progress in node number, if needed.

The genetic correlation between seed-branch length and node number varied in the magnitude and the sign in the different populations. The smallest estimates were obtained in populations 1 and 5. Populations 2, 3, and 6 showed intermediate estimates. In population 4, the genetic correlation coefficient between seed-branch length and node number was -0.61, on an F_3 family mean basis. Estimates were not possible in the F_2 generation for that population. Population 4 is a cross involving 'Chicken Maize' and 'Dwarf Broomcorn'. 'Chicken Maize' had about twice the number of nodes of 'Dwarf Broomcorn', but its seed-branch length was much smaller. It was suggested that the genes in this cross controlling seed-branch length and node number, or at least some of those genes, might be in close linkage.

The genetic correlation estimates of head length and seed weight, branch length and seed weight, and node number and seed weight were generally small, except for a few populations. Relatively high and negative estimates were observed between head length and seed weight and seed-branch length and seed weight in population 3. The genetic correlation estimates, for head length and seed weight and node number and seed weight, were relatively high and positive in population 6.

Summary and Conclusions

Phenotypic, genetic, and environmental correlation coefficient estimates were calculated for five characters in six populations of sorghum. These estimates were obtained from the F_2 generation on an individual plant basis and from the F_3 generation on a family mean

basis. Estimates of the environmental and the genetic correlation
coefficients were obtained by two methods: the pooled and the geo-
metric mean methods. The pooled method resulted in some undefined
estimates and the geometric mean method resulted in some complex
numbers for such estimates. Tests of significance were accomplished
for the phenotypic and the environmental correlations in the F_2
generation, based on the pooled method, and in the F_3 generation.

The phenotypic and the environmental correlations for each of
the F_2 generation, based on the pooled method, and the F_3 generation
had similar significances and signs. Differences were found between
the phenotypic correlations, as well as the genetic correlations, in
the two generations. It was suggested that such differences might be
due to the difference in the environment. The genetic correlations
were calculated on an individual plant basis in the F_2 generation,
and on a family mean basis in the F_3 generation. Perhaps this was
the reason for obtaining differences in the sign and the magnitude
of these two estimates.

In general, head length and seed-branch length showed the highest
genetic correlation in both generations. In all cases these estimates
of correlation coefficients were positive. It was concluded that
selection for either head length or seed-branch length should result
in rapid progress in the other character. The genetic correlation
coefficient of head width and the other characters did not follow
any regular pattern in most populations. It was found earlier that
head width was completely lacking in additive gene action. Consequent-
ly, it was concluded that selection for head width based on the other
characters, or vice versa, would not accomplish any desirable progress.

Head length and node number showed relatively higher estimates of the genetic correlation than seed-branch length and node number regardless of sign. Relatively low estimates of the genetic correlation coefficients were found for seed weight and the other characters. It was concluded that selection for seed weight based on the other characters, or vice versa, would not lead to any desirable progress.

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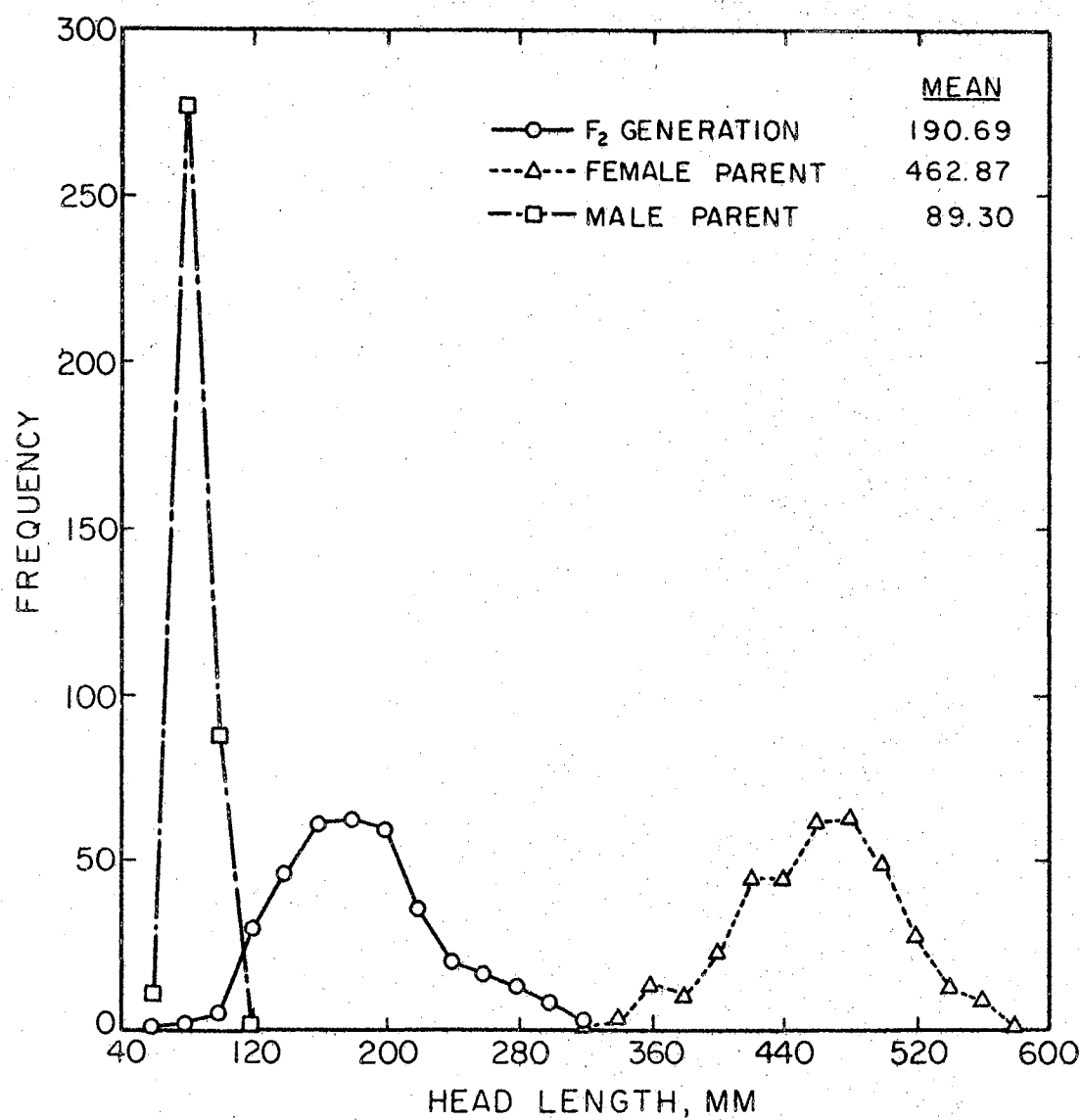   Foundations. The University of Chicago Press.
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APPENDIX

Figure 1. Frequency Distributions of Head Length for the
Parents and the F_2 Generation of Population 1,
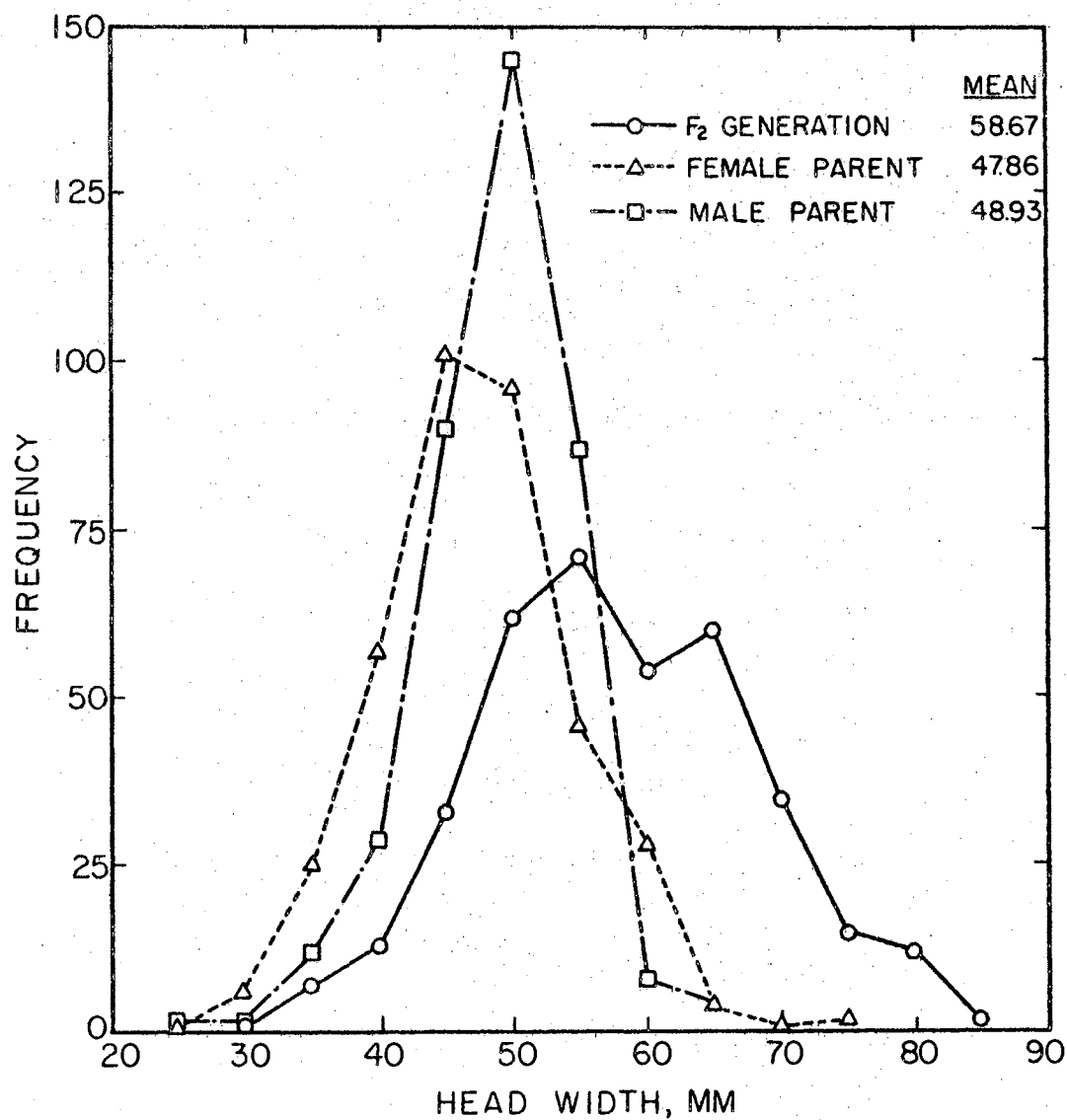Woodward Big Head x Chicken Maize.

Figure 2. Frequency Distributions of Head Width for the
Parents and the F_2 Generation of Population 1,
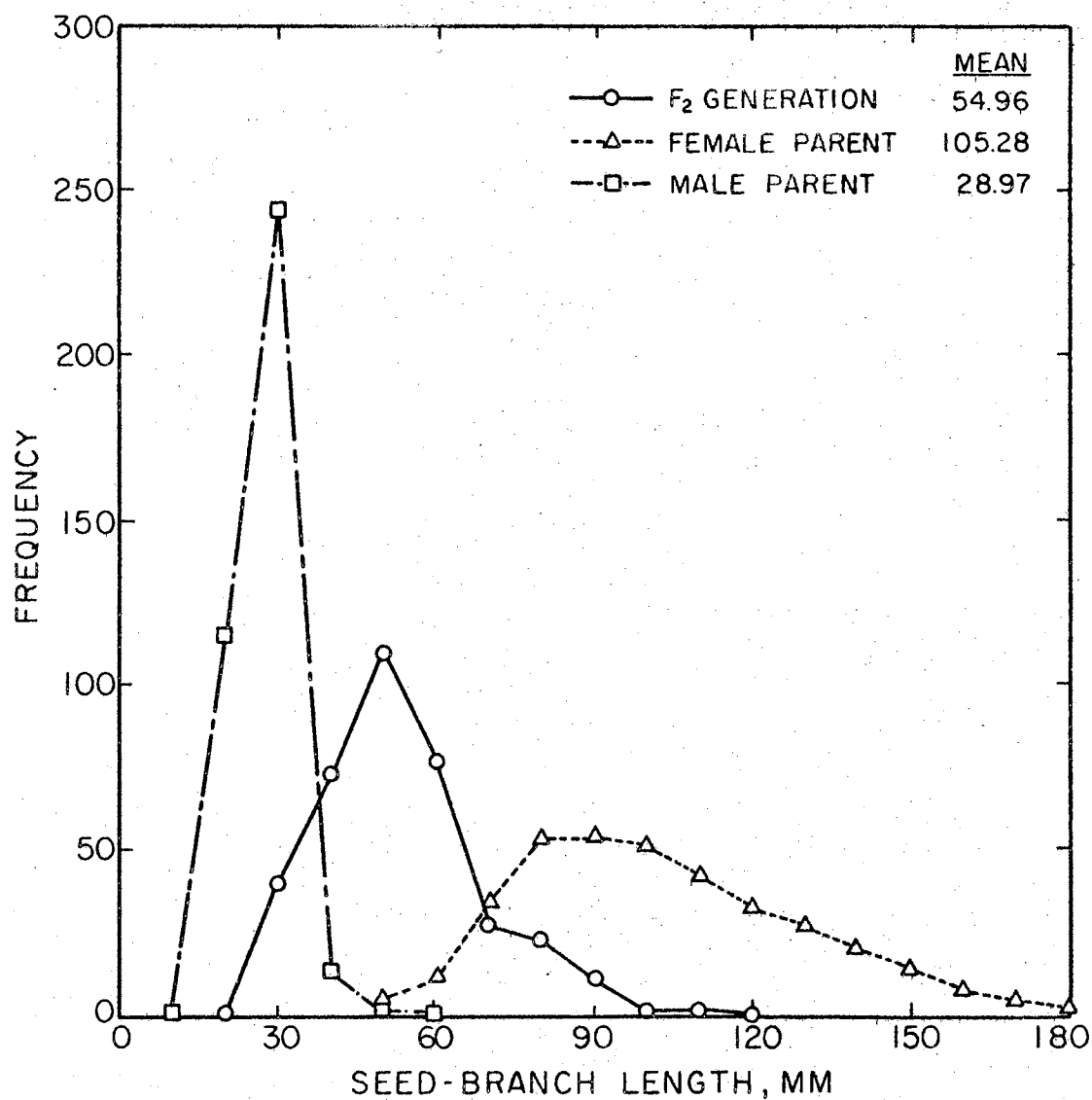Woodward Big Head x Chicken Maize.

Figure 3. Frequency Distributions of Seed-Branch Length for the Parents and the F_2 Generation of Population 1, Woodward Big Head x Chicken Maize.
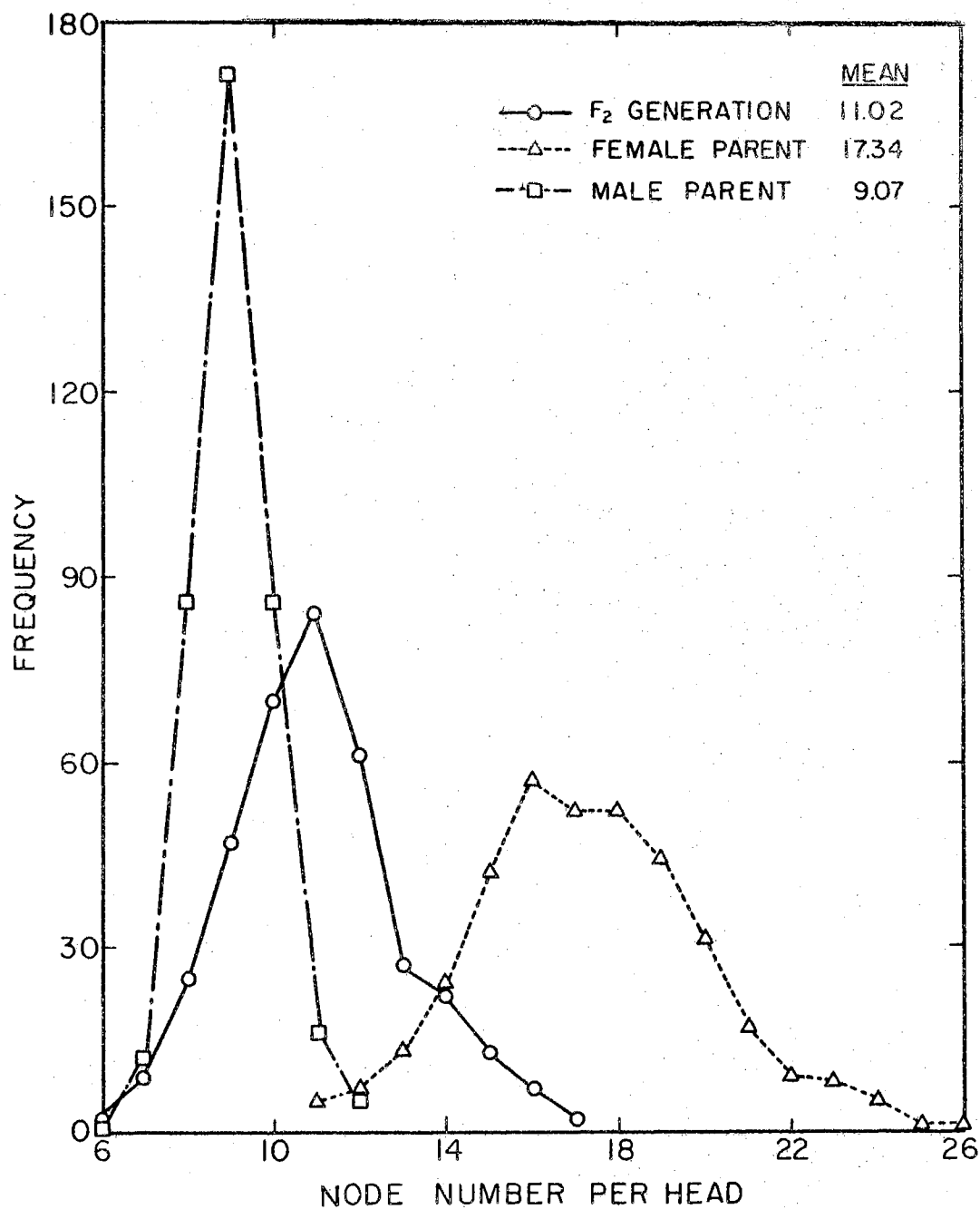
Figure 4. Frequency Distributions of Node Number per Head
for the Parents and the F_2 Generation of
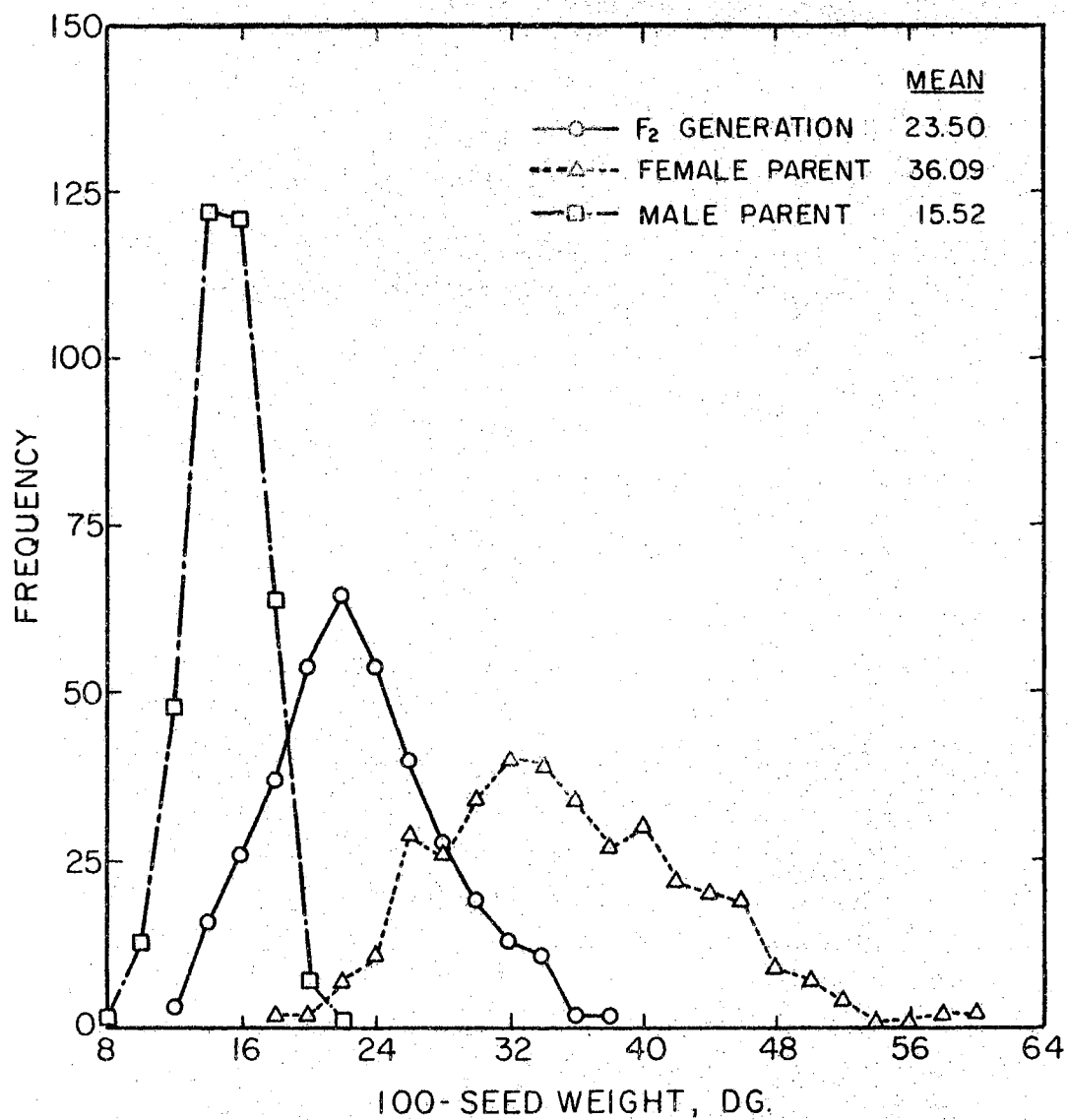Population 1, Woodward Big Head x Chicken
Maize.

Figure 5. Frequency Distributions of 100-Seed Weight for
the Parents and the F_2 Generation of Population
1, Woodward Big Head x Chicken Maize.

VITA

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