I. INHERITANCE OF SEED WEIGHT IN A GRAIN SORGHUM [(SORGHUM BICOLOR (L.) MOENCH)] CROSS.

II. INHERITANCE OF GERMINATION RATE IN A GRAIN SORGHUM [(SORGHUM BICOLOR (L.) MOENCH)] CROSS.

III. DOSAGE EFFECT OF WAXY GENE (wx) ON MALTOSE PRODUCTION AND DEGREE OF HYDROLYSIS OF THREE GRAIN SORGHUM [(SORGHUM BICOLOR (L.) MOENCH] VARIETIES AND THEIR F_1 HYBRIDS.

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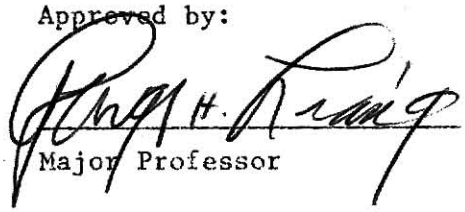

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Inheritance of Seed Weight in a Grain Sorghum [(*Sorghum bicolor* (L.) Moench)] Cross.

SUMMARY

To gain a better understanding of the inheritance of seed weight, two sorghum grain [*Sorghum bicolor* (L.) Moench] varieties of contrasting seed weight, their F_1, F_2, F_3 and first generation backcrosses were studied.

The population means and variances were used to estimate the heritability, the minimum number of genetic factors, and to determine the nature of gene action involved in the inheritance of seed weight.

Heritability of seed weight was of moderate magnitude (50%), revealing that selection in the F_2 could be effective in increasing the mean of seed weight.

A minimum of 2-3 genetic factors appeared to control the expression of this trait.

Gamble's method (1962) was used to estimate the gene actions. Dominance x dominance and additive x dominance types of epistasis were the only significant and important gene effects in the inheritance of kernel weight for this cross. Additive and dominance gene actions appeared to have a minor contribution.

Phenotypic correlations, estimated in segregating and non-segregating populations, indicated that kernel number was more importance than kernel weight in determining total yield. However, kernel number and kernel weight had a negative and in some instances significant correlation in all generations, except in the F_2.

Plant height was significantly correlated with kernel weight and grain yield, suggesting that selection of short plants without sacrificing kernel weight and grain yield, may be quite difficult.

INHERITANCE OF SEED WEIGHT IN A GRAIN SORGHUM [*Sorghum bicolor* (L.) Moench] CROSS

INTRODUCTION

The effectiveness of selection depends primarily on the magnitude of heritable variability present in segregating populations for the trait being selected. An understanding of the genetic basis of quantitative variability is necessary for efficient utilization of available germplasm in a plant breeding program.

The heritability of a character describes the extent to which it is transmitted from one generation to the next. This parameter is a very valuable tool when the breeders use it in conjunction with other parameters in predicting the magnitude of the genetic gain that can be achieved through selection.

The production of high-yielding hybrids in sorghum has been the main objective in the breeding programs. A major obstacle has been the low heritability of yield in early generations. However, heritability estimates reported by several workers have indicated that certain components of grain yield in sorghum are more heritable than yield itself.

Although much has been learned concerning the inheritance of several plant characters in grain sorghum, only a few studies on the inheritance of seed size have been reported. Malm (1968) has concluded that usually large seeded parents produced the highest yielding grain sorghum hybrids. He also pointed out that a breeder, using the same exotic material he used, should make significant progress in selecting for grain yield by screening on the basis of kernel size within segregating populations.

Swarup and Chaugale (1962) studied the inheritance of seed size in grain sorghum and reported a high value of heritability for 100-seed weight (85.4%) calculated in the broad sense by using the formula proposed by Hanson, Robinson and Comstock (1956).

Beil and Atkins (1967) obtained moderately high heritability values for 100-seed weight in crosses between Reliance x North Dakota Madam sorghum No. 158 and Redlan x North Dakota Madam sorghum No. 158, from 58.8 to 75%. But, a lower progress was predicted for seed weight as compared with those obtained with other agronomic traits. Chung and Liang (1970) estimated heritability for kernel weight in F_3 and F_4 progenies from selected F_2 plants of three crosses, Redlan x Martin, KS7 x Combine Kafir 60 and Redland x Combine 7078. They reported a moderately high heritability value which ranged from 17.6 to 86.7%. Voight et al. (1966) estimated the heritability for seed size to be slightly in excess of 60% in a grain sorghum cross between 'Bigseed' and "Norghum', when they used the formula proposed by Warner (1952) and concluded that considerable progress could be achieved in shifting mean seed size by selecting large-seeded F_2 plants. Sindage and Swarup (1970) reported a broad sense estimate of heritability for 100-seed weight of 59.9% calculated by using the method proposed by Weber and Worthy (1952). Chiang and Smith (1967) obtained a low heritability value for 100-seed weight (13.2%) in a diallel analysis. They concluded that the expected gain by selection for this character should be very low magnitude.

Ali-Khan and Weibel (1969) used the F_2 variance method to estimate the value of heritability for several agronomic characters in grain sorghum. Heritabilities for 100-seed weight were 22% in the cross between

'Redlan' and 'Plainsman' and 30% in the cross between 'Combine Kafir 60' and 'Combine 7078'.

Liang and Walters (1968) found a very low heritability value for kernel weight in three crosses as 24% for Redlan x Martin and for Redlan x Combine 7078, and 33% for Plainsman x KS7. Fanous et al. (1971) also obtained a low heritability of 13 to 47% for 100-seed weight in five crosses of grain sorghum, when calculated by the regression method, whereas the estimates were larger (66 to 84%) when they utilized the variance component method. Mukuru (1973) working with four populations of grain sorghum found the heritability estimate ranged from 16 to 39%.

To determine the number of genetic factors in the expression of kernel weight, could help to predict if a yield increase could be obtained and whether it would be easier to select for kernel weight than for yield itself. Voight et al. (1966) concluded that a minimum of 3 or 4 genes or blocks of genes, additive in their effect, appeared to control seed size. Chiang and Smith (1967) found that seed size appeared to be governed by two genetic factors.

The relative magnitude of the estimates of gene effects have a direct bearing on the breeding procedure to be adopted for agronomic traits in a particular crop. Voight et al. (1966), in their study with two parental lines and derived populations, found that genetic variability was, almost entirely, due to additive gene action, without evidence for dominance or epistasis as an important contribution to seed size. However, Beil and Atkins (1967) observed a gross deviation from the strictly additive gene action for seed weight. Liang and Walters (1968) indicated that additive gene effect had a minor contribution to the inheritance of

kernel weight in grain sorghum, whereas dominance appeared to be important in the inheritance of several agronomic traits. Also, additive x additive and dominance x dominance were the important types of epistasis. Mukuru (1973), working with four populations of grain sorghum, found a positive and significant estimate of additive and dominance gene effect for kernel weight in all the populations. It was apparent that mode of the genotypic variance for seed weight arose from dominance effect. Likewise, Nayakar (1973) in his study with six populations of grain sorghum found that dominance gene effect was the significant genetic component in the inheritance of 1000-kernel weight. The additive x additive and dominance x dominance gene effects were also important. His general conclusion was that all types of gene effects were favorable for the exploitation of heterosis.

A knowledge of correlation that exists between important characters may facilitate the interpretation of the results and provide the basis for planning more efficient breeding programs. Several workers have estimated correlations among several agronomic traits in inbred lines, hybrids of grain sorghum, but the results are not always consistent. Swarup and Chaugale (1962), working with 70 varieties of sorghum, concluded that seed weight did not show any genotypic correlation with grain yield. Ali-Khan and Weibel (1969) found that grain yield and kernel weight were inversely correlated and the increase in yield in the grain sorghum hybrid was mainly due to the increase in the kernel number per head. Liang (1967) and Liang et al. (1969) in two studies, estimated genotypic and phenotypic correlations among several traits in segregating populations and in pure lines of grain sorghum. In the first study kernel weight showed

a low correlation with grain yield (r_p = 0.234, r_g = 0.253). In contrast, the second study revealed a positive and significant correlation between both characters. An inverse, but developmentally induced relationship, was reported by them between kernel weight and kernel number. Beil and Atkins (1967) found a positive and in some instances significant genotypic correlation between yield and 100-seed weight in two crosses of grain sorghum. Malm (1968) reported kernel weight to be positively associated with protein percentage and significantly correlated with grain yield. Mukuru (1973) observed that transgressive segregation was toward the parent with lower kernel weight.

Data regarding heritability and different types of gene action in other crops indicate that the magnitude of these genetic parameters varies from location to location and from year to year for the same cross and from cross to cross. Anand and Torrie (1963) reported a high heritability for seed weight in three soybean crosses, 53, 65 and 84%, respectively. Seed weight was not correlated with seed yield. Gamble (1962a, 1962b) found that the additive effects were important for kernel row number, ear diameter, and seed weight in corn. Sharma and Knott (1964) studied the inheritance of kernel weight in a wheat cross; the heritability ranged from 37 to 69% when they used different methods of estimation. Probably, four genes were responsible for the expression of kernel weight. Sun et al. (1972) estimated heritability for kernel weight, in six spring wheat crosses, and obtained a range from 51 to 85%. Additive and dominance effects were more important in determining kernel weight than epistatic effect. Heterosis was greater in crosses of more distantly related parents and ranged from -4.3 to 31.2% as calculated as the increase of F_1 above mid-parent value. Brown (1973), in wheat, also obtained a wide

range for heritability of seed size, from 23.8 to 80.2%. He determined the minimum gene number to be two, acting in additive manner. Ketaka et al. (1976) reported a moderately high heritability value for kernel weight (65%) in crosses between two winter wheat cultivars. The additive gene effect was the main source of variation for kernel weight.

The objective of the present study was an attempt to gain a better understanding of the mode and magnitude of the inheritance of seed weight to assess the possibility of changing or improving seed size through hybridization and selection.

MATERIALS AND METHODS

The parental varieties chosen for this study were PL-1 as parent No. 1 (P_1) and Combine Kafir-60 as parent No.2(P_2) Combine Kafir-60, an early-maturing ($ma_1Ma_2ma_3Ma_4$) and three dwarf ($dw_1Dw_2dw_3Dw_4$) grain sorghum variety which has relatively small seeds that averaged 26 grams per 1,000 seeds. PL-1, also a three dwarf variety ($dw_1dw_2Dw_3dw_4$), originally introduced from Ethiopia but converted to combine height, possesses large seeds which averaged 56 grams per 1,000 seeds.

The two varieties were crossed and the F_1 plants obtained were self pollinated and also backcrossed to each parent to produce the F_2, first and second backcross generations (B_1 and B_2). Twenty-nine F_2 plants were grown and selfed in field conditions to obtain the F_3 families. A photograph of seeds of the parental varieties and their F_1 hybrid is shown in Fig. 1.

Parents, F_1, F_2, B_1, B_2, and F_3 populations were planted at Ashland (Riley County) Experimental Station during the summer of 1975. Each cross was considered as a unit in the planting scheme, randomized in two blocks in rows of 6 meters long and spaced 76 cm apart. The seeds were planted by hand, each row was thinned so that the remaining plants were about 15 cm apart within each row.

The plants were harvested individually, but only those in full competition were used in the analysis. The main head on each plant was harvested and threshed. The total weight for each panicle was recorded and the kernel number per head was also obtained. A 250-seed sample was taken from each plant by using an electronic seed counter and the weight was recorded in grams.

The plant height was measured on an individual plant basis as the distance between the base of the stem and ligule of the flag leaf.

PROCEDURE OF ANALYSIS

The biometrical analyses were conducted with untransformed data. For validity of this analysis the scale should be such that the gene effect appears to be additive, no genotype-environment interaction; the variances should be independent of the means and the phenotypic values must follow a normal distribution.

A scaling test for additive gene action was made by using the formula proposed by Mather (1971); three quantities were calculated as follows:

$$A = 2\bar{B}_1 - \bar{P}_1 - \bar{F}_1;\ \bar{B} = 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1;\ \text{and}\ C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2.$$

When the gene effects are additive on the average, these quantities should not be significantly different from zero. If they deviate from zero then use of transformation to correct for non-additivity is suggested. Deviation of F_2 from F_1 was calculated by using the formula:

$$F_2 \text{ deviation} = F_2 - \frac{1}{2}[F_1 + \frac{1}{2}(P_1 + P_2)].$$

Significant F_2 deviations indicate the presence of epistatic effects.

The data obtained from each population was plotted in a frequency distribution table and represented graphically in histograms. Means and mean squares were calculated for each population. The mean squares for the non-segregating populations (P_1, P_2, F_1) were averaged to obtain an estimate of the environmental variance (σ_E^2) which in turn was subtracted from the variance of the segregating populations (F_2, B_1, B_2) to obtain an estimate of the genotypic variance (σ_g^2). The method outlined by Warner (1952) was used to estimate the heritability. This method involves the total F_2 variance and those of the summed backcrosses:

$$h^2 = \frac{2VF_2 - (VB_1 + VB_2)}{VF_2} = \frac{1/2(D)}{1/2(D) + 1/4(H) + E}$$

The minimum gene number involved in the expression of seed size, for this particular cross, was obtained by using the formula used by Burton (1951) and suggested by Sewall Wright:

$n = [0.25(0.75 - h+h^2)D^2]/ F_2^2 - F_1^2$ where $D = \overline{P}_2 - \overline{P}_1$, and $h = (\overline{F}_1 - \overline{P}_1)/D$

$\overline{P}_1$ = The mean of the smallest parent

$\overline{P}_2$ = The mean of the largest parent

$\overline{F}_1$ = The mean of the F_1 population

σF_2^2 = The variance of F_2 population

σF_1^2 = The variance of F_1 population

Also, a formula modified by Weber (1950) and cited by Brown (1973) was used in obtaining this estimate:

$$n = (P_2 - P_1)^2/8(VF_2 - \frac{VP_1 + VP_2 + VF_1}{3})$$ (This formula assumes no dominance effect)

In estimating the exact number of genes controlling seed weight the observed distribution of the F_2 data was fitted into the expected segregation ratio for partial dominance with 2 and 3 gene pairs. The expected values for partial dominance were calculated by interpolation between expected segregation ratios for complete and no dominance (additive). The significance of the deviation, between observed and expected, was tested by using a chi-square test; with 4 degree of freedom at 1 and 5% of probability. The average degree of dominance was estimated by utilizing Mather's formula (1971): $\frac{\sqrt{H}}{D}$

The nature of gene action in governing seed size was determined by using the method constructed by Hayman (1958) and modified by Gamble (1962a, 1962b). The equations giving the estimates of the gene effects

in terms of the generation means are:

$m = \overline{F}_2$

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

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

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

$ad = -1/2\ \overline{P}_1 + 1/2\ \overline{P}_2 + \overline{B}_1 - \overline{B}_2$

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

Where a and d are additive and dominance gene effects, aa, ad and dd are additive by additive, additive by dominance, and dominance by dominance types of epistatic gene effects. The significance of the various gene effects for this model were computed by calculating standard error from the variance of the corresponding population means.

A comparison of the observed and calculated F_1 means reveals the nature and degree of dominance expressed in the inheritance of this trait. The extent of agreement between observed and calculated F_2 means furnishes an indication of the nature of gene action.

The theoretical means presented in Table 2 were calculated using the following formulas:

$$\text{Theoretical arithmetic } F_1 = \frac{\overline{P}_1 + \overline{P}_2}{2}$$

$$\text{Theoretical arithmetic } \overline{F}_2 = \frac{\overline{P}_1 + 2\overline{F}_1 + \overline{P}_2}{4}$$

$$\text{Theoretical arithmetic } \overline{B}_1 = \frac{\overline{F}_1 + \overline{P}_1}{2}$$

$$\text{Theoretical arithmetic } \overline{B}_2 = \frac{\overline{F}_1 + \overline{P}_2}{2}$$

$$\text{Theoretical geometric } \overline{F}_1 = \text{Antilog of } \frac{\log \overline{P}_1 + \log \overline{P}_2}{4}$$

$$\text{Theoretical geometric } \overline{F}_2 = \text{Antilog of } \frac{\log \overline{P}_1 + 2\log \overline{F}_1 + \log \overline{P}_2}{4}$$

$$\text{Theoretical geometric } \overline{B}_1 = \text{Antilog of } \frac{\log \overline{F}_1 + \log \overline{P}_1}{2}$$

$$\text{Theoretical geometric } \overline{B}_2 = \text{Antilog of } \frac{\log \overline{F}_1 + \log \overline{P}_2}{2}$$

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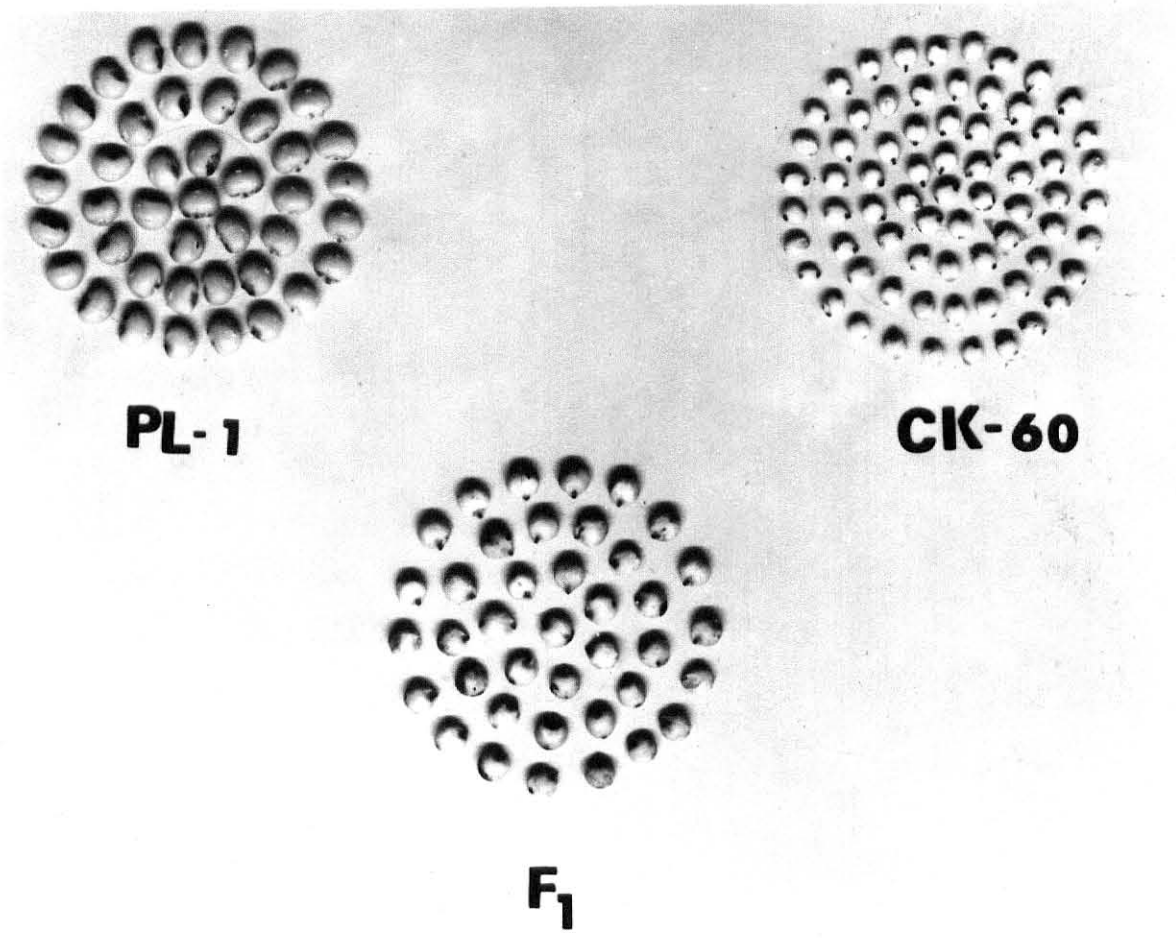

Fig. 1. Comparison of seed size of two parental lines (PL-1, CK-60) and their F_1 progeny.

RESULTS AND DISCUSSION

The observed and expected frequency distribution for the parental varieties and their F_1 and F_2 derivatives are presented in Table 2. Tests of goodness of fit indicated that P_1, P_2 and B_2 populations followed the normal distribution, while B_1, F_2 and F_3 populations deviated significantly from normality.

The observed distributions for each of the seven populations were also depicted in histograms (Fig. 2 and Fig. 3). Kernel weights of the parental varieties occupy two extremes in the scale of measurement. The F_1 showed a tendency toward the parent with heavier kernel weight indicating partial dominance may govern the inheritance of kernel weight. Although the observed frequency distribution for the F_2 population did not fit well in the test of normality, it appeared quite smooth and unimodal with a slightly skewness toward the large-seeded parent. The unimodal distribution suggests that a multiple-factor inheritance could be involved for kernel weight. Likewise, the F_3 distribution was smooth, less spread and showed little skewness.

Population means in Table 2 demonstrated that F_1 mean deviated significantly from the mid-parent value, indicating heterosis and that a considerable amount of nonadditive gene action was involved in the expression of this character. The F_2 mean did not agree with either the arithmetic or with the geometric means. Likewise, the F_2 mean deviated significantly from F_1 mean in the negative direction (Table 4), suggesting the presence of epistasis. Furthermore, in the scaling test, as shown in Table 4, the quantities A, B and C differed significantly from 0, which

Table 1. Observed and expected frequency distribution for kernel weight (g/1,000) of two parental lines, F_1, F_2, F_3, first (B_1) and second backcross (B_2).

Population	Number Observed and Expected*/Class - Class mid-point, Original Data																		n	$\bar{x}$	S_D	C.V. (%)	Probability (x^2)
	16	19	22	25	28	31	34	37	40	43	45	48	51	54	57	60	63	66					
P_1(PL-1)																							
Exp.												1	2	6	9	10	8	4	40	59.2	4.3	7.3	.5-.75
Obs.												3	2	2	9	9	10	5					
F_1(PL-1xCK60)																							
Exp.										2	6	5							13	46.2	2.3	5.0	1/
Obs.										2	4	7											
F_2																							
Exp.	2	4	9	18	31	47	59	65	64	53	38	24	13	7	3				437	37.4	7.6	20.2	.01
Obs.	4	8	12	13	14	39	50	56	62	78	48	33	14	5	1								
F_3																							
Exp.		4	10	21	37	50	55	48	33	18	8	3	1						288	33.5	6.0	17.9	.01
Obs.		6	17	21	33	46	32	52	39	27	9	4	2										
B_1(F_1xPL-1)																							
Exp.				2	4	6	8	10	8	7	5	4	2	1	0	0			57	37.8	7.3	19.3	.01
Obs.				2	3	8	7	4	5	4	6	4	5	4	4	1							
B_2(F_1xCK60)																							
Exp.	1	3	8	15	23	26	25	18	10	4	1	0							134	31.3	5.7	18.1	.05-.1
Obs.	1	2	11	23	20	19	22	14	14	6	1	1											
P_2(CK60)																							
Exp.	0	2	10	19	14	5													50	25.7	2.9	11.5	.1-.25
Obs.	3	1	8	19	18	1																	

*Expected values based on normal distribution, using calculated means and variances for each population.
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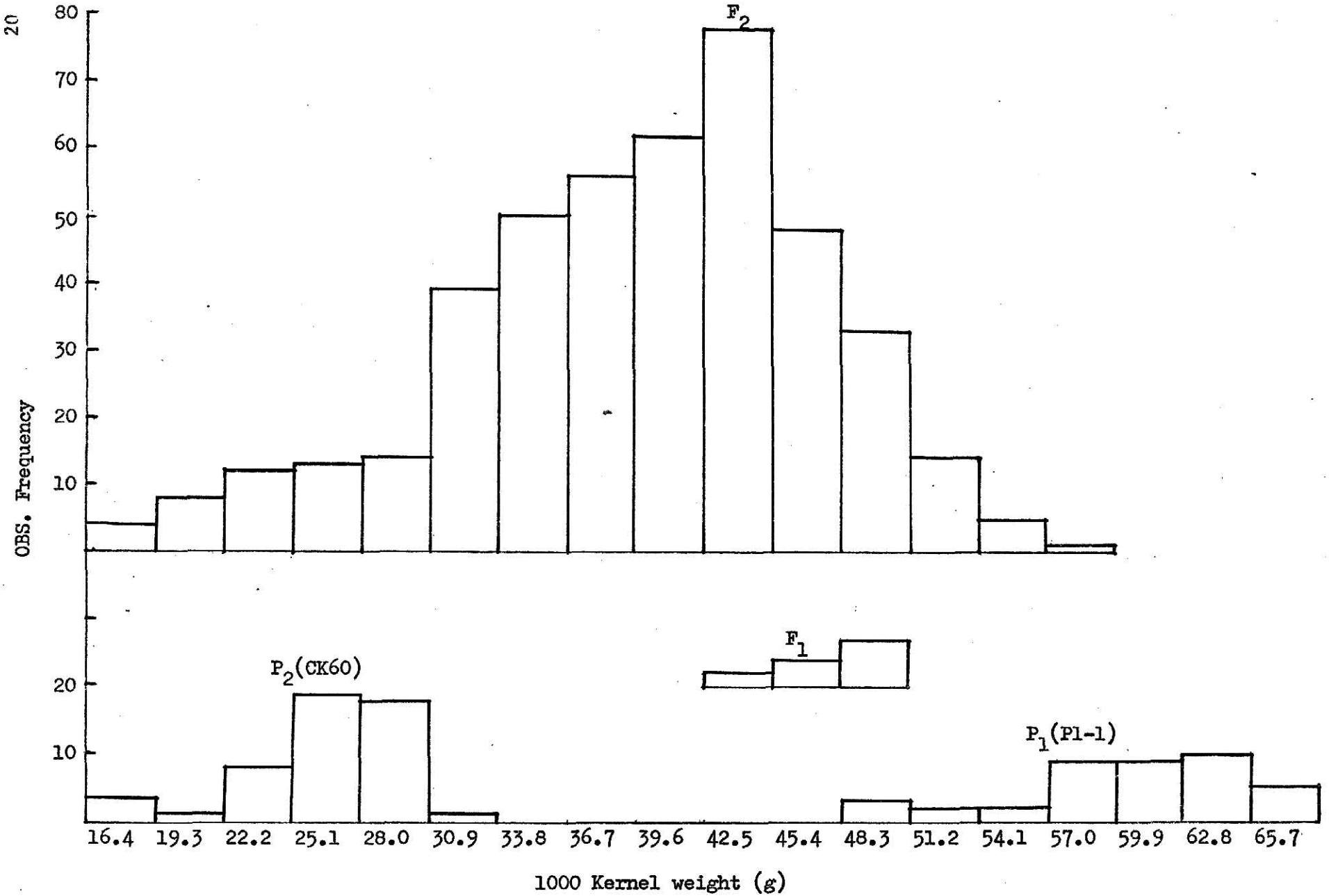

Fig. 2. Frequency distribution for kernel weight of two parental lines (P_1, P_2), their F_1 and F_2 derivatives.

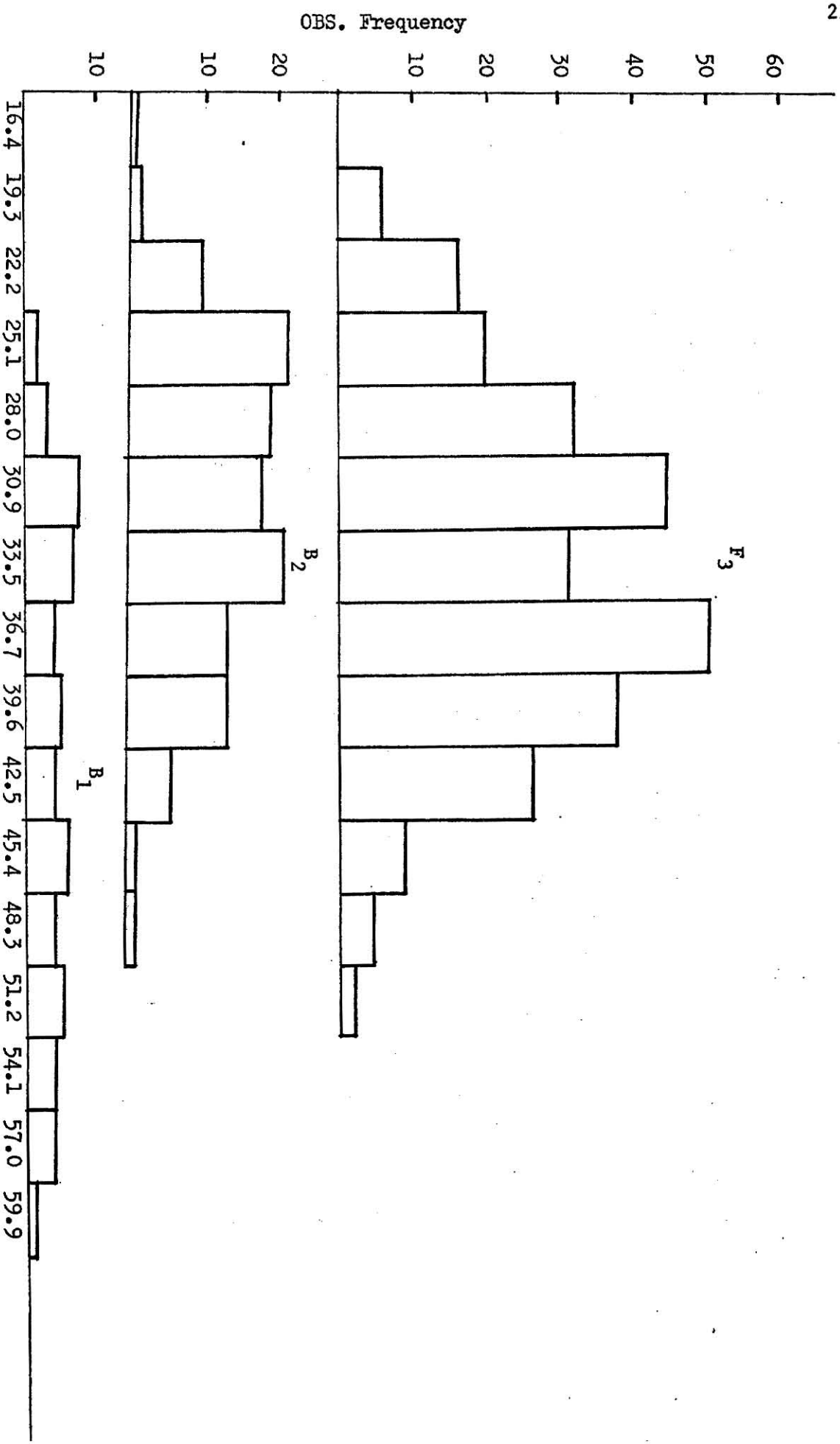

Fig. 3. Frequency distribution for kernel weight of first (B_1), second (B_2) backcross and F_3 population.

Table 2. Observed means, theoretical means (arithmetic and geometric), phenotypic variances, and estimated environmental and genetic variances for kernel weight of seven sorghum populations.

Populations	Obs. mean (g/1,000)	Theo. mean		Variance		
		Arith.	Geom.	Phenotypic	Environ.[1]	Genotypic
P_1 (PL-1)	59.2 ± 0.69			18.9		
P_2 (CK60)	25.7 ± 0.41			8.84	12.3	
F_1	46.2 ± 0.64	41.9	38.7	5.34		
F_2	37.4 ± 0.36	44.1	42.3	57.05		44.7
B_1 (F_1xPL-1)	37.8 ± 0.97	52.2	51.9	53.4		41.1
B_2 (F_1xCK60)	31.3 ± 0.49	35.9	34.5	32.1		19.8
F_3	33.5 ± 0.35			35.7		

[1] Environmental variance = $\frac{(n_1 - 1)V_{P1} + (n_2 - 1)V_{P2} + (n_3 - 1)V_{F1}}{(n_1 - 1)+(n_2 - 1)+(n_3 - 1)}$

Table 3. Estimates of heritability and minimum number of genetic factors involved in the inheritance of kernel weight, and expected genetic progress through selections.

Cross	Heritability	Number of genetic factors	Expected genetic progress[3/]
PL-1 x	h^2 = 50%	n = 2-3[1/]	G_s = 20.8%
Combine Kafir-60		n = 3[2/]	

[1/] Calculated by utilizing Wright's formula

[2/] Weber's formula (1950)

[3/] $G_s = i \cdot \sigma_p \cdot h^2$

Table 4. Scaling test, F_2 deviation, estimates of gene effects, and average degree of dominance for kernel weight in the cross of PL-1 x Combine Kafir-60.

Scaling Test			F_2 deviation	Gene effects						Avg. degree of dominance
A	B	C		m	a	d	aa	ad	dd	
-29.2**	-9.3**	-27.7**	-6.9**	37.4	6.5	-7.8	-11.5	-10.3**	50.5**	0.78

* significant at 5% probability level

** significant at 1% probability level

corroborated the nonadditive gene action. Population means of the backcrosses showed respective relations with the recurrent parental means.

Estimated phenotypic, genotypic, and environmental variances for each population are shown in Table 2. The variances were used to estimate the heritability for kernel weight is shown in Table 3. The heritability, being 50%, was moderately high in magnitude and might have resulted, in part, from the large differences in kernel weights between the two parental varieties. Since the concept of heritability is associated with the relative influences of heredity and environment on variations in a character, heritability of 50% estimated on individual plant basis indicates that improvement of seed weight by selection should be possible. Expected genetic advance under selection is shown in Table 3 and we note a considerable progress is expected. However, we must be cautious in inferring the results to other crosses because both PL-1 and Combine Kafir 60 are highly selected varieties; these varieties and their immediate derivatives should be considered as the population from which the inference was drawn.

The magnitude of heritability estimated in this experiment is in agreement with other reports (Beil and Atkins, 1967; Chung and Liang, 1970; Voight et al., 1966). Voight et al. (1966) also reported that a significant progress could be achieved in shifting the mean seed size by selecting large-seeded F_2 plants. Conversely, Beil and Atkins (1967) and Chiang and Smith (1967) concluded that increasing of seed weight is expected to be small through selection. Using the formulas used by Burton (1966), and that cited by Brown (1973) the number of gene pairs

controlling seed weight was estimated to be 2-3 as a minimum number in this particular cross. However, an exact estimate of the effective number of genes could not be obtained by fitting the observed distribution of the F_2 data into the expected segregation ratio for partial dominance. Mainly, due to bias introduced in the expected values which were obtained by interpolation between complete and no dominance, two alternatives of known segregation ratios.

Similarly, Voight et al. (1966) reported that a minimum of 3-4 genes appears to be involved in the inheritance of seed size. From all the data available, it seems that relatively few gene pairs govern the seed weight, although genes showing little or no dominance are not detected.

Six genetic parameters indicating gene actions were estimated by Gamble's (1962) mean approach and the results are presented in Table 4. Dominance x dominance and additive x dominance types of epistasis were the only significant parameters among the six estimated, revealing that epistatic gene effects are important in the basic genetic mechanism of kernel weight inheritance in this particular cross.

The digenic d x d epistasis would be expected if both parents contain the same dominant genes, that is, some genes for greater seed weight are dominant in both parents as are others for less seed weight. Additive x dominance gene effect was also of considerable magnitude, but negative. This indicates that a diminishing effect due to this type of gene action could occur. The magnitude of a, additive gene effect, despite it being positive, was not significant and appears to have a minor contribution to the inheritance of kernel weight. Likewise, dominance gene effect was

also not significant.

Although Voight et al. (1966) reported that genetic variability for kernel weight was almost entirely due to additive gene action, Liang and Walter (1968) indicated a minor contribution of the additive gene effect to the inheritance of kernel weight while dominance, additive x additive and dominance x dominance were more important than additive gene action for kernel weight. Mukuru (1973) found a positive and significant estimate of additive and dominance gene effect for kernel weight for all the populations studied. Likewise, Nayakar (1973) demonstrated that dominance gene effect was the important gene action in the inheritance of kernel weight along with additive x additive and dominance x dominance types of gene effects.

Estimates of genetic parameters by the mean approach tend to have a large standard error and not directly comparable to the estimates obtained by variance methods. Nevertheless the estimates of genetic parameters obtained by Gamble's approach may provide information where other methods do not. For example, Warner's method requires the assumption that absence of epistasis, which does not seem to be realistic. The significance of dominance x dominance and additive x dominance types of epistasis, if true, suggests that the magnitude of heritability estimated by Warner's approach was inflated by the presence of epistasis. Furthermore, presence of epistasis implies that we should emphasize family selection in our breeding programs aimed at the improvement of seed weight.

Differences in results by various workers could be attributed to the methods as well as the materials used. Nonadditive gene effects appear to be more important than that of additive if the parental varieties have an intensive selection history. To be cautious, each cross and its

descendants should be viewed as a separate population and the information obtained from each population should refer to itself only.

Phenotypic correlation coefficients shown in Table 5 demonstrated that kernel number appears to be more important than kernel weight in contributing to the total grain yield because it has a positive and significant correlation with grain yield. Kernel number, however, had negative correlation and in some instances significant with kernel weight in all generations except the F_2 population where the plants were segregating.

The negative correlation between kernel number and kernel weight has been reported by Adams (1967) in many crops and viewed as a compensation between yield components. The negative relationship between yield components such as kernel number and kernel weight are believed to be developmentally induced, especially under stress conditions in which the two developing components compete for common and limited nutrient and water supply. In other words, yield results as an integration of its components which are, in turn, interdependent to a certain degree. Plasticity among yield components, in which variation in one component tends to be compensate for variations in others, has an adaptive value to plants because it facilitates the possibility of maintaining the yield in an adequate level.

The level of heterozygosity of the genetic material may also affect the direction and intensity of the correlations between yield components. In non-segregating populations, the correlations between kernel weight and kernel number was negative, but positive and significant in F_2. The correlations for individual classes in F_2 were also positive and

Table 5. Phenotypic correlations between kernel weight, kernel number, and grain yield of two parental varieties and their F_1, F_2, and F_3 derivatives. Also the correlations of these traits with plant height in F_2 population.

Populations	Character	Character		
		Kernel number	Grain yield	Plant height
PL-1	Kernel weight	-.35	.23	----
	Grain yield	.83**		----
Combine Kafir-60	Kernel weight	.51*	-.21	----
	Grain yield	.71**		----
F_1	Kernel weight	-.26	.04	----
	Grain yield	.95**		----
F_2	Kernel weight	.36**	.71**	.63**
	Grain yield	.84**		.46**
	Kernel number			0.25
F_3	Kernel weight	-.34**	.11	
	Grain yield	.88**		

* significant at 5% probability level
** significant at 1% probability level

Table 5a. Phenotypic correlations between kernel weight, kernel number, and grain yield in five F_2 classes.

Class No., g/1,000 Interval	Character	Character		
		Kernel Number	Grain Yield	Plant Height
1(18-25.7)	Kernel weight	0.65*	0.72**	0.35
n=10 obs.	Grain yield	0.94**		
	Plant height	0.04	0.06	
2(25.8-33.5)	Kernel weight	0.35	0.46	0.36
n=19 obs.	Grain yield	0.88**		
	Plant height	0.40	0.53*	
3(33.6-41.3)	Kernel weight	0.40*	0.43**	0.36*
n=40 obs.	Grain yield	0.98**		
	Plant height	0.12	0.11	
4(41.4-49.1)	Kernel weight	0.44**	0.48**	0.57**
n=39 obs.	Grain yield	0.99**		
	Plant height	0.46**	0.50**	
5(49.2-56.9)	Kernel weight	0.88*	0.87**	0.93**
n=7 obs.	Grain yield	0.99**		
	Plant height	0.82**	0.78**	

* significant at 5% probability level
** significant at 1% probability level

significant, indicating that the correlation obtained, considering the F_2 as a whole, represented a pool of all of these individual correlation values.

Plant height showed positive and highly significant correlation with kernel weight, kernel number and grain yield. If such relationship holds true, it may be difficult to select for short plants without sacrificing kernel weight, kernel number and consequently, grain yield.

An understanding of character association, particularly association between yield components, are helpful in a breeding program. One of the objectives in this experiment is to select the 3-dwarf types (either Dw_2 or Dw_3) with large kernel weight and high kernel number from the recombinants among the offspring. However, F_3 data suggested that a simultaneous improvement of kernel weight and kernel number is not possible because of the mutual competition of these two characters for common metabolites.

Table 6. Kernel weight (g/1,000), kernel number per panicle, grain yield (g/plant), and plant height (cm) of the parental lines, their F_1, F_2, and F_3 derivatives.

Population	Kernel Weight (g/1,000)	Kernel Number per panicle	Grain Yield (g/plant)	Plant Height (cm)
PL-1	59.2	789	45.6	68.5
Combine Kafir-60	25.7	2,653	68.2	52.4
F_1	46.2	2,241	103.2	121.4
F_2	37.4	1,273	49.2	82.6
F_3 - 1 (F_2-1 plant)	39.6	1,164	45.7	67.1
F_3-1	32.8	1,224	39.6	26.1
F_3-2 (F_2- 2 plant)	32.5	1,787	58.7	28.7
F_3-3(F_2-3 plant)	28.3	1,331	34.3	26.1
F_3-3	35.2	1,027	40.3	77.0
F_3-5 (F_2-5 plant)	27.1	1,456	36.4	23.1
F_3-6 (F_2-6 plant)	35.8	866	31.7	40.9
F_3-6	33.1	1,417	46.5	26.9
F_3-7 (F_2-7 plant)	26.8	1,715	44.6	51.2
F_3-8 (F_2-8 plant)	30.4	1,483	44.5	51.9

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Inheritance of Germination Rate in a Sorghum [Sorghum bicolor (L.) Moench] Cross

SUMMARY

Inheritance of germination rate was studied in the F_1, backcrosses and F_2 derivatives from the cross of two grain sorghum [Sorghum bicolor (L.) Moench] varieties, 'Combine Kafir-60' and 'PL-1', which differed in this characteristic.

Heritability for germination rate, calculated on the basis of original data, was of moderate magnitude (44.8%), suggesting that a larger proportion of the variation observed in their trait was environmental in origin. Estimate of genetic advance indicated that selection for this trait would be ineffective.

The minimum number of genes controlling germination rate was estimated to be 1. The marked increase in the germination rate of F_1 over the parental values indicated the presence of heterosis. This suggests over dominance in the action of genes is responsible for the expression of this trait.

Germination rate did not show any significant correlation with seed weight.

INHERITANCE OF GERMINATION RATE IN A SORGHUM [*Sorghum bicolor* (L.) Moench] CROSS

INTRODUCTION

Good stand in grain sorghum is of considerable importance because of its direct influence on the yield. The general ability of sorghum seed to germinate well and the ability to produce a faster growing seedling would not only allow early planting and better weed control, but should on the average make an early harvest possible.

It has frequently been observed that seed lots of sorghum with equal laboratory germination, when grown in field conditions may give greatly different stands, especially under adverse environmental conditions. Recognized factors that can contribute to the failure of sorghum seed to germinate or emerge are usually encountered within a few months after harvest.

The experience of some sorghum breeders is that large seeds of some lines tend to germinate less as compared with cultivars with normal seed size. To increase yield, it may be desirable to transfer the gene(s) controlling large seeds to locally adapted cultivars without inducing any adverse response in other traits.

The main objective in this study is to determine whether germination rate in grain sorghum is controlled by genetic factors and to find out to what degree selection can be effective in improving this characteristic.

Almost nothing has been reported on the inheritance of germination rate in grain sorghum. There is a belief among some breeders that most of

the variation observed in this character must be environmental in origin. On the other hand, some workers have postulated that the inheritance of germination rate should be simple, with very few genes governing its expression. Some of the factors that have been reported to affect seed germination, seedling emergence and seedling stand are temperature, soil type, depth of seeding, seed maturity, moisture content and seed injury.

Robbins and Porter (1946) reported that sorghum seeds were able to germinate at 50 and 60 percent of moisture content. On the other hand, mature sorghum seeds with moisture content of 15% or less, were unaffected in viability by exposure to temperature between 33°C and -20°C. Desay (1958) studied some of the factors influencing germination in nine strains of sudan grass; he found the germinability was high in seeds harvested at complete maturity, the earliest emergence of seedlings was observed at higher temperature, and there was a significant variation among strains of sudan grass in germination and seedling emergence. Pinthus and Rosenblum (1961) determined that the minimum temperature required for germination of sorghum seeds was between 8°C and 10°C. The hybrid 'RS610' was superior to the varieties 'D.D. Yellow Sooner' and 'Martin' in germination and seedling emergence at low temperature.

In trying to find out the effect of freezing on seed viability in grain sorghum, Rosenow et al. (1962) found the germination of seed having high moisture content to be considerably affected by lower freezing temperatures. Seeds from Atlas and RS610 were more tolerant than Plaisman seed to freezing. Similarly, Gritton and Atkins (1963) reported a greater tolerance to freezing treatment for 'Combine Kafir-60' than other entries.

Evans and Stickler (1961) indicated that germination of 'Midland', 'KS602', 'RS608', and 'RS610' decreased as moisture tension increased. Phillips and Youngman (1971) observed that seeds sown with 8% moisture content emerged less than seeds with 11 or 14% moisture. They concluded that low initial seed moisture content combined with low soil temperature affected greatly the emergence in grain sorghum and also grain yield, especially under dry land conditions.

Mayer and Mayber (1963), in corn, obtained no differences in germination due to seed size, regardless of hybrid, planting depth and temperature.

In grain sorghum, Suh et al. (1974) observed no significant differences in 14 agronomic characteristics between the resulting crops from two seed weights.

It has been observed in seed samples, freshly harvested and dried, fails to germinate satisfactorily unless a special treatment is given. The problem has been related to dormancy which varies among strains grown in the same area and harvested at the same time. Dormant seeds were observed by Goodsell (1957) in samples from Combine Kafir-60 which germinated only 5 to 10%, even though a test with tetrazolium indicated that the seeds were 100% viable. The dormancy was attributed to the presence of some inhibitory agent present in the seed coat. Clark et al. (1967, 1968) have studied the dormancy in grain sorghum. They postulated mechanisms acting in dormancy. There was no difference in germination response of seeds of 'Combine Kafir-60' and 'Feterita' when germinated immediately after harvest, without drying. However, Feterita germinated

100% when the seeds were dried to approximately 12% moisture. Results of germination test of seeds, from Combine Kafir-60, 'Combine Shullu' and their F_1 cross, suggested that pericarp and testa were involved in dormancy.

Several workers have tried to study to what extent heredity may affect the differences in germination. Pinnell (1949), in corn, concluded that, on the average, double cross germinated best followed by single crosses and inbred lines. Also, wide differences between inbred lines were found and these differences appeared to be heritable in some crosses. He postulated the inheritance of germination seemed rather complex. The maternal effect was of great importance in determining seedling stand in both single and double crosses and probably the nature of the endosperm could be involved in the portion of the inheritance directly related to the maternal effect.

Shrivastava and Pinnell (1963) estimated the heritability for germination percentage by utilizing parental, F_1 and F_3 generations of four crosses. A very low value of heritability was obtained for the field experiment, from 22 to 40% in three of the crosses, and for the cross Combine Kafir-60 x Plainsman a negative value resulted. These results indicated that germination is greatly influenced by the environment.

Liang and Walter (1968) and Liang et al. (1969) determined the heritability for germination in two different studies. In the first, they applied the formula suggested by Warner (1952) to the crosses 'Redlan x Martin', 'Redland x Combine 7078', and 'Plainsman x KS7'. The heritability values obtained were 80, 67 and 52%, respectively. The dominance effect and additive x dominance gene effects appeared to be very important for germination. In the second study, they utilized F_3 and F_4 lines derived

from two crosses, 'Redland x Martin' and 'Combine Kafir-60 x KS7'. The heritability was determined by parent-offspring regression, parent-offspring correlation and variance components. The estimated values for one population were 34, 77 and 75% and 34, 56 and 48% for the other. A negative correlation between germination with yield and protein was found in both populations. Likewise, Tovar and Liang (1975) found a negative correlation between germination and protein content; r = -0.082 and -0.073, in the original and arcsine transformed data for 40 single cross hybrids.

Maunder (1965) in a program of transferring red seed color to white kafir-hegari derivatives, observed a positive effect of seed color in improving germination in an otherwise weak line.

MATERIALS AND METHODS

Two grain sorghum varieties, chosen on the basis of their contrasting germination, were used as parents in this study. One of the parental lines, 'PL-1', is a three dwarf ($dw_1dw_2Dw_3dw_4$) grain sorghum cultivar with large seeds and an average germination of 60%, but ranging from 55 to 70%. The other parents, 'Combine Kafir-60', is also a three dwarf ($dw_1Dw_2dw_3dw_4$) grain sorghum cultivar with relative small seeds and an average germination of 85%.

Crosses between the two varieties were made in greenhouse during 1974-75 season, and the F_1 was backcrossed to each of the parent (P_1 and P_2) to produce the first and second backcross generation: $B_1(P_1 \times F_1)$ and $B_2(P_2 \times F_1)$. Seeds produced by self-pollination of the F_1 plants were composited to provide the F_2 material. Parents, F_1, F_2, B_1 and B_2 populations were planted at Ashland (Riley county) Experimental Station during the summer of 1975. Each cross was considered as a unit in the planting scheme and randomized in two bloacks in rows of 6 meter long and spaced 76 cm apart. The main head of plant in full competition was harvested and threshed.

Samples of fifty seeds, from each plant in each population, were taken and treated with fungicide (Spergon) before planting. The seeds were planted in flats containing sand, at 2 cm depth in the greenhouse condition in December 1975. Ten flats were utilized in each trial and repeated for 8 times. Data were taken on individual plant basis; 40

plants were included for each parent and their F_1; 116 plants for the F_2 and 83 and 96 plants for the first and second backcross, respectively.

The total number of seedlings emerged was recorded for a 7 day period. The germination percentage and its arcsine transformation were obtained from each population.

PROCEDURE OF ANALYSIS

The biometrical analysis were conducted with untransformed data assuming that the scale should be such that the gene effect appear to be additive, absence of genotype-environment interaction, independence of variances and means and that the phenotypic values must be normally distributed.

The data obtained from each population was plotted in a frequency distribution table and represented graphically in histogram.

The means and variances were calculated for each population. The environmental variance (σE^2) was obtained by averaging the mean square values of non-segregating populations (P_1, P_2 and F_1). Then, it was subtracted from the variance of segregating populations (F_2, B_1 and B_2) to obtain an estimate of the genotypic variance (σg^2).

A formula suggested by Warner (1952) was utilized to estimate the heritability for germination rate. Only, the variance of the F_2 and those of the backcross were included to determine this value.

$$h^2 = \frac{2VF_2 - (V_{B1} + V_{B2})}{VF_2} = \frac{1/2D}{1/2D + 1/4H + E}$$

However, the method required to make the assumptions that non-heritable component of the variance of the F_2, and the backcrosses are of comparable magnitude and that epistasis is negligible.

The estimate of the minimum gene number governing the germination percentage was obtained by utilizing the formula utilized by Burton (1950)

and proposed by Sewall Wright (1921):

$$n = \frac{[0.25(0.75 - h + h^2)\ D^2]}{\sigma F_2^2 - \sigma F_1^2}; \text{ where } D = \overline{P}_2 - \overline{P}_1$$

and

$$h = \frac{\overline{F}_1 - \overline{P}_1}{D} \quad .$$

$\overline{P}_1$ = The mean of the smallest parent.

$\overline{P}_2$ = The mean of the largest parent.

$\overline{F}_1$ = The mean of F_1 generation.

σF_2^2 = Variance of F_2 generation.

σF_1^2 = Variance of F_1 generation.

An estimate of the degree of dominance was determined by using the formula utilized by Beil and Atkins (1967) and proposed by Griffing (1950).

$$hp = \frac{(\overline{F}_1 - \overline{MP})}{(\overline{P} - \overline{MP})} \text{ where;}$$

hp = dominance value

$\overline{F}_1$ = observed mean of the F_1

$\overline{MP}$ = mid-parent value

$\overline{P}$ = Mean of the greatest parent

Deviation of F_2 from F_1 was calculated using the formula:

$$F_2 \text{ deviation} = \overline{F}_2 - 1/2[\overline{F}_1 + 1/2(\overline{P}_1 + \overline{P}_2)] \quad .$$

Heterosis for this cross was calculated as the percentage increase of F_1 performance above the mean parental performance. The expectation

of heterosis is:

Heterosis = $F_1 - 1/2(P_1 + P_2)$; this estimate assumes that linkage is absent. Also, heterosis was estimated as the percentage increase of F_1 performance above the better parent performance.

A comparison of observed and calculated means for F_1 and F_2 furnishes information about degree of dominance and nature of gene action in the inheritance of a trait.

The theoretical means were calculated, using the following formulas:

Theoretical arithmetic $\quad \overline{F}_1 = \dfrac{\overline{P}_1 + \overline{P}_2}{2}$

Theoretical arithmetic $\quad \overline{F}_2 = \dfrac{\overline{P}_1 + 2\overline{F}_1 + \overline{P}_2}{4}$

Theoretical geometric $\quad \overline{F}_1 = \text{antilog of } \dfrac{\log \overline{P}_1 + \log \overline{P}_2}{2}$

Theoretical geometric $\quad \overline{F}_2 = \text{antilog of } \dfrac{\log \overline{P}_1 + 2\log \overline{F}_1 + \log \overline{P}_2}{4}$

RESULTS AND DISCUSSION

The observed and expected values as well as the observed frequency distribution for the parental lines and derivatives are given in Table 1 and represented graphically in Fig. 1, 2 and 3. The goodness of fit to normality was tested, using chi-square test. The calculated chi-square values indicate a good agreement to normality for P_1, F_1, B_1 and B_2, but F_2 and P_2 do not fit so well into a normal distribution.

The parental lines chosen for this study did not exhibit greater contrast in germination as shown by the overlapping of some of the frequency classes in the observed distribution (Fig. 1).

The average germination for F_1 was higher than the better and the mid-parent. The mean germination rate for F_2 was 10% less than that of F_1, with its distribution displaying toward positive direction, i.e., towards the parent with high germination.

Transgressive segregation for high as well as low germination rate was also observed in the F_2, revealing the just few genes should be involved in the inheritance of germination rate in this particular cross. However, only the second backcross (B_2) displayed some degree of association with the recurrent parent, since its average germination rate did not deviate significantly from the averages of the F_1 and recurrent line.

A comparison of the observed and calculated F_1 means reveals the nature and degree of dominance present in the inheritance of a trait.

Table 1. Observed and expected frequency distribution for germination rate (%) of parents, their F_1, F_2, first (B_1) and second backcross (B_2).

Population	Number observed and expected values* in each class Class Mid-Point, Original Data															n	$\bar{x}$	S_D	C.V. (%)	Probl. of chi-square
	28	33	38	43	48	53	58	63	68	73	78	83	88	93	98					
P_1(PL-1)																				
Exp.					1	1	3	4	6	7	7	5	4	2		40	74.2	11.1	15.0	0.5-0.75
Obs.					1	1	4	2	4	6	9	7	4	1						
F_1(PL-1 x CK60)																				
Exp.												2	4	5	3	19	91.9	5.6	6.1	0.25-0.1
Obs.												1	7	5	6					
F_2																				
Exp.							2	5	9	16	21	22	19	13	7	114	82.0	10.3	12.6	0.01-0.025
Obs.							1	2	6	8	26	21	33	12	5					
B_1(F_1 x PL-1)																				
Exp.								2	4	9	11	13	12	8	4	63	82.9	9.7	11.7	0.25-0.50
Obs.								5	2	7	8	12	17	7	5					
B_2(F_1 x CK60)																				
Exp.									1	4	9	16	19	17	10	76	88.1	8.3	9.4	0.05-0.1
Obs.									5	2	5	14	13	24	13					
P_2(CK60)																				
Exp.										1	4	8	19	6	2	40	86.8	6.6	7.6	0.01
Obs.										1	6	6	13	10	4					

*Expected values based on normal distribution using calculated means and variances of each population.

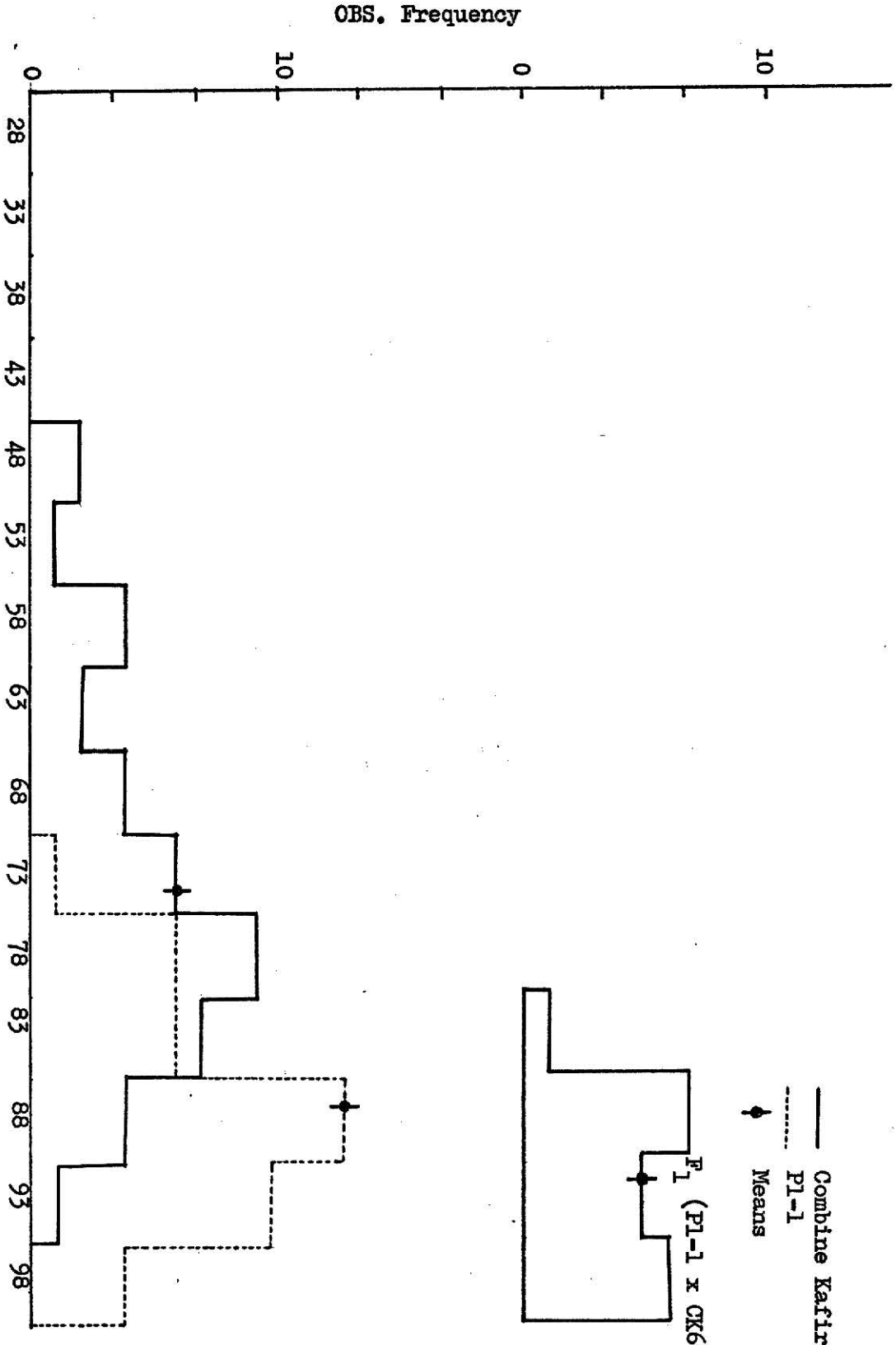

Fig. 1. Frequency distribution for germination rate (%) of two parents and F_1 cross.

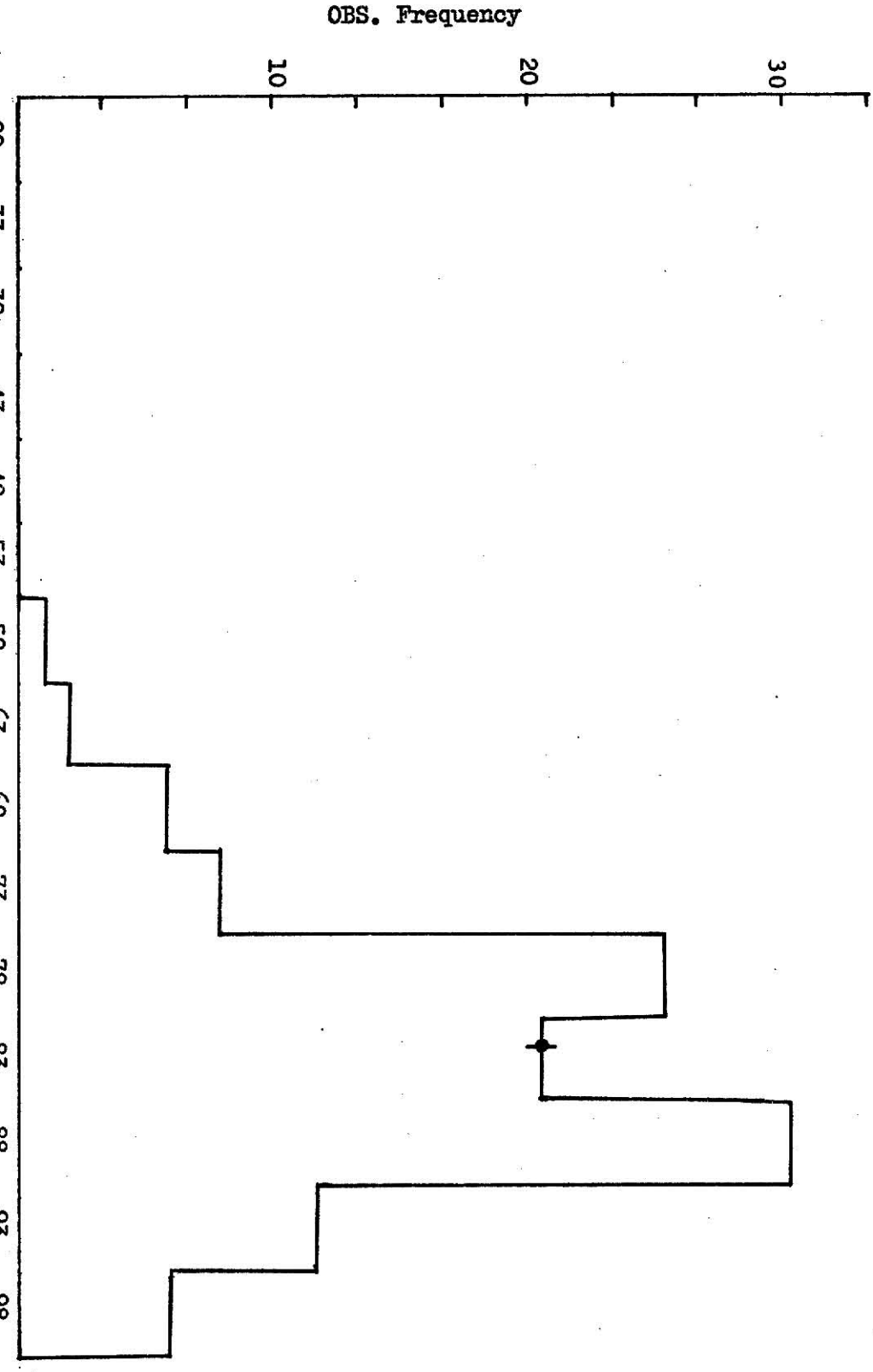

Fig. 2. Frequency distribution of germination rate (%) for F_2 generation.

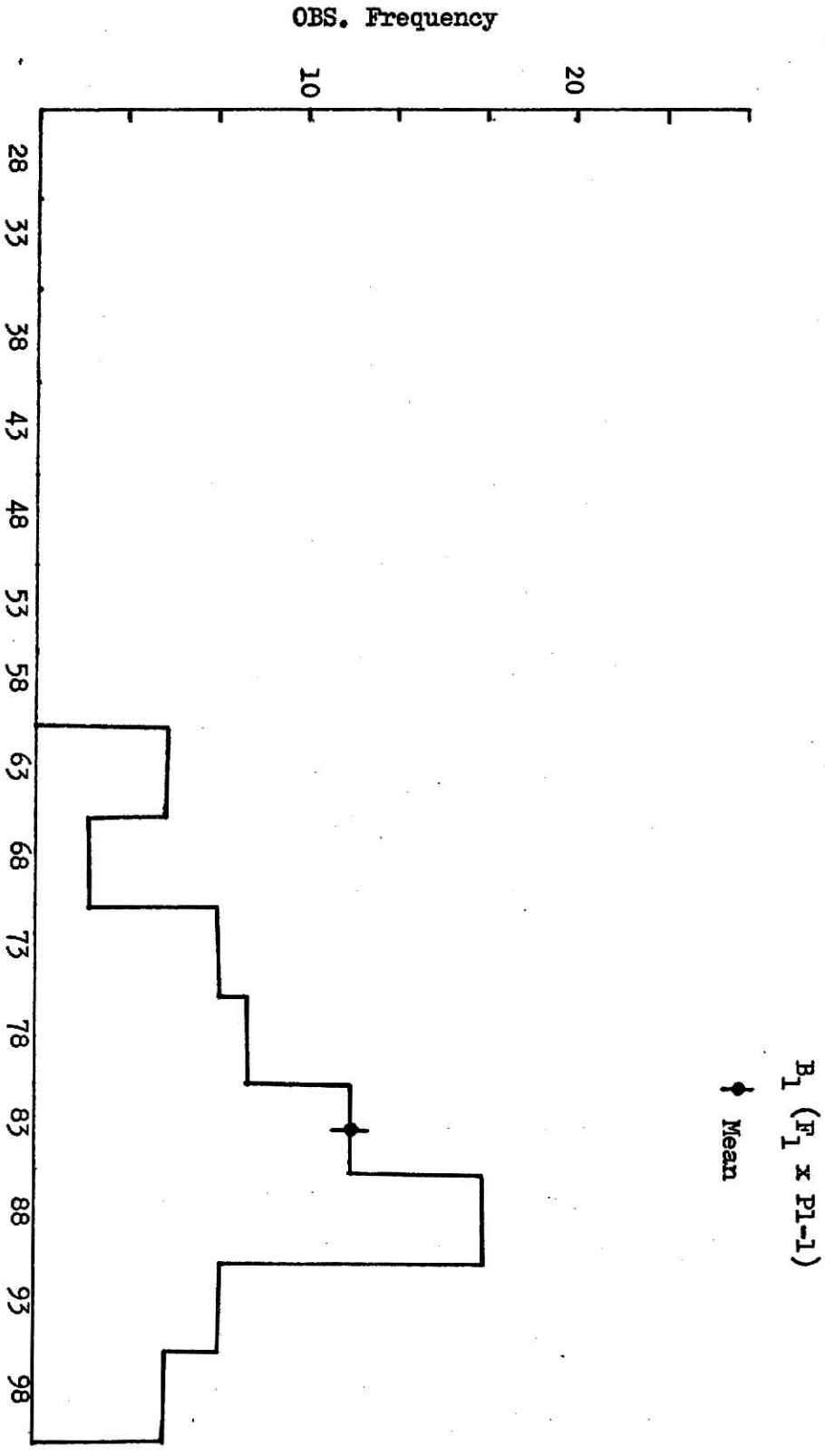

Fig. 3. Frequency distribution for germination rate (%) of first backcross (B_1).

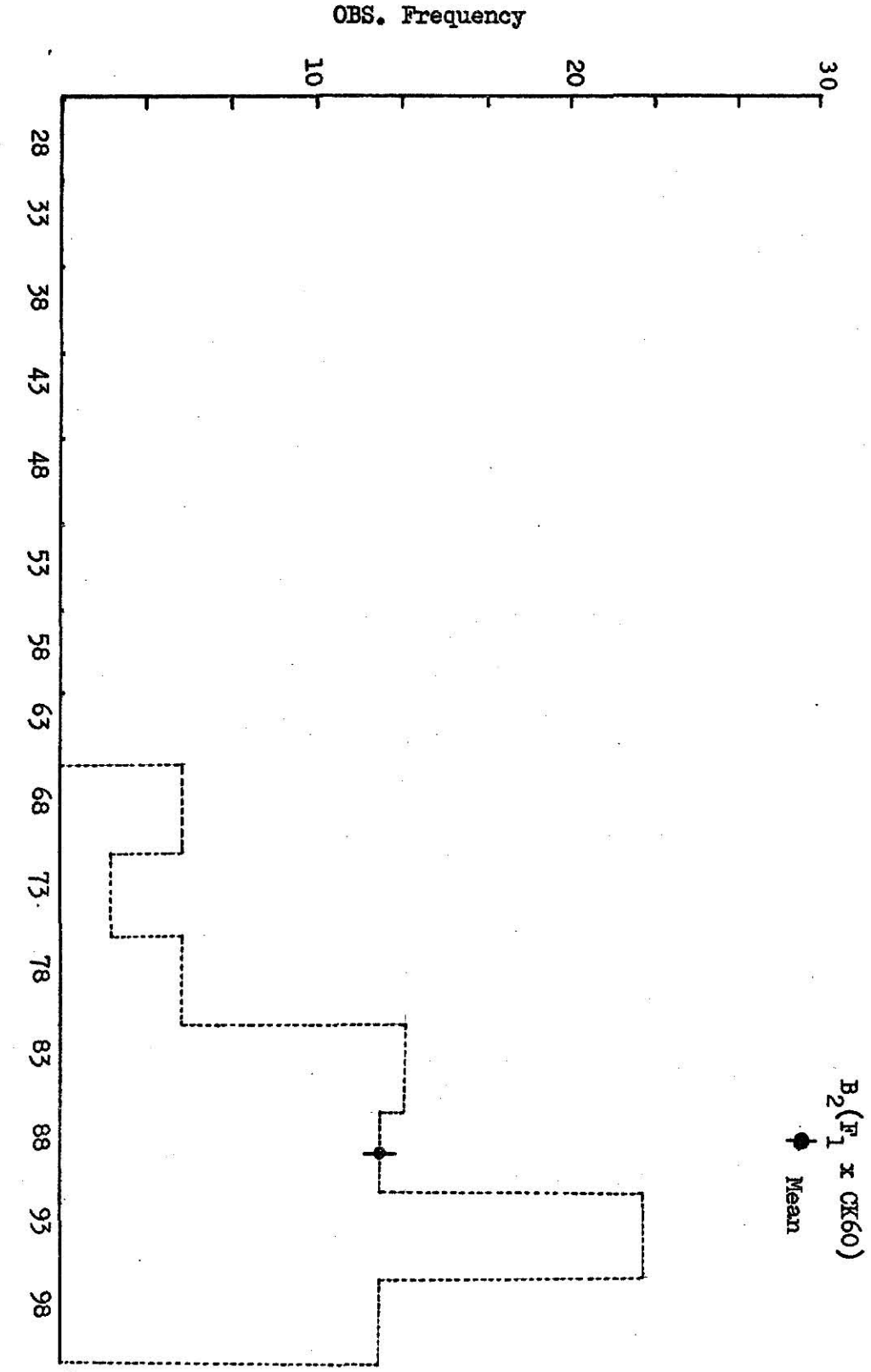

Fig. 4. Frequency distribution for germination rate (%) of second backcross (B_2).

An examination of the means in Table 2, shows that the arithmetical and geometrical means are significantly different from the mean of F_1. The marked increase in the germination rate of F_1 over the two parents indicates the presence of heterosis, meaning that overdominance is involved in the action of genes conditioning this trait. Also, the discrepancy between calculated and observed means of the F_2 demonstrates the presence of some sort of non-additive gene action.

Estimated phenotypic, genotypic and environmental variances for each of the siz populations are shown in Table 2.

Heritability estimate for germination rate, calculated on the basis of original data, is given in Table 3. It was of moderate magnitude (44.8%), signifying that most of the variation observed in environmental in origin. However, the increase in the environmental variance was due to the phenotypic variance observed for PL-1, one of the parental lines which still might be heterozygous for the gene(s) controlling this trait.

The expected genetic progress is shown in Table 3. It was seen that an increase of only 11.6% can be achieved by selecting top 5% of the F_2 plants with high germination rate. This progress is considerably low, despite the moderate heritability value observed for this trait, which may be due to some sort of non-additive genetic effects. It is a known fact that whenever heterosis is of high magnitude, a loss of part of such increase in the F_2 generation is expected.

Shrivastava and Pinnel (1963) reported a very low value of heritability for germination, ranging from 22 to 40% in three crosses

and negative for the fourth cross: Combine Kafir-60 x Plainsman.

Using the formula proposed by Wright and cited by Burton (1966) the minimum number of genes controlling germination rate was estimated to be 1. The nature of the F_2 distribution was of little value in determining the number of genes involved in the inheritance of this trait, since more than 50% of the F_2 variance was non-genetic or environmental.

The F_2 deviation from the F_1 was negative and significant, thus, indicating the presence of epistatic gene effects. The estimate of degree of dominance (H_p) calculated by the formula suggested by Griffing (1950) indicated overdominance.

The analysis of the results preclude a definite conclusion relative to the type of gene action involved in the inheritance of a germination rate. Breeding schemes such as family selection should be considered as an alternative possibility to a hybridization program, because of the low heritability observed for this trait. The family selection would be effective in the case where the environmental deviation constituted a larger part of the phenotypic variance for the trait.

Germination percentage did not show any correlation with seed weight ($r_p = 0.10$), consequently, the size of the seed had no effect on the germination, at least, in the genetic material utilized in this study. Therefore, it will be possible to select large-seeded plants without inducing negative response in the germination.

Table 2. Observed means, theoretical means (arithmetic and geometric), phenotypic variances, and estimated environmental and genetic variances for germination percentage of six sorghum populations.

Populations	Obs. mean (germ. %)	Theo. mean Arith.	Theo. mean Geom.	Variance Phenotypic	Variance Environ.[1/]	Variance Genotypic
P_1(PL-1)	74.2±1.87			124.2		
P_2(CK-60)	86.8±1.04			43.6	73.9	
F_1	91.9±1.28	80.5	80.3	30.5		
F_2	82.0±0.96	86.2	85.9	105.5		31.6
B_1(F_1xPL-1)	82.9±1.22			94.5		20.6
B_2(F_1xCK-60)	88.1±1.04			69.6		0.0

[1/] Environmental variance = $$\frac{(n_1 - 1)V_{P1} + (n_2 - 1)V_{P2} + (n_3 - 1)V_{F1}}{(n_1 - 1)+(n_2 - 1)+(n_3 - 1)}$$

Table 3. Estimate of heritability and minimum number of genetic factors involved in the inheritance of germination rate, and expected genetic progress through selection.

Cross	Heritability (h^2)	Number of genetic factors	Expected genetic progress[2/] (%)
PL-1xCK-60	44.8	n = 1[1/]	11.6%

[1/] Calculated by utilizing Wright's formula.

[2/] $G_s = i\sigma p \cdot h^2$

Table 4. Estimate of degree of dominance, F_2 deviation and heterosis observed for germination rate of the cross PL-1 x Combine Kafir-60.

Estimate of dominance (hp)[1/]	F_2 deviation	Heterosis %	
		Over mid-parent	Over better parent
hp = 1.8	-4.2±1.47**	14.2**	5.9 ns

[1/] Estimate obtained using the Griffing's formula

ns - non-significant

** - significant at 1% level of probability

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DOSAGE EFFECT OF WAXY GENE (wx) ON MALTOSE PRODUCTION AND DEGREE OF HYDROLYSIS OF THREE SORGHUM GRAIN [Sorghum bicolor (L.) MOENCH] VARIETIES AND THEIR F_1 HYBRIDS

SUMMARY

To study the dosage effect of waxy gene (wx) on the amount of maltose and degree of hydrolysis directly observed by scanning electon microscopy, purified starch from three grain sorghum [Sorghum bicolor (L.) Moench] varieties (two starchy endosperm - 'Combine Kafir-60' and 'PL-1', and one waxy-'Texioca 63'), F_1 and reciprocal crosses were subjected to hydrolysis by α-amylase for 48 hours.

Doses of wx gene had a significant effect on the rate and degree of hydrolysis of purified starch from endosperm genotypes wxwxwx, Wxwxwx, WxWxwx and WxWxWx.

Genotypes with three doses of waxy genes had the highest release of maltose as compared to those having 2, 1 and 0 doses, respectively. Similarly, genotypes with 2 doses of waxy genes produced more maltose than those with 1 dose. Crosses having PL-1 as female parent had the lowest release of maltose.

In general, there was a good agreement between the amount of maltose produced in the analysis of the supernatant and degree of hydrolysis of starch granules observed by scanning electron microscopy.

Obvious differences, in mode and degree of hydrolysis, were observed among starches of the parental lines. Waxy starch was most readily digested by the enzyme. Differences between F_1 and reciprocal crosses were mainly in degree of hydrolysis. The highest degree of hydrolysis

was observed in crosses having Texioca-63 used as female parent. Those with PL-1 as female parent had the lowest degree of hydrolysis.

DOSAGE EFFECT OF WAXY GENE (wx) ON MALTOSE PRODUCTION AND DEGREE OF HYDROLYSIS OF THREE SORGHUM [Sorghum bicolor (L.) Moench GRAIN VARIETIES AND THEIR F_1 HYBRIDS

INTRODUCTION AND LITERATURE REVIEW

Sorghum grain has been important in world agriculture for centuries. In the United States, sorghum grain has become, in relatively short time, a major aspect of the economy of Southwest Plains regions.

The favorable price of sorghum grain, as compared to concentrate feeds, has long made it the prime energy source for feeders in the Southwest. This economic incentive coupled with the availability of a wide genetic diversity in sorghum world collection has been a stimulus for grain sorghum breeders to develop varieties, hybrids with improved nutritive value and quality.

The use of lines with different types of grain (white, pearly, and corneous) and lines having grain with different pericarp color or different endosperm types could be effectively utilized in breeding program to improve the food quality of grain sorghum. However, it is necessary to define the feed and food quality in terms of chemical and physical attributes of sorghum grain in order to develop reliable methods for predicting quality which in turn can be used in the plant breeding program to assess the real potential value of germplasm available in the world collection of sorghum.

The structural characteristics of the sorghum caryopsis has been important in determining the suitability of the kernel as animal feed or for a particular industrial process involved. The proportions of

corneous and floury endosperms in the peripheral endosperm are of particular importance in wet-milling process of extraction of starch.

Rooney (1970b) studied the differences in starch recovery from 'Martin' 'Kafir-60', '7078', 'Tx 414', and four hybrids in which these varieties were parents. Grain from Martin and its hybrids gave significantly lower starch recovery and higher starch population than grain from other varieties and those hybrids in which Martin was not present.

Hoseney et al. (1974) characterized the sorghum kernel structure of a group of varieties by using the scanning electron microscope. They observed the soft endosperm to be characterized by large intergranular spaces and round starch granules which are covered with a thin sheet of protein containing relatively large spherical protein bodies.

In contrast, the hard endosperm possesses a tightly packed structure without air spaces, the starch granules are polygonal and encased in a dense proteinaceous matrix containing the protein bodies composed mainly of Kafrin, a protein low in lysine.

Hinder and Eng (1970) emphasized the advantages of the waxy grain sorghum type over non-waxy regular starch when the grain is to be fed steam-flaked, micronized or after dry or moist heat treatment.

Ruminant response to varieties of sorghum with different nutritional values is economically important to the livestock industry.

McCollough (1973) compared the feeding value of 13 hybrid sorghum with that of two hybrid corn, all representing seven types of endosperm. Steers fed all-waxy sorghum grain had the highest daily gain and the same feed conversion as steer fed yellow dent corn and hetero yellow endosperm sorghum hybrids. On the other hand, steer fed bird-resistant

sorghum grain gained significantly less than those fed yellow dent corn, all waxy and hetero-yellow endosperm hybrids.

McGinty and Riggs (1968) reported no significant differences in the coefficients of digestibility for ground grain of four sorghum varieties. In two experiments, Tx-09, 7078, waxy feterita, and Tx-2536 had higher coefficients of digestibility for dry matter than Kaoliang and Dorset No. 28. In vitro data indicated no differences in the digestibility of the endosperm of these varieties, but, digestibility was reduced when the pericarp from Kaoliang and Dorset No. 28 was added to the endosperm of any of the four varieties.

Sanford et al. (1970) observed differences in ruminal carbohydrate digestibility among four endosperm types. The rank was floury (90.1%), waxy (75%), normal (68.1%) and corneous (48.4%).

Sherrod et al. (1973) compared two in vitro techniques with % in vitro dry matter disappearance (IVDMD) to estimate digestible energy (DE) of bird resistant, corneous, intermediate, and floury sorghum grain types.

Scanning electron microscopy (SEM) have been used by many researchers, in studying some characteristic of the endosperm, cell wall, and in investigating starch hydrolysis by amylases.

Alpha-amylase is an endogeneous enzyme that hydrolyzes α-(1 4)-D-glucopyranosidic linkages in amylaceous polymer in random fashion, fragmenting glucans to D-glucose and oligo-saccharides (Whelan, 1964). Robyt and French (1967) related the differences in the patterns of α-amylase hydrolysis of amylase to the increase in reducing value. The differences in the curves were interpreted as due to differences in the degree of multiple attack which was determined by the ratio of the reducing value of the oligosaccharide fraction to that of the polysaccharide fraction.

Davis and Harbers (1974) utilized scanning electron microscopy to observe differences in endosperm structure and degree of starch hydrolysis of three grain types, waxy, yellow endosperm and bird resistant. Starch granules in soft endosperm of yellow and bird resistant type were smooth and spherical, while those in a waxy variety were irregular in shape. They also observed a different type of hydrolysis on split kernel immersed in rumen fluid, being point-surface attack on the starch from waxy grain, linear track hydrolysis on that from yellow endosperm and minor point hydrolysis on that from bird resistant type. Similarly, they compared the degree of hydrolysis on purified starch treated with porcine amylase at different rates. Waxy starch was more readily hydrolyzed than starch of yellow grain type, while the bird resistant sorghum grain starch showed substrate inhibition.

Harbers and Davis (1974) found that the nature of hydrolysis differed greatly between starch granules of waxy and yellow endosperm, subjected to digestion in the gastro intestinal tract of rats and pigs.

Sullins et al. (1974) related the great solubility of the waxy kernel with the fact that waxy starch was more susceptible to enzymatic attack, probably due to less peripheral endosperm area. Also, they concluded that the improved efficiency of feed lot cattle fed waxy sorghum was associated with these characteristics.

Some researchers have reported on the inheritance of waxy endosperm in several crops. In grain sorghum, Karper (1933) concluded that waxy gene behaves as simple Mendelian recessive, since the segregation ratio of F_2 gave a good 3:1 ratio. He reported xenia in the endosperm starch of F_1 seed developed from emasculated waxy flower when pollen carrying the dominant normal starchy gene fertilized an ovule carrying the recessive

waxy gene. Dominance of the starch gene was apparently complete.

Ellis et al. (1974) demonstrated the dosage effect of waxy gene on some chemical, physical properties and digestibility of two cultivar of grain sorghum. Lines with contrasting waxy and normal endosperm were used to derive homogeneous populations of grain with endosperm genotypes WxWxWx, WxWxwx, Wxwxwx, and wxwxwx. Amylose content of the starch from these four genotypes were 24, 23, 17 and 0%, respectively. In vitro digestibility of purified starch, ground grain pretreated with pronase, and ground grain increased significantly with each additional dose of the waxy allele.

Sullins et al. (1974) found that genotypes with 1, 2 and 3 doses of the wx gene showed an alteration in the distribution of protein in the endosperm. The peripheral endosperm area was neither dense nor thick in the waxy and hetero waxy genotype as compared to the nonwaxy WxWxWx.

This study was undertaken to determine the dosage effect of the waxy gene on the amount of maltose released, degree and kind of hydrolysis exerted by porcine pancreatic alpha amylase enzyme on isolated starch from three sorghum varieties, their F_1 and reciprocal crosses.

MATERIALS AND METHODS

The parental varieties chosen for this study were 'Combine Kafir-60' and 'PL-1', both having intermediate and starchy endosperm, and 'Texioca-63' with floury and waxy endosperm.

Combine Kafir-60 and Texioca-63 possess white pericarp, on contrast, PL-1 has yellow pericarp. Seeds of these varieties were planted and grown in individual pots under greenhouse conditions during the fall of 1975. Manual crosses among these varieties were made to obtain all the possible F_1 and reciprocal crosses, the parental lines were selfed.

Seeds from each individual cross were harvested, threshed and dried. Starch was isolated from each variety and their F_1 and reciprocal crosses by using a simple wet-milling method. A 2g grain sample was soaked overnight in water at 5-8°C; then coarsely ground in a mortar and sieved through a 100-mesh screen. Material remaining on the screen was reground and screened several times, then suspended in water, centrifuged at 450 x g with separation of the protein layer with a spatula. This procedure was repeated at least four times until the starch appeared pure. Purified starches were dried overnight in an oven at 36°C and bottled for later use.

Porcine pancreatic α-amylase sigma enzyme was utilized in this in vitro study. It was diluted to 2.97 I.U. activity per ml in 0.02 M phosphate buffer (pH 6.9) containing 0.006 NaCl (one I.U. releases one micromole of reducing units, calculated as maltose, per minute at 25°C).

A standard solution of maltose (2 μmoles/ml) was prepared by dissolving 0.721 g of sigma M-2250 maltose in 100 ml of H_2O, then diluted (1→10) in saturated Benzoic acid. A reducing sugar standard curve was

obtained with the maltose standard using dinitrosalicylic acid (DNS) method according to Miller (1959).

The readings were made in a Coleman Junior spectrophotometer at 50 mμ against a blank containing buffer without enzyme. The calibration curve with maltose (0.4-2 μmoles) was used to convert colorimeter reading to units of activity.

Samples of purified starch (20 mg) from each of the genotypes and from Sigma potato starch (as control) were placed in 25-ml Erlenmeyer flasks with 4.0 ml of enzyme, incubated 48 hr at 25°C in a Dubanoff metabolic shaker. The solutions were then poured in tubes and centrifuged for 10 min at 10,000 x g.

Also, purified starch from the parents were incubated but, in absence of the enzyme. The supernatant was decanted then 0.1 and 0.2 ml were removed according to Miller's method and tested for amounts of maltose.

Similarly, 0.1, 0.2, 0.3 and 0.4 ml of the supernatant were used to compare the rate of hydrolysis of the parental lines.

Residual starch was dried overnight in a oven at 36°C. All the samples were mounted on double-stick tape and coated with 150 Å of gold palladium and observed with ETec Autoscan scanning electron microscopy at 2000 x of magnification. Polaroid film was used to photograph the scanned image. Results were expressed in moles of maltose released per minute and analyzed statistically using AARDWARK program.

L.S.D. was used to test differences between means of paired treatments and also to test the differences among groups of genotypes classified according to the doses of waxy (wx) gene.

Sigma potato starch (Type III) having 100% amylose, was considered as control in the experiment. The average production of maltose for each endosperm genotype was expressed in terms of increase in percentage over the control (100%).

RESULTS AND DISCUSSION

Maltose production from purified starch of two starchy endosperm varieties, Combine Kafir-60 and PL-1 was compared to that of Texioca-63, a waxy endosperm variety as shown in Fig. 1. These sorghum varieties showed different rates of hydrolysis at the same substrate/enzyme ratio. Waxy sorghum grain starch released a higher amount of maltose than did the two normal endosperm varieties.

The dosage effects of waxy gene (wx) on the amount of maltose released by the enzymatic hydrolysis of isolated starch of these varieties and their F_1 and reciprocal crosses are given in Table 1 and 2.

Different doses of wx gene showed a significant effect on the amount of maltose produced from purified starch of the endosperm genotypes; wxwxwx, Wxwxwx, WxWxwx and WxWxWx. The genotype with 3 doses of wx was the most efficient and had 63, 105 and 53% of increase as compared to 2, 1 and 0 doses in the cross between Combine Kafir-60 by Texioca-63. Likewise, the same order was observed in the cross between PL-1 by Texioca-63 with 89, 119 and 64% of increase of the genotype with 3 doses over those with 2, 1 and 0 doses.

The differences between F_1 and its reciprocals of these two crosses were highly significant, indicating that endosperm genotypes with two doses of wx gene had more maltose released than endosperm with one dose of wx gene. However, hybrids with 2 doses of wx gene (Wxwxwx) did not exceed the amount of maltose produced by either of the parental lines having normal endosperm, although the degree of hydrolysis observed for the hetero waxy hybrids were consistently higher than that in Combine Kafir-60

and PL-1. Crosses having PL-1 as female parent had the lowest release of maltose probably due to presence of some kind of negative gene interaction.

The starchy gene (Wx) was incomplete dominant over waxy (wx) in both crosses, because the F_1 performance was close to the parent with starchy endosperm type.

The release of maltose, as a product of the hydrolytic action of α-amylase, offers an accurate index of digestibility. Maltose released used in conjunction with some other in vitro techniques should provide sorghum breeder basic information necessary to improve the feed efficiency of sorghum grain.

It is quite evident that different doses of waxy genes affect significantly the degree of digestion of starch, thus breeders should take advantage of waxy genes and develop hetero-waxy grain sorghum hybrids providing better feed efficiency.

Fig. 2 to 13 are the photomicrographs of granules from purified starch for each variety and their crosses with other. These photographs reveal differences in degree and pattern of hydrolysis after 48 hr incubation period with α-amylase (20 mg starch/sample). Purified starch of the parental lines incubated without enzyme (Fig. 2, 3 and 4) did not show any hydrolysis, thus, confirming the absence of endogeneous amylase adsorved to starch grain. Starch granules in the waxy endosperm were of irregular shape, while those in the normal endosperm were polygonals.

The photomicrographs 5 to 7 show clear differences in mode and degree of hydrolysis among purified starch of the parental lines treated with α-amylase. The waxy starch was most readily digested by the enzyme as shown in Fig. 7. A concentric shell structure can be clearly seen in

starch granules as a result of the hydrolysis. The differences between Combine Kafir-60 and PL-1, two normal endosperm varieties, were both in pattern and degree of hydrolysis. The predominant form of enzymatic attack in Combine Kafir-60 was of a large and irregularly shaped holes, while that in PL-1 was of radial erosion type. The degree of hydrolysis was slightly high in Combine Kafir-60.

Similarly, F_1 and its reciprocal crosses differed mainly in the amount of hydrolysis rather than in pattern. The highest hydrolysis was observed in crosses having Texioca-63 (waxy endosperm type) as female parent while those crosses with PL-1 as female had the lowest degree of hydrolysis and showed mostly a point and linear tract hydrolysis. With few exceptions, there was a good agreement between the degree of enzymatic attack observed in the photomicrographs of starch granules and the amount of maltose produced in the supernatant analysis.

This study showed that the amount of maltose produced as well as the degree of hydrolysis directly observed on the starch grains, were affected significantly by variation in doses of waxy (wx) gene in the endosperm genotype.

Genotype with 3 doses of wx gene had the highest release of maltose in comparison to that of 2, 1 and 0 doses. Likewise, genotype with 2 doses produced significantly more maltose than those having one dose.

In general, there was a good agreement between the production of maltose and the degree of hydrolysis observed in the photomicrographs.

The release of maltose offers an accurate index of digestibility which used in conjunction with the Scanning electron microscopy provides the breeders with useful information in developing suitable Sorghum varieties for livestock.

Table 1. Dosage effect of waxy gene (wx) on the amount of maltose produced by purified kernel starch of two sorghum varieties, their F_1 cross and reciprocal crosses treated with α-amylase.

Var. and Cross	Endosperm Type	Approx. Prop. of Amylop: Amylose	Avg. Prod. of Maltose (μmoles)	Doses of Waxy Gene	Increase Relative to Check(%)
Texioca	waxy	100 amylop	1.33	3	165
Texioca x CK60	heterowaxy	unknown	0.82	2	102
CK60 x Texioca	heterowaxy	unknown	0.48	1	60
CK60	normal (starchy)	75:25	0.91	0	112
Amylose[1/]	----------	100 amylose	0.81	-	100

L.S.D. (.05) = 0.054 μmoles of maltose
L.S.D. (.01) = 0.069 μmoles of maltose

[1/] Potato starch free of amylopectin used as control.

Table 2. Dosage effect of waxy gene (wx) on the amount of maltose produced by purified kernel starch of two sorghum varieties and their F_1 cross and reciprocal cross treated with α-amylase.

Var. and Cross	Endosperm Type	Approx. Prop. of Amylop: Amylose	Avg. Prod. of Maltose (μmoles)	Doses of Waxy Gene	Increase Relative to Check(%)
Texioca	waxy	100 amylop	1.33	3	165
Texioca x PL-1	heterowaxy	unknown	0.62	2	76
PL-1 x Texioca	heterowaxy	unknown	0.38	1	46
PL-1	normal (starchy)	75:25	0.82	0	101
Amylose[1/]		100 amylose	0.81	-	100

L.S.D. (.05) = 0.054 μmoles of maltose
L.S.D. (.01) = 0.069 μmoles of maltose

[1/] Potato starch free of amylopectin used as control.

Table 3. Amount of maltose produced (µmoles) from purified kernel starch of two sorghum varieties, their F_1 cross and reciprocal cross treated with α-amylase.

Var. and Cross	Endosperm Type	Approx. Prop. of Amylop: Amylose	Avg. Prod. of Maltose (µmoles)	Increase Relative to Check(%)
CK60	normal (starchy)	75:25	0.91	112
CK60 x PL-1	"	unknown	0.83	103
PL-1 x CK60	"	unknown	0.38	46
PL-1	"	75:25	0.82	101
Amylose[1/]	---	100 amylose	0.81	100

L.S.D. (.05) = 0.054 µmoles of maltose
L.S.D. (.01) = 0.069 µmoles of maltose

[1/] Potato starch free of amylopectin used as control.

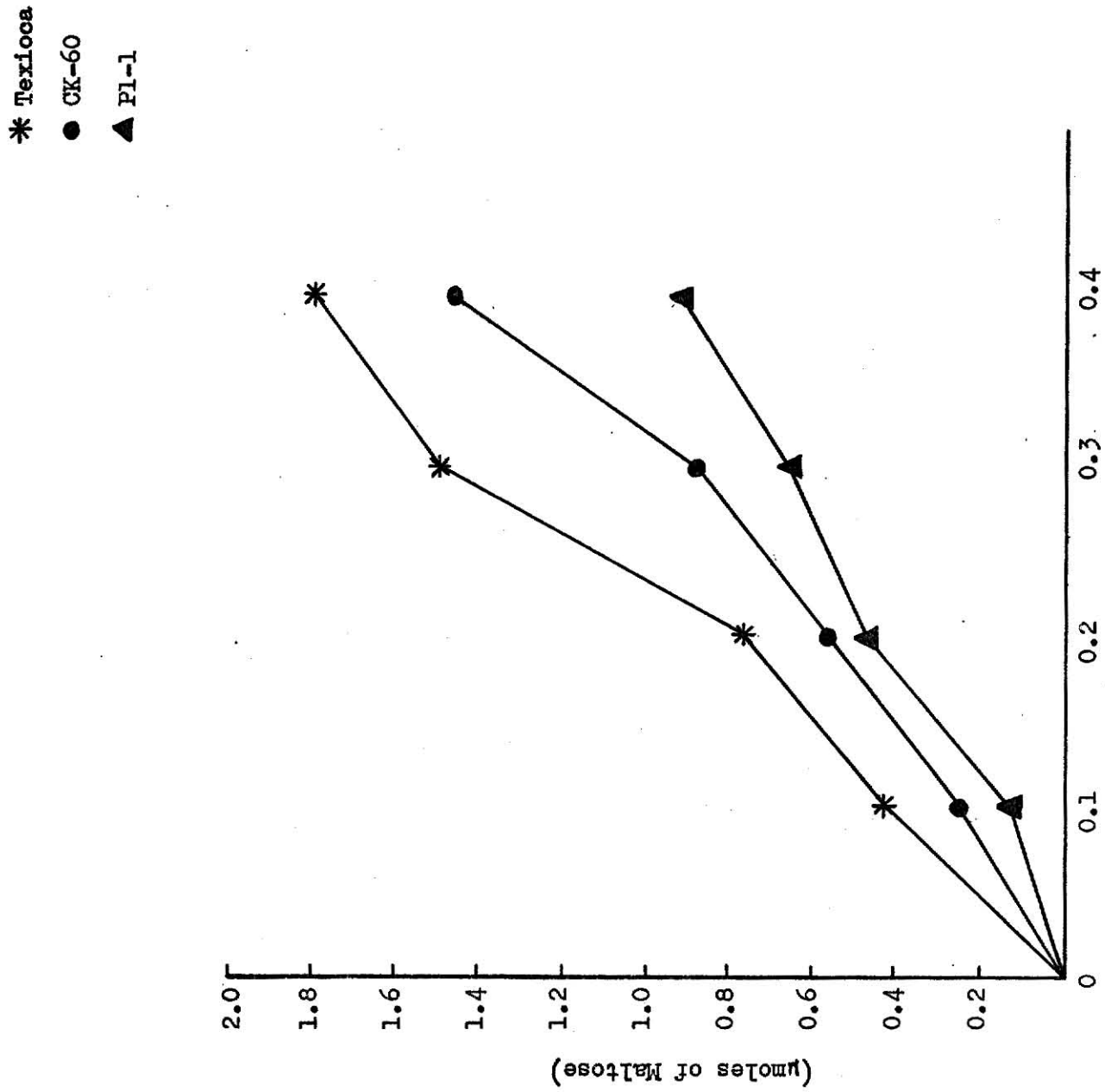
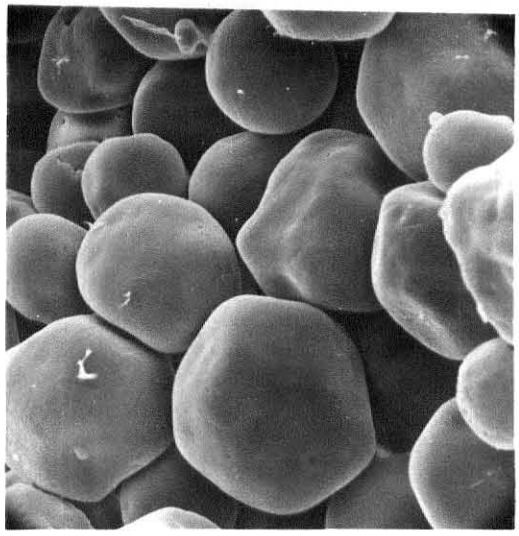


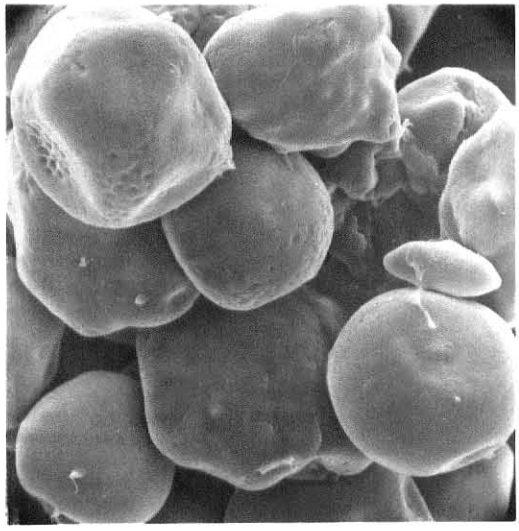
Fig. 1. Maltose production from purified starch of two starchy and one waxy sorghum varieties after 48 hr. of incubation with alpha-amylase.

Fig. 2 Scanning electron photomicrograph of starch granules isolated from Combine Kafir-60 (starchy endosperm Sorghum) incubated without α-amylase (2000x).

Fig. 3 Scanning electron photomicrograph of starch granules isolated from PL-1 (starchy endosperm Sorghum) incubated without α-amylase (2000x).

Fig. 4 Scanning electron photomicrograph of starch granules isolated from Texioca-63 (waxy endosperm Sorghum) incubated without α-amylase (2000x).





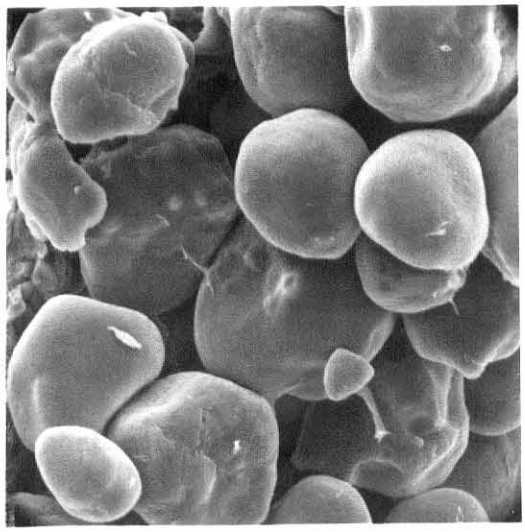
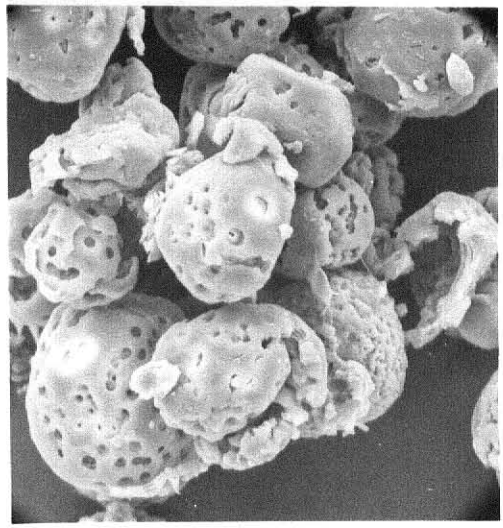
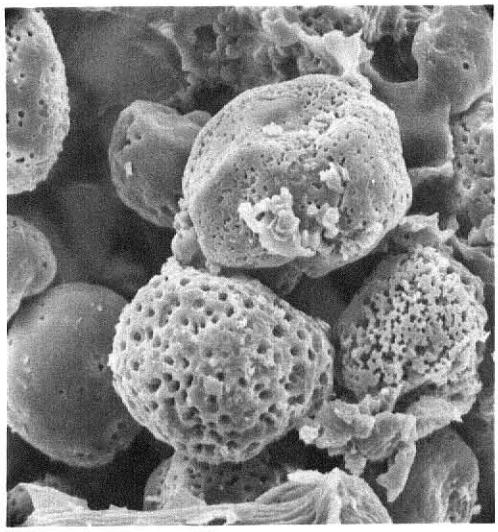


Fig. 5 Scanning electron photomicrograph of starch granules isolated from Combine Kafir-60 (starchy endosperm Sorghum) treated with α-amylase (2000x).

Fig. 6 Scanning electron photomicrograph of starch granules isolated from PL-1 (starchy endosperm Sorghum) treated with α-amylase (2000x).

Fig. 7 Scanning electron photomicrograph of starch granules from Texioca-63 (waxy endosperm Sorghum) treated with α-amylase (6000x).





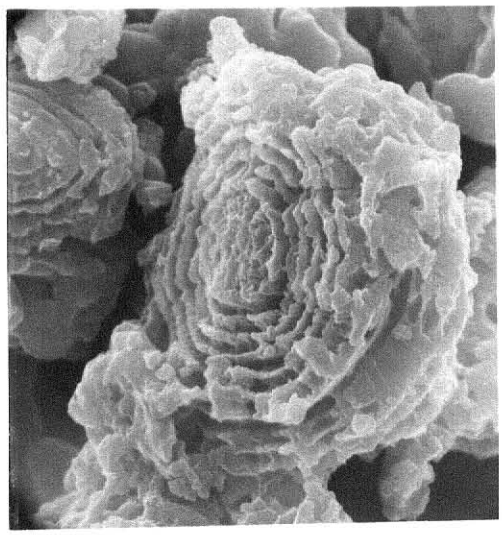
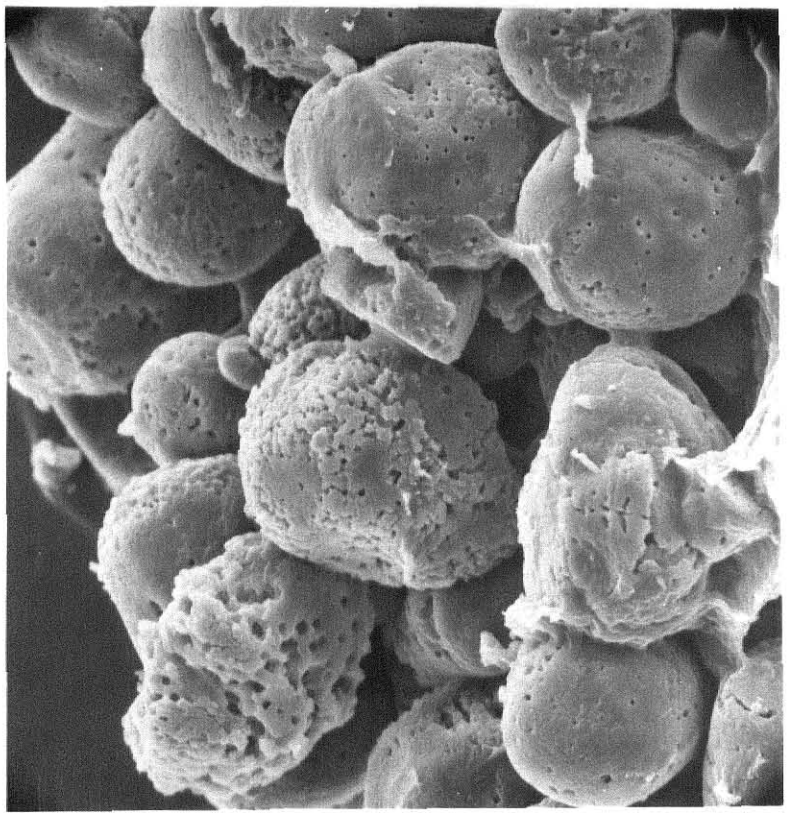


Fig. 8 Scanning electron photomicrograph of starch granules isolated from Combine Kafir-60 x Texioca-63 cross (heterowaxy endosperm with 1 dose of waxy gene) treated with α-amylase (2000x).

Fig. 9 Scanning electron photomicrograph of starch granules isolated from Texioca-63 x Combine Kafir-60 cross (heterowaxy endosperm with 2 doses of waxy gene) treated with α-amylase (2000x).



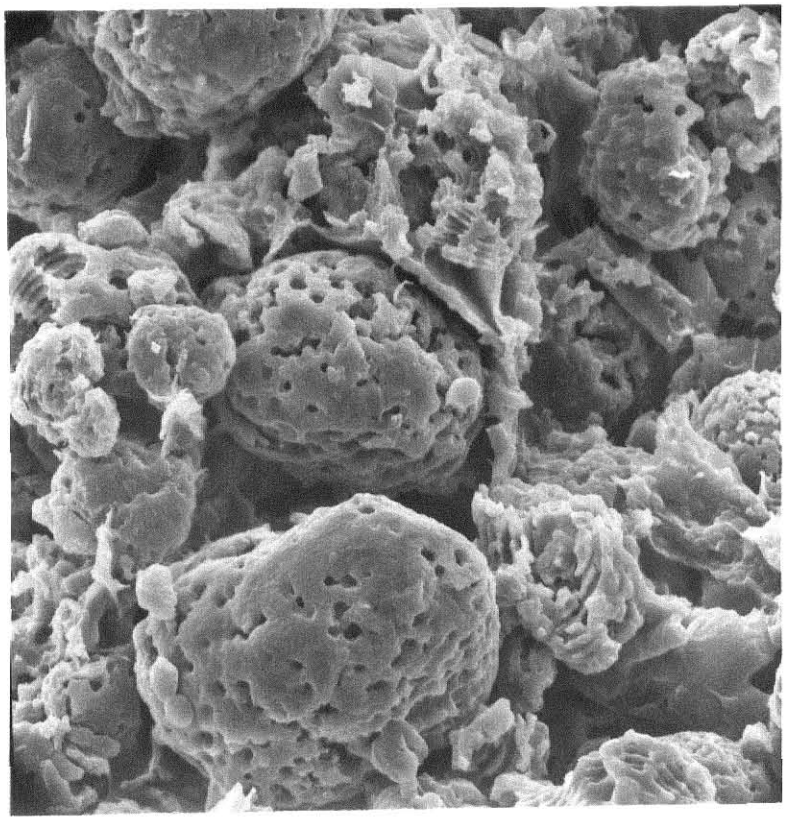
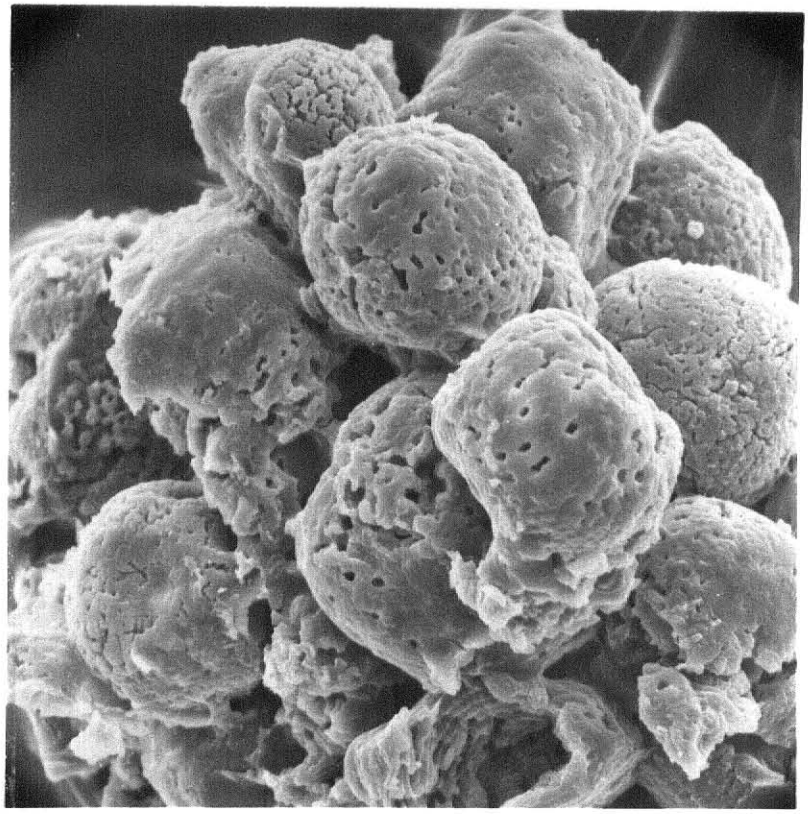


Fig. 10 Scanning electron photograph of starch granules isolated from PL-1 x Texioca-63 cross (heterowaxy endosperm with 1 dose of waxy gene) treated with α-amylase (2000x).

Fig. 11 Scanning electron photomicrograph of starch granules isolated from Texioca-63 PL-1 cross (heterowaxy endosperm with 2 doses of waxy gene) treated with α-amylase (2000x).



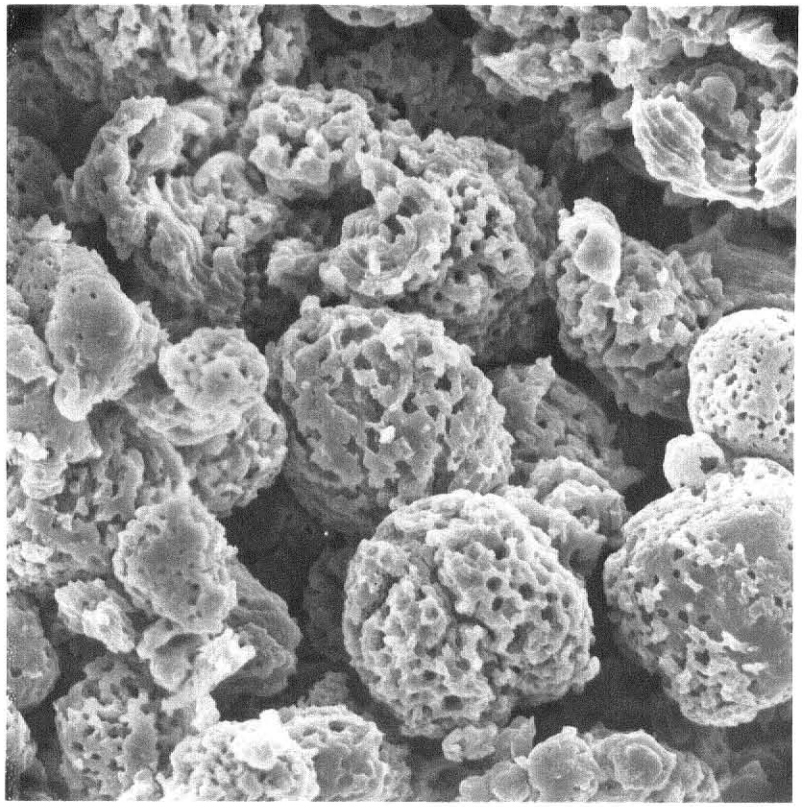
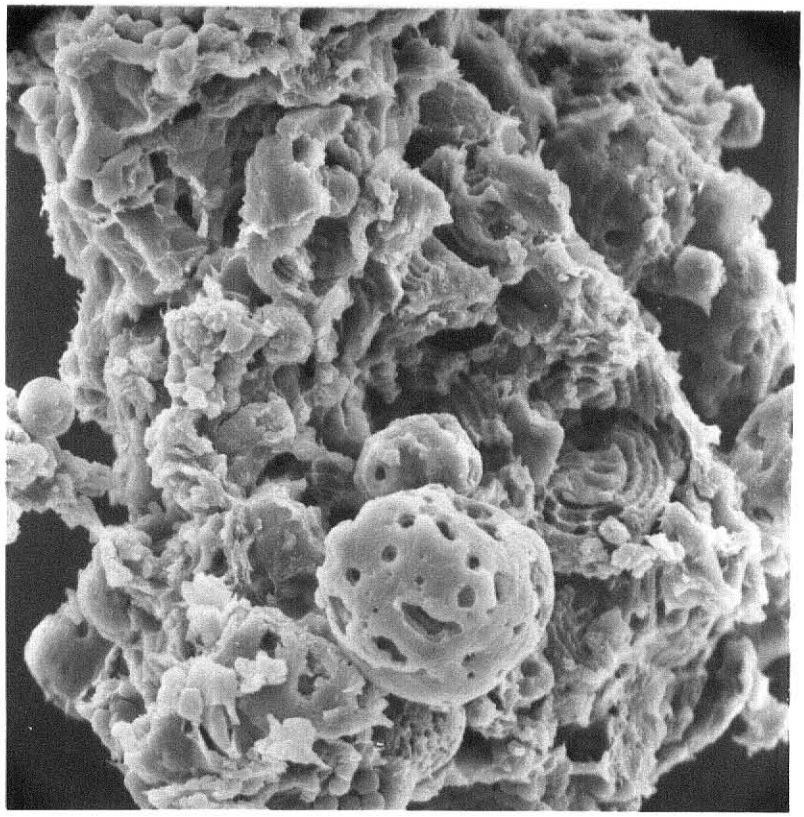
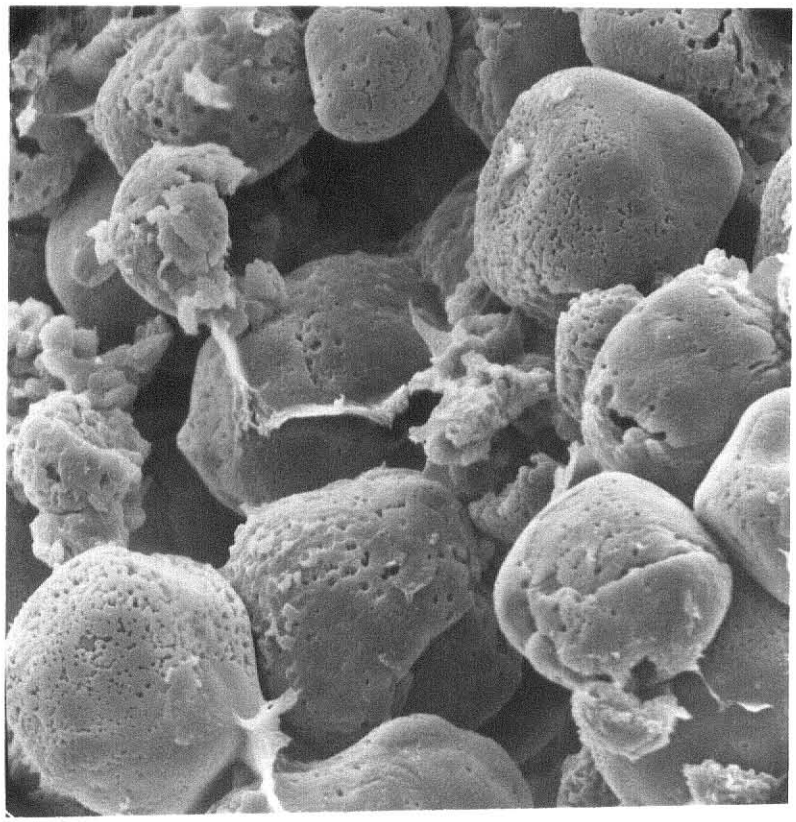


Fig. 12 Scanning electron photomicrograph of starch granules isolated from Combine Kafir-60 x PL-1 cross (starchy endosperm) treated with α-amylase (2000x).

Fig. 13 Scanning electron photomicrograph of starch granules isolated from PL-1 x Combine Kafir-60 cross (starchy endosperm) treated with α-amylase (2000x).





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I. INHERITANCE OF SEED WEIGHT IN A GRAIN SORGHUM [(*SORGHUM BICOLOR* (L.) MOENCH)] CROSS.

II. INHERITANCE OF GERMINATION RATE IN A GRAIN SORGHUM [(*SORGHUM BICOLOR* (L.) MOENCH)] CROSS.

III. DOSAGE EFFECT OF WAXY GENE (*wx*) ON MALTOSE PRODUCTION AND DEGREE OF HYDROLYSIS OF THREE GRAIN SORGHUM [(*SORGHUM BICOLOR* (L.) MOENCH)] VARIETIES AND THEIR F_1 HYBRIDS.

by

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B.S., Central University of Venezuela, 1967

AN ABSTRACT OF A MASTER'S THESIS

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ABSTRACT

The production of grain sorghum hybrids with high yielding and improved nutritive values has been the main objective in breeding programs. The first part of this investigation was to study the mode of inheritance for seed weight and germination rate in a grain sorghum cross.

Two sorghum varieties, 'Combine Kafir-60' and 'PL-1' were chosen for this study. Manual crosses between them were carried out and the F_1 plants obtained were selfed and also backcrossed to each of the parent to produce the F_2, first and second backcross generations. Twenty-nine F_3 families were also included in the experiment.

These populations were planted at Ashland Experiment Station (Riley County) during the summer of 1975.

Data for seed weight and germination percentage were taken on the individual plant basis and the biometrical analyses were conducted with untransformed data. The population means and variances for each population were used to estimate heritability, minimum gene number and to determine the nature of gene action involved in the inheritance of these traits.

Estimates of heritability for seed weight and germination rate were both of moderate magnitude, being 50.0 and 44.8%, respectively. However, a significant genetic gain by selection was indicated only for seed weight.

A minimum of 2-3 genetic factors appeared to control the inheritance of seed weight while only one factor was estimated for germination rate.

Two types of epistasis, dxd and axd were the only significant and important gene effects in the inheritance of seed weight; overdominance appeared to be more important for germination rate than other gene effects.

Kernel number and kernel weight had a negative and in some instances significant correlation in all the populations except in the F_2. Plant height was positively and significantly correlated with grain yield and its components, suggesting that selection for short plants, without sacrificing yield may be difficult. Seed weight did not correlate with the germination rate.

A second study was conducted to investigate the dosage effect of waxy (wx) gene on the rate and degree of hydrolysis exerted by α-amylase in three sorghum varieties and their three F_1 hybrids.

The parental lines were 'Combine Kafir-60' and 'PL-1', both of intermediate and normal endosperm, and 'Texioca-63' with floury and waxy endosperm. Starch extracted from each endosperm genotype and potato starch was incubated with porcine-alpha amylase.

Results indicated that the rates of enzymatic hydrolysis, degree and pattern of digestion were significantly affected by the doses of waxy gene. Endosperm genotypes with three doses of waxy gene (wxwxwx) had the highest release of maltose and endosperm genotypes with two doses of waxy gene (Wxwxwx) yielded more maltose than those with one dose of waxy gene (WxWxwx). Crosses with PL-1 as female parent had the lowest release of maltose.

The relationship between maltose release and doses of waxy gene were confirmed by the degree of hydrolysis directly observed by scanning electron microscope.