THE INTERACTION OF YIELD COMPONENTS TOWARDS THE EXPRESSION OF YIELD IN GRAIN SORGHUM (Sorghum bicolor Linn. MOENCH)

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
B. H. ZAKRI
1973

ABSTRACT

THE INTERACTION OF YIELD COMPONENTS
TOWARDS THE EXPRESSION OF YIELD IN GRAIN
SORGHUM (SORGHUM BICOLOR LINN.) MOENCH

by

B. H. Zakri

The roles of yield components, namely, number of heads per unit area (X), number of seeds per head (Y) and average seed weight (Z) towards the expression of the complex trait, grain yield per unit area (W), were examined in a population of grain sorghum (Sorghum bicolor, Linn. MOENCH) varieties. Y was the component most strongly associated with W, followed by X and Z respectively. If W is regarded as the volume of a rectangular parallelepiped with X, Y and Z as its edges, Y should be assigned to be its longest edge since by convention the volume is changed least by changes in its longest edge and changed most by its shortest edge. It follows then that the development of a high Y is essential for yield stability in this particular region.

The response of grain yield (W) to varying stand densities were analyzed. At the location where soil moisture during the growing period was adequate, W was linear across stand densities. Compensatory reactions among the yield

components, especially between X and Y, were responsible for maintaining the yield linearity. However, at the location where soil moisture was limiting, there was an optimum stand density beyond which yield would decline. Intense interplant competition for a share of the limiting input was the essential cause for this yield reduction.

THE INTERACTION OF YIELD COMPONENTS TOWARDS
THE EXPRESSION OF YIELD IN GRAIN SORGHUM
(*Sorghum bicolor* Linn. MOENCH)

by

B'.ʳ H. Zakri

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Crop and Soil Sciences

1973

ACKNOWLEDGEMENTS

The author wishes to express his sincere gratitude to Dr. J.E. Grafius for his guidance, encouragement, patience and constructive criticism during the course of this study, and in the preparation of the manuscript.

Dr. D. H. Smith's review of the manuscript is greatly appreciated.

The author also wishes to extend his indebtedness to The Training Division, Majlis Amanah Rakyat (M.A.R.A.) of Kuala Lumpur, Malaysia, for their generous financial support during his stay in the United States.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Continued . . .)

LIST OF FIGURES

THE INTERACTION OF YIELD COMPONENTS TOWARDS THE EXPRESSION OF YIELD IN GRAIN SORGHUM VARIETIES

Introduction

In multicellular organisms most characters are complex in nature such that each of these traits is controlled by an array of genes or gene systems. It is believed that for certain complex traits such as yield in grain crops, genes responsible for yield itself need not exist; it is in fact a consequence of the actions and reactions of two or more yield components, each of which has its own unique gene system. It has been shown in stress-free environments that the individual yield components are either uncorrelated or the correlation tends to be small indicating that independent gene systems are involved.

The concept of the component approach enables the breeder to simplify a complex trait into its subdivisions. In grain sorghum, grain yield per unit area (W) could be partitioned into its three individual components namely, number of heads per unit area (X), number of kernels per head (Y) and the average kernel weight (Z). Yield is the product of these components, that is W = XYZ.

One might initially be apprehensive in accepting the theory that genetic systems are operating in a multiplicative fashion. However, it is a rational proposition when one takes into consideration that the individual components of yield are sequentially developed. In grain sorghum, the number of heads per unit area as represented by tillers during the vegetative stage, is the first component to be morphologically laid down. This is followed closely in the next phase by the number of kernels per head. Fertilization and seed set initiate the development of kernel size, thus rounding up the final phase of the sequence. Each component is uniquely developed within the time scale, after allowing for some degree of overlapping between the first two phases. Hence, it follows that yield is the product of number of heads per unit area X number of kernels per head X average kernel size.

The object of this study is to ascertain the interacting roles of the yield components in relation to the eventual expression of yield under conditions of varying stand densities.

REVIEW OF LITERATURE

a) Yield Components Interaction

A complex trait in a crop plant can be defined as an entity comprised of several individual components. Grafius (1956, 1965) visualized a complex trait such as yield in small grains as a geometric construct in the form of a parallelepiped, designating the volume as yield (W), with the edges X, Y and Z as the three yield components namely, number of panicles per unit area/per plant, average number of kernels per panicle and average kernel weight, respectively. The three-dimensional model elucidates how W could be altered by changes in X, Y and Z and consequently, how yield could be engineered to suit a given environment by manipulating the individual yield components.

Whitehouse et al. (1958) partitioned the yield of wheat into the following components: weight per kernel, kernel per spikelet, spikelets per ear and ears per plant. There were no significant correlations between the components implying that they are independent of each other.

Hutchinson (1940) observed that in cotton, some yield components are more stable than others when they are subjected to environmental variations, and consequently found that selection was more effective for certain components only.

He also provided data to show the adverse association between certain components which he called "physiological incompatabilities."

Adams (1967) later termed the above phenomenon as "Yield Component Compensation." Negative associations among yield components occur when the plant is subjected to stress and it is a form of within - plant adjustments which is prevalent in well-adapted varieties. The whole process seems to have an air of accomodation in it, whereby if one component in a given environment is not subscribing to its fullest genetic potential towards the fulfillment of the ultimate (complex) trait, the "deficiency" would be made up in the form of a greater contribution by another component in the system. Adams (1967) presented an elaborate thesis on the subject of yield component compensation. He postulated that negative correlations among principal components of a complex trait are developmental rather than genetic in itself, and the phenomena are caused by genetically independent components developing in a sequential pattern.

Working in oats, Maddur (1972) found that a negative correlation existed between the tiller number (X) and the kernels per tiller (Y), which he attributed to intraplant competition due to stress. However, he noted that this association helps maintain the linearity of yield to adversities in the environment.

Stickler and Wearden (1965) observed that grain yield in sorghum were constant across stand densities because of

inter compensations among individual yield components particularly between number of heads per unit area and the average number of kernels per head. Yield superiority was mainly associated with more heads per unit area (greater tillering capacity).

Working with sorghum under dry land conditions, Karchi and Rudich (1966) also reported that yield superiority was due primarily to increased number of heads per unit area rather than to changes in head weight. X and Y were mostly free of environmental effects; however, Z was strongly affected by environmental conditions prevailing at the time of kernel maturation, in this case, inadequate soil moisture. They also found that plot yields were constant at different seedling densities, largely due to changes in X. Yield per unit area (W) was directly associated with X and inversely proportional to YZ.

The findings of the two later groups seem to be in accord with the analyses of Thomas, Grafius and Hahn (1970a, 1970b) on correlated sequential characters: In a stress situation, the expression of a complex trait is greatly influenced genetically by the earliest component being fixed in the developmental sequence. They analyzed yield components data in wheat,barley and rice, and observed that the degree of true direct genetic control diminishes for characters fixed later along the sequence.

b) The Effect of Stand Density on yield and yield components

Under conditions of adequate soil moisture, Robinson et al. (1964), Porter et al. (1960), Grimes and Musick (1960), found no effect of populations ranging from 64,000 to 312,000 plants per acre on the grain yield of sorghum. When water is not a growth-limiting factor, high plant densities with maximum ground cover usually results in better utilization of incoming energy and added nutrients.

Grimes and Musick (1960) explained that tolerance to varying stand densities in grain sorghum is due to their tendency to tiller and produce larger heads at low plant populations and smaller heads combined with some plants not producing heads at high plant densities. Working on sorghum under irrigation, Nelson (1952) found no significant yield differences with populations varying from 72,000 to 228,000 plants per acre. As remarked earlier, Stickler and Wearden (1965), Karchi and Rudich (1966) found that the stability of grain yields across stand densities was attributed to inter-compensation among yield components, especially heads per unit area and seeds per head.

In drier conditions, moisture is a limiting factor and tends to restrict plant growth during the initial or for most parts of the growing season. Mathews and Barnes (1940), Bond et al. (1964) observed that the size of a sorghum crop is determined to a great extent by the amount of soil moisture at the initial growing stage. Working under various cultural practices, Brown and Shrader (1959) noted that the optimum plant population varied with the availability of soil moisture. With 6 inches of initial soil moisture (ISM) stand densities of 13,000 to 15,000 plants per acre produced the maximum yields. With 10 inches ISM, 60,000 plants per acre produced the highest yields. With 14 inches ISM, the optimum population is 90,000 plants per acre. Mann (1965) concluded that plant populations apparently have greater effect on yield than do row spacings, and he found that under dryland conditions, seeding rates of more than 4 lbs. per acre generally results in yield reduction. He observed that there was no significant difference in yield between 21-inch and 42-inch rows. However, the narrower row spacing showed advantages over the broader one in competition with weeds as well as for prevention of wind erosion.

MATERIALS AND METHODS

Thirty varieties of grain sorghum were grown in 1972 at two locations in Michigan, namely at the counties of Kalamazoo (Location 1) and Branch (Location 2). The annual precipitation for the two locations is given in Table 1. Precipitation from May 1 through September 30 for Location 1 and Location 2 were 17.17 and 16.34 inches respectively.

While the rainfall distribution between the two areas may not be significantly different, the amount of soil moisture retained during the growing season would vary due to differences in soil type. The soils at both locations were marginal to sub-marginal for good crop production. At Location 1, the soil type was Sumner (formerly Warsaw) loam while at Location 2, it was Boyer gravelly sandy loam. The water-holding capacity was better for the soil at Location 1 than at Location 2. The quadratic relationship between grain yield and stand density evident at Location 2 (Table 5) strongly hinted the existence of an environmental stress at this particular location during the year the experiment was conducted. Soil moisture was believed to be the limiting input, assuming that all other inputs are adequate.

In each location, the experiment was designed as a rectangular lattice of k (k+1) treatments with 6 replications. There were 180 original plots per location. Each plot is

TABLE 1. TOTAL PRECIPITATION AND DEPARTURES FROM NORMAL (1972)

Station	Jan. Prec.	Jan. Dep.	Feb. Prec.	Feb. Dep.	March Prec.	March Dep.	April Prec.	April Dep.	May Prec.	May Dep.	June Prec.	June Dep.
Location 1 (Kalamazoo)	1.49	-.77	.90	-1.11	3.08	.55	2.93	-.15	3.44	-.32	1.60	-2.13
Location 2 (Branch)	1.55	-.39	.62	-1.22	3.13	.65	3.86	.49	3.35	-.33	-.49	-1.73

Station	July Prec.	July Dep.	Aug. Prec.	Aug. Dep.	September Prec.	September Dep.	October Prec.	October Dep.	November Prec.	November Dep.	December Prec.	December Dep.	Annual Prec.	Annual Dep.
Location 1 (Kalamazoo)	2.43	-.88	4.41	1.33	5.29	2.27	2.78	-.23	3.03	.43	4.24	2.15	35.62	1.14
Location 2 (Branch)	2.36	-1.07	3.26	.22	4.88	1.63	2.57	.00	3.35	.87	3.31	1.49	34.73	.61

Note: Units are in inches. Normals for both stations are climatological normals based on the period 1931-1960.

Source of Data: Climatological Data - Michigan Annual Summary 1972, Vol. 87(13):202. U.S. Dept. of Commerce, National Oceanic & Atmospheric Administration.

made up of a single row, 10 feet long, with 30 inch row spacing.

The following measurements were made throughout the course of the study.

1) Stand density of plants per plot
2) Percentage of bird damage - later in the statistical analyses, all relevant variables were corrected for this value.
3) Yield per plot (W) - heads were harvested, dried, threshed, cleaned and weighed.
4) Number of heads per unit area (X) i.e. the number of heads per plot were counted prior to harvest.
5) Number of kernels per head (Y). This was computed by using the equation $Y = \frac{W}{XZ}$
6) Average kernel weight (Z). A 3 gram sample per plot was counted using an electronic seed counter and the average kernel weight was calculated.

To measure the influence of stand density on yield and yield components, the values for yield per unit area (W) and seeds per head (Y) have to be adjusted for variation in percentage of bird damage.

i) Original regression model of $R_{W.s}$

$$\hat{W} = b_o + b_1X_s + b_2\, X_{BD}$$

$$b_o = \hat{W} - b_1X_s - b_2\, X_{BD}$$

Adjusted model:

$$\hat{W}_{adj} = W_{obs} - b_2 (X_{BD} - \bar{X}_{BD})$$

$$= b_o' + b_1X_s$$

$$\text{where } b_o' = b_o - b_2 \bar{X}_{BD}$$

ii) Original regression model of $R_{y,s}$

$$\hat{Y} = b_o + b_1X_s + b_2 X_{BD}$$

$$b_o = \hat{Y} - b_1X_s - b_2 X_{BD}$$

Adjusted model:

$$\hat{Y}_{adj} = Y_{obs} - b_2 (X_{BD} - \bar{X}_{BD})$$

$$= b_o' + b_1X_s$$

$$\text{where } b_o' = b_o - b_2\bar{X}_{BD}$$

Suits (1957) suggested that the dummy variable is a useful and simple method of introducing into a regression analysis information contained in variables that are not conventionally measured on a numerical scale in the course of an experiment.

In this case, an attempt is made to establish the relationship of W and stand density in the sorghum population.

However, the population is heterogenous with respect to the inclusion of 30 different entries in the experiment. Thus any description of the influence of stand density on W must also take into account the variation among entries.

Since entry is a nominal scale variable, numerical values must be assigned to it before it can be fitted into a regression equation. Hence, 29 dummy variables are created for the 30 entries, with the following properties:

R_1 = 1 in Entry 1
= 0 in all other entries except Entry 30
= -1 in Entry 30

R_2 = 1 in Entry 2
= 0 in all other entries except Entry 30
=-1 in Entry 30

Similar assignments are made to all others of the 29 dummy variables. A 30th dummy variable is not necessary since the last value is determined by difference. An additional dummy variable would only result in n equations and n + 1 unknowns and in matrix algebraic terms, this is known as singularity. Suits (1957), Draper and Smith (1967) and Cohen (1968) gave proof and further details concerning this aspect of statistics.

The data matrix is as follows:

$$
\begin{array}{c} \\ W_1 \\ W_2 \\ W_3 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ W_{29} \\ W_{30} \end{array}
=
\begin{bmatrix}
X_o & X_s & R_1 & R_2 & R_3 & \cdots & R_{29} \\
1 & \text{real value} & 1 & 0 & 0 & \cdots & 0 \\
1 & '' & 0 & 1 & 0 & \cdots & 0 \\
1 & '' & 0 & 0 & 1 & \cdots & 0 \\
\cdot & \cdot & \cdot & & & & \\
\cdot & \cdot & \cdot & & & & \\
\cdot & \cdot & \cdot & & & & \\
\cdot & \cdot & \cdot & & & & \\
1 & '' & 0 & 0 & 0 & \cdots & 1 \\
1 & '' & -1 & -1 & -1 & \cdots & -1
\end{bmatrix}
$$

The model would then be:

$$\hat{W} = b_oX_o + b_1 X_s + c_1R_1 + c_2R_2 + \ldots + c_{29}R_{29}$$

The Least Square method is used to test the significance of the model.

To consider the possibility of a quadratic relationship, the following model is also tested:

$$\hat{W} = b_oX_o + b_1X_s + b_2X_s^2 + c_1R_1 + \ldots + c_{29}R_{29}$$

RESULTS

Tables 2 and 3 provide the analysis of variance of the regression of grain yield per unit area (W) and yield components (X,Y,Z) on stand density. As expected, the entry differences are significant for all dependent variables (i.e. W,X,Y and Z) in both locations. In Location 1, variance due to stand density is significant for heads per unit area (X) and seeds per head (Y) but not for yield per unit area (W) nor average kernel weight (Z). In Location 2, only the linear regression of W on stand density and that of X on stand density are significant.

The quadratic effect of stand density on yield and yield components are tested and as shown in Tables 4 and 5, the pattern of significance seems to follow that observed in tables 2 and 3.

The effects of stand density on yield at each location are graphed in Figures 1 and 2. A quadratic relationship could be fitted at Location 2, while no significant influence of stand density on W is found at Location 1.

Figures 3 and 4 show the response of yield and its three components to varying stand density. At Location 1, the linearity of W is maintained by the counter-directions between X and Y. Z appears to be unaffected. At Location 2 there is an upper limit to W, beyond which the yield declines. The behavior of W seems to be mainly determined by X.

The correlation coefficients for yield and yield components are presented in Table 6. Yield per unit area (W) is most strongly correlated with seeds per head (Y), followed by heads per unit area (X). However, the association of W with average kernel weight (Z) is not significant in either location.

Significant negative correlations are observed in both locations for X vs. Y and Y vs. Z. However, only Location 1 indicates a significant negative correlation for X vs. Z.

The variance analyses of tables 7 and 8 provide a description of the variation in yield per unit area (W) which is accounted for by its yield components. In both locations, the regression is significant. In tables 9 and 10, the degree of importance of each individual component on yield is evaluated. Since the computations were based on adjusted values, the R_2 (.77 and .74 respectively) tend to be of a smaller value. In all three statistics, namely beta weight, partial correlation coefficient and R^2 deletes, Y is found to be the most important component associated with W.

X and Z follow in that order. These results correspond with the correlation coefficients shown in Table 6.

Tables 11 and 12 consist of the mean values of W,X,Y and Z in relation to the frequencies of stand density. At Location 1 (Table 11), W is constant across stand density. However,at Location 2 (Table 12), yield peaks at a stand density of 38 plants per plot. This could also be derived by differentiating the regression equation with respect to W:

$$W = 2.60\ X_s - .034X_s^2$$

$$\frac{dW}{dX_s} = 2.60 - .068X_s$$

$$X_s = \frac{2.6}{.068} = 38.24$$

Table 13 provides the distribution of plus and minus deviations from the population mean of the five top varieties. Note the consistence of the plus signs for Y at both locations.

In Table 14,W,X,Y and Z for the top five varieties are expressed as percentage of the mean at both locations. For each variety, component compensation is evident along with high values for Y (except for P500A).

The values of W,X,Y and Z relative to their means at each location are provided in Tables 15 and 16.

Table 2. Analysis of variance on the regression of yield (W) and yield components (X,Y,Z) on stand density. (Location 1)

Source	df	Mean Squares			
		W	X	Y	Z
Entries	29	968.74**	142.35**	349895.39**	.00004**
Stand Density	1	586.18	2668.60**	1059578.00**	.000004
Residual	149	325.68	57.62	104954.40	.0000055

**= P<.01

Table 3. Analysis of variance on the regression of yield (W) and yield components (X,Y,Z) on stand density. (Location 2)

Source	df	Mean Squares			
		W	X	Y	Z
Entries	29	648.43**	183.14**	420749.66**	.00003**
Stand density	1	2829.02**	3446.70**	227688.41	.000001
Residual	130	350.01	73.59	109298.64	.000008

**= P<.01

Table 4. Analysis of variance on the quadratic relationship of yield (W) and yield components (X,Y,Z) on stand density (Location 1)

Source	df	Mean Squares			
		W	X	Y	Z
Stand density (Q)	2	400.09	1443.67**	661097.84**	.000005
Residual	148	326.44	56.53	103889.11	.000006

**= P<.01

Table 5. Analysis of variance on the quadratic relationship of yield (W) and yield components (X,Y,Z) on stand density. (Location 2)

Source	df	Mean Squares			
		W	X	Y	Z
Stand density (Q)	2	1890.04**	1724.27**	124724.70	.000004
Residual	129	345.35	74.14	109977.23	.000008

**= P<.01

Table 6. Simple correlation coefficients for yield and yield components. Each population/location comprises 30 entries.

	Location 1	Location 2
r_{wx}	.229**	.278**
r_{wy}	.585**	.596**
r_{wz}	-.064	-.151
r_{xy}	-.393**	-.425**
r_{xz}	-.202**	-.030
r_{yz}	-.391**	-.496**

**= P<.01

Table 7. Analysis of variance on the multiple regression of yield per unit area (W) on heads per unit area (X), seeds per head (Y) and average seed weight (Z). Location 1. R_2 = .77

Source	df	Mean Squares
Regression	3	20689.37**
Error	176	107.94

**=P<.01

Table 8. Analysis of variance on the multiple regression of yield per unit area (W) on heads per unit area (X), seeds per head (Y), and average seed weight (Z). Location 2. $R_2 = .74$

Source	df	Mean Squares
Regression	3	17207.16**
Error	157	117.76

**=P<.01

Table 9. Multiple Regression Statistics for yield per unit area (W) as the dependent variable and heads per unit area (X), seeds per head (Y) and average seed weight (Z), as the independent variables (Location 1)

Variable	Beta weights	Sig. level	Partial corr. coefficients	R_2 deletes
X	.75	<0.0005	.79	.37
Y	1.07	<0.0005	.87	.05
Z	.51	<0.0005	.66	.58

$R_2 = .77$

$R = .88$

The R^2 deletes measures the regression of W without the designated variable.

Table 10. Multiple regression statistics for yield per unit area (W) as the dependent variable and heads per unit area (X), seeds per head (Y) and average seed weight (Z) as the independent variables. Location 2.

Variable	Beta weights	Sig.level	Partial corr. coefficients	R^2 deletes
X	.66	<0.0005	.76	.38
Y	1.00	<0.0005	.84	.11
Z	.28	<0.0005	.43	.68

R^2 = .74

R = .86

The R^2 deletes measures the regression of W without the designated variable.

Table 11. Mean values of yield per unit (W), heads per unit area (X), seeds per head (Y), average seed weight (Z) in relation to frequency of stand density. Figures obtained from observations of 30 entries. Location 1. (n = 180)

Stand category	Frequency	$\bar{X}$ (#)	$\bar{Y}$ (#)	$\bar{Z}$ (gms)	$\bar{W}$ (bushels)
6	1	18	1933	.0183	41.73
8	1	21	1406	.0203	44.39
13	1	38	1210	.0236	70.16
14	2	42	948	.0259	58.23
16	1	51	681	.0173	31.37
17	4	40	1193	.0238	62.52
18	3	50	1186	.0217	57.25
19	3	39	994	.0284	59.31
20	3	35	1329	.0250	68.64
21	6	40	1489	.0228	59.33
22	8	43	1312	.0231	73.14
23	6	43	1011	.0243	60.00
24	2	45	1167	.0219	68.17
25	12	46	1123	.0232	65.53
26	11	44	1302	.0233	75.00
27	7	43	1240	.0246	77.32
28	6	44	1230	.0249	74.94
29	11	47	1278	.0221	75.72
30	7	50	1250	.0222	74.86
31	6	43	1292	.0210	63.77
32	13	50	1191	.0215	71.65
33	4	52	1146	.0197	65.18

Table 11 (Continued . . .)

Stand Category	Frequency	X (#)	Y (#)	Z (gms)	W (bushels)
34	9	52	1087	.0227	68.63
35	8	56	991	.0221	69.05
36	4	52-	1101	.0238	77.67
37	3	49	1066	.0218	63.88
38	5	53	944	.0226	58.39
39	3	52	1206	.0205	72.26
40	5	48	1117	.0228	67.51
41	1	49	1161	.0226	74.90
42	3	53	895	.0216	59.55
43	4	50	1284	.0212	73.54
44	2	54	957	.0211	59.55
45	3	53	1312	.0208	78.96
46	3	54	1069	.0225	72.33
47	1	54	1102	.0250	85.05
48	2	54	994	.0193	59.79
51	3	52	1239	.0212	75.54
56	1	63	1157	.0227	94.92
57	1	71	1044	.0217	92.20
59	1	61	1292	.0204	91.92
Average of preceding values		47	1179	.0226	69.06

Table 12. Mean values of yield per unit area (W), heads per unit area (X), seeds per head (Y), average seed weight (Z) in relation to frequency of density. Figures obtained from observations of 30 entries. Location 2 (n = 161)

Stand category	Frequency	X (#)	Y (#)	Z (gms)	W (bushels)
10	1	48	1079	.0189	74.94
11	1	35	1353	.0240	57.14
12	1	31	1300	.0233	76.77
15	3	49	680	.0238	46.32
16	2	34	1160	.0257	46.17
17	1	44	1165	.0244	65.61
18	3	37	1173	.0229	56.90
19	9	41	1198	.0231	71.09
20	3	41	811	.0248	44.12
21	4	43	1003	.0244	60.56
22	6	37	957	.0217	67.93
23	9	45	1362	.0210	71.66
24	15	43	1286	.0219	67.50
25	11	46	1046	.0232	60.98
26	11	42	1244	.0233	66.22
27	6	53	895	.0243	59.14
28	6	51	1144	.0237	77.59
29	6	54	928	.0251	69.03
30	12	48	1131	.0237	70.59
31	5	48	1378	.0243	73.55
32	7	39	1270	.0235	68.46
33	3	53	1022	.0229	66.56

Table 12 (Continued ....)

Stand Category	Frequency	X (#)	Y (#)	Z (gms)	W (bushels)
34	7	57	1021	.0228	72.75
35	3	51	1127	.0240	72.20
36	5	45	1257	.0228	71.23
37	4	60	1268	.0212	84.26
38	2	55	1120	.0261	87.85
39	2	48	1670	.0183	84.60
40	1	64	584	.0300	64.62
41	1	31	1457	.0227	63.28
42	4	69	672	.0235	59.22
43	1	59	1203	.0207	82.12
44	2	68	785	.0249	75.45
48	3	54	955	.0249	72.58
50	1	30	1528	.0250	69.91
Average of preceding values		47	1130	.0232	67.91

Table 13. Plus and minus deviations from the mean of the 5 top entries.

Location 1			Location 2			Average		
X	Y	Z	X	Y	Z	X	Y	Z
+	+	-	-	+	+	-	+	+
+	+	+	-	+	-	+	+	-
+	+	-	-	+	+	+	+	-
+	+	-	-	+	-	-	+	-
-	-	+	-	+	+	-	-	+

Table 14. Number of heads per unit area (X), number of seeds per head (Y), average kernel weight (Z) and average yield per unit area (W) expressed as percentage of the mean at both locations. The entries are the best 5 varieties among a population with minimal bird damage (<10%)

Entry	X %	X %	Z %	W %
1. NK 180	93.01	128.43	100.4	118.67
2. BR 100	108.28	106.28	97.9	109.68
3. P550 BR	101.10	104.10	99.1	108.34
4. 1015 BR	99.10	129.92	85.0	108.16
5. P500A	94.61	98.34	104.7	105.68
$\bar{X}$ of top 5 as % of 2 location means	99.22	113.41	97.42	110.10

Table 15. Number of heads per unit area (X), number of seeds per head (Y), average seed weight (Z) and average yield per unit area (W) expressed as percentage of the location means. The entries are the best 5 varieties among a population with minimal bird damage (<10%) Location 1.

Entry	X %	Y %	Z %	W %
1. NK 180	100.4	119.9	98.3	120.27
2. BR 100	113.5	100.2	100.0	116.95
3. P550 BR	101.00	108.6	96.9	110.41
4. 1015 BR	100.0	117.3	86.4	104.80
5. P500 A	91.97	95.9	105.7	101.90
Mean of top 5 as % of location means	101.37	108.38	97.46	110.86

Table 16. Number of heads per unit area (X), number of seeds per head (Y), average seed weight (Z), and average yield per unit area (W) expressed as percentage of the location means. The entries are the best 5 varieties among a population with minimal bird damage (<10%). Location 2.

Entry	X	Y	Z	W
1. NK 180	81.1	137.2	102.5	117.16
2. BR 100	97.6	112.6	96.2	102.64
3. P550 BR	95.7	99.4	101.7	106.27
4. 1015 BR	92.9	142.9	83.5	111.51
5. P500 A	92.0	100.9	104.2	109.4
Mean of top 5 as % of location means	91.82	118.6	97.6	109.4

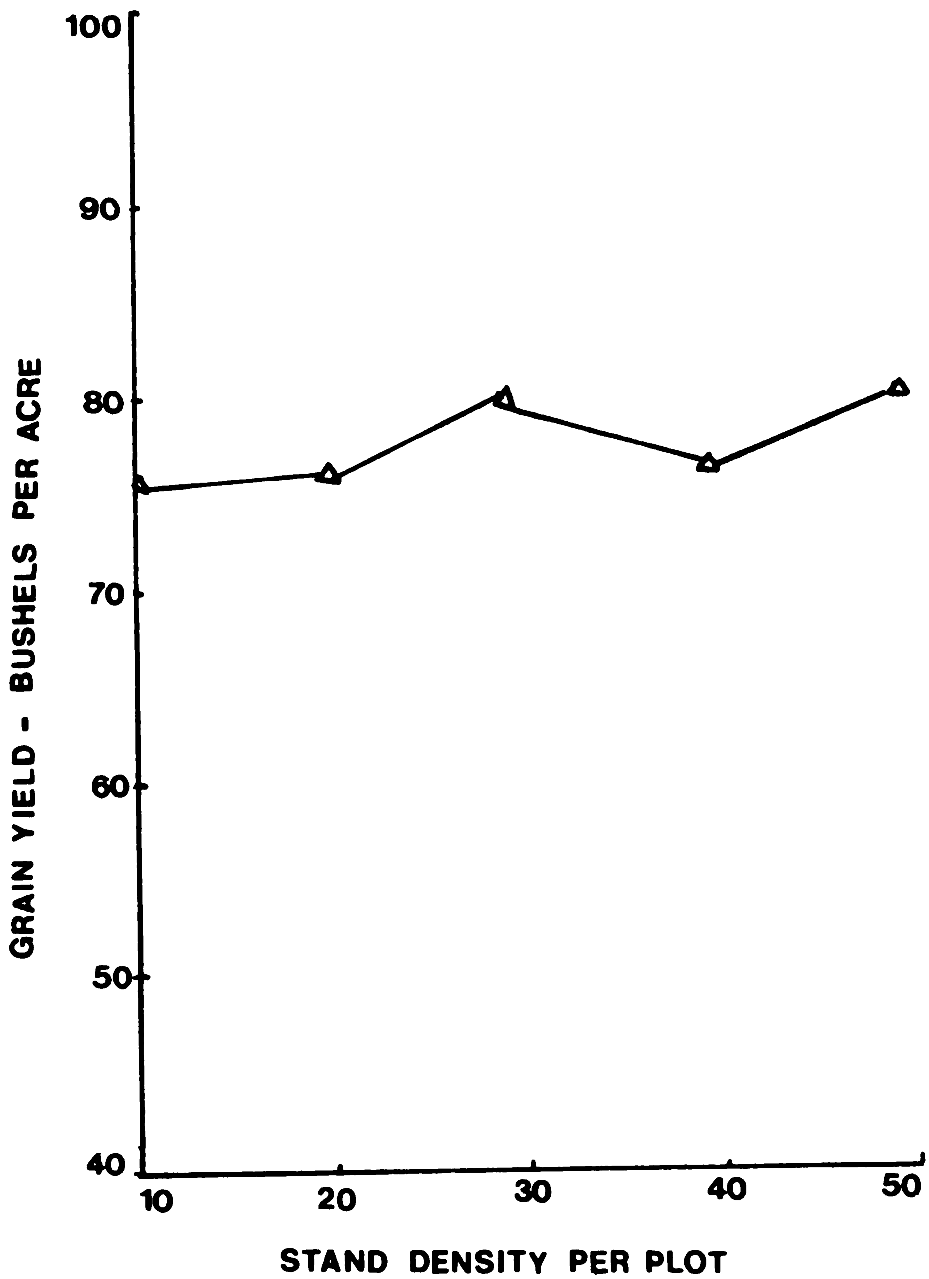

Figure 1. Grain Yield as affected by stand density (Location 1)

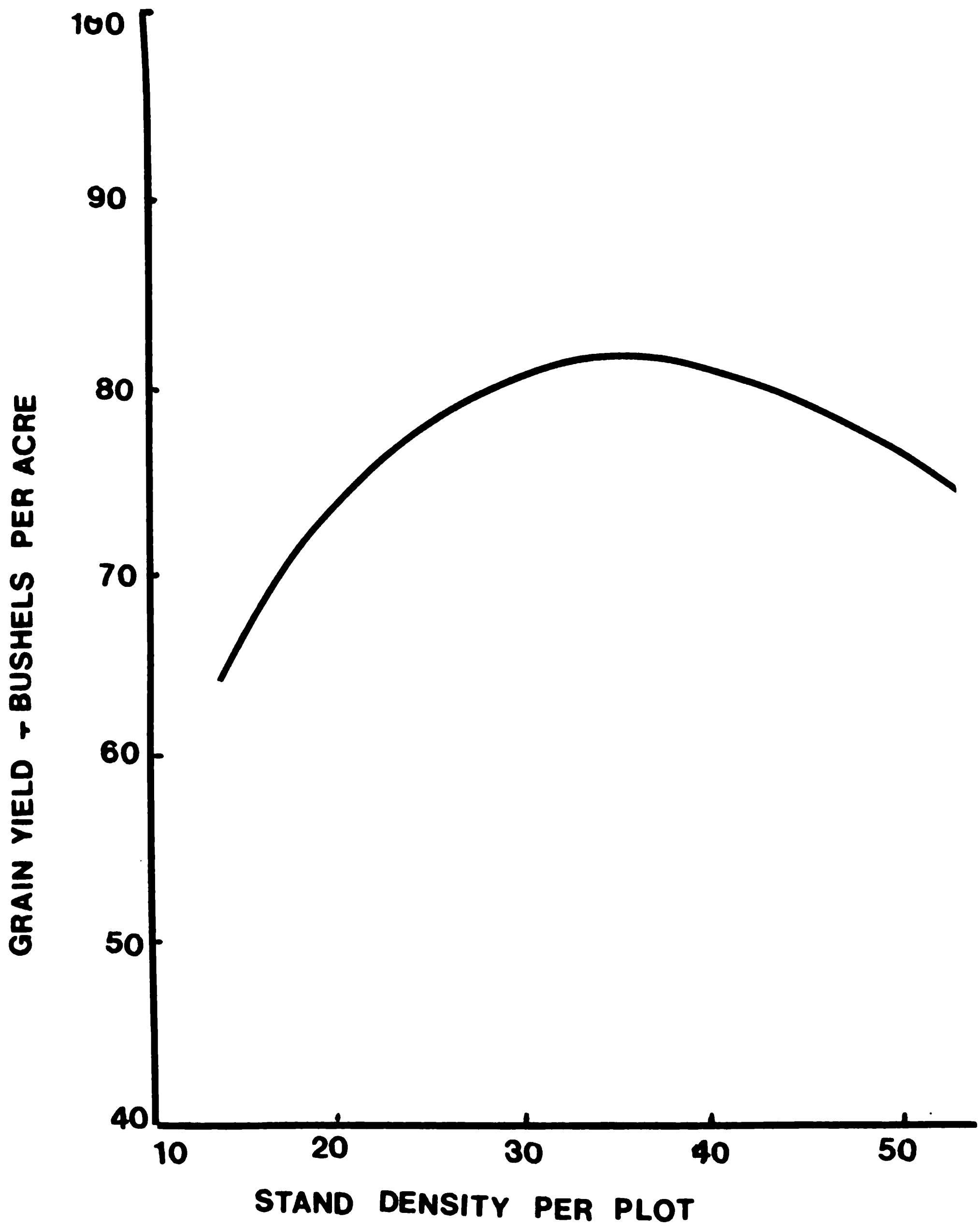

Figure 2. Grain yield as affected by stand density (Location 2).

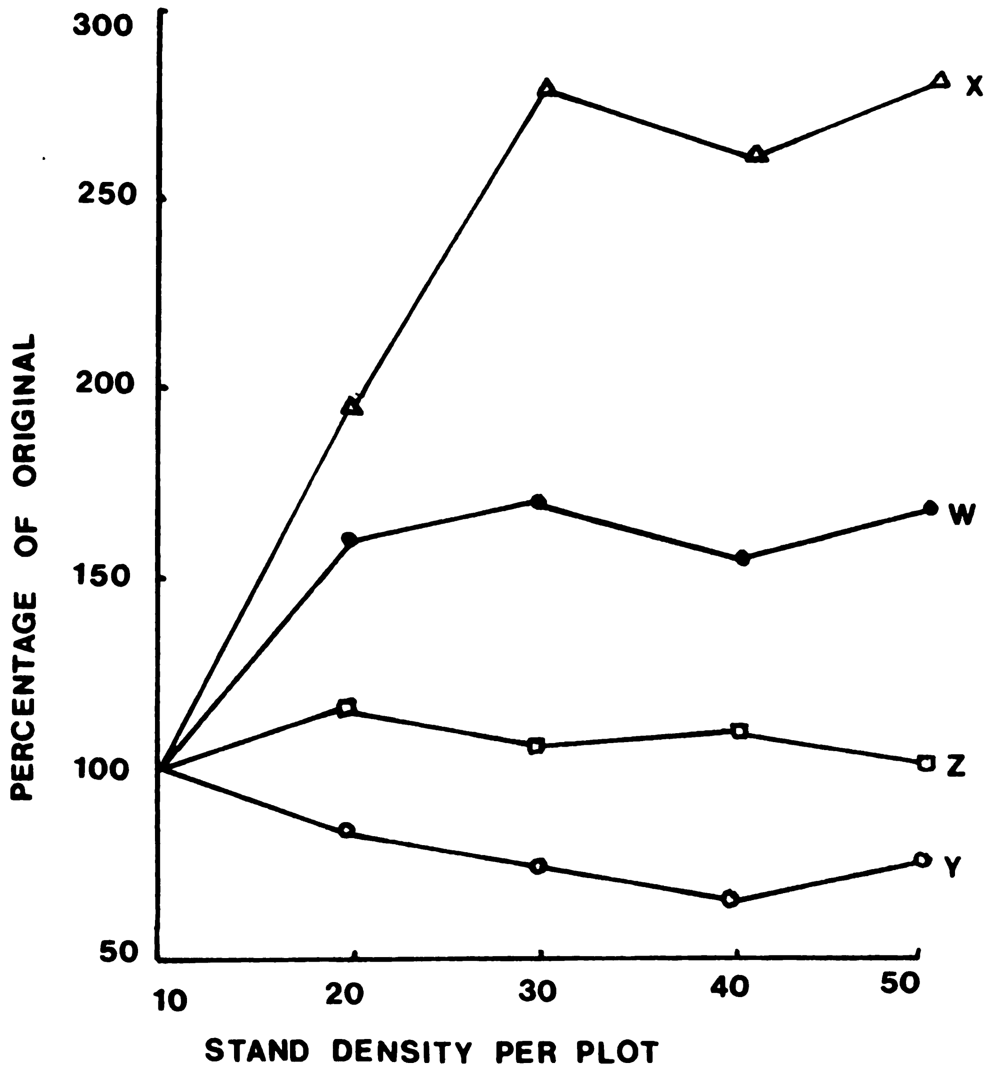

Figure 3. Yield and yield components as affected by stand density (Location 1)

** = P<.01

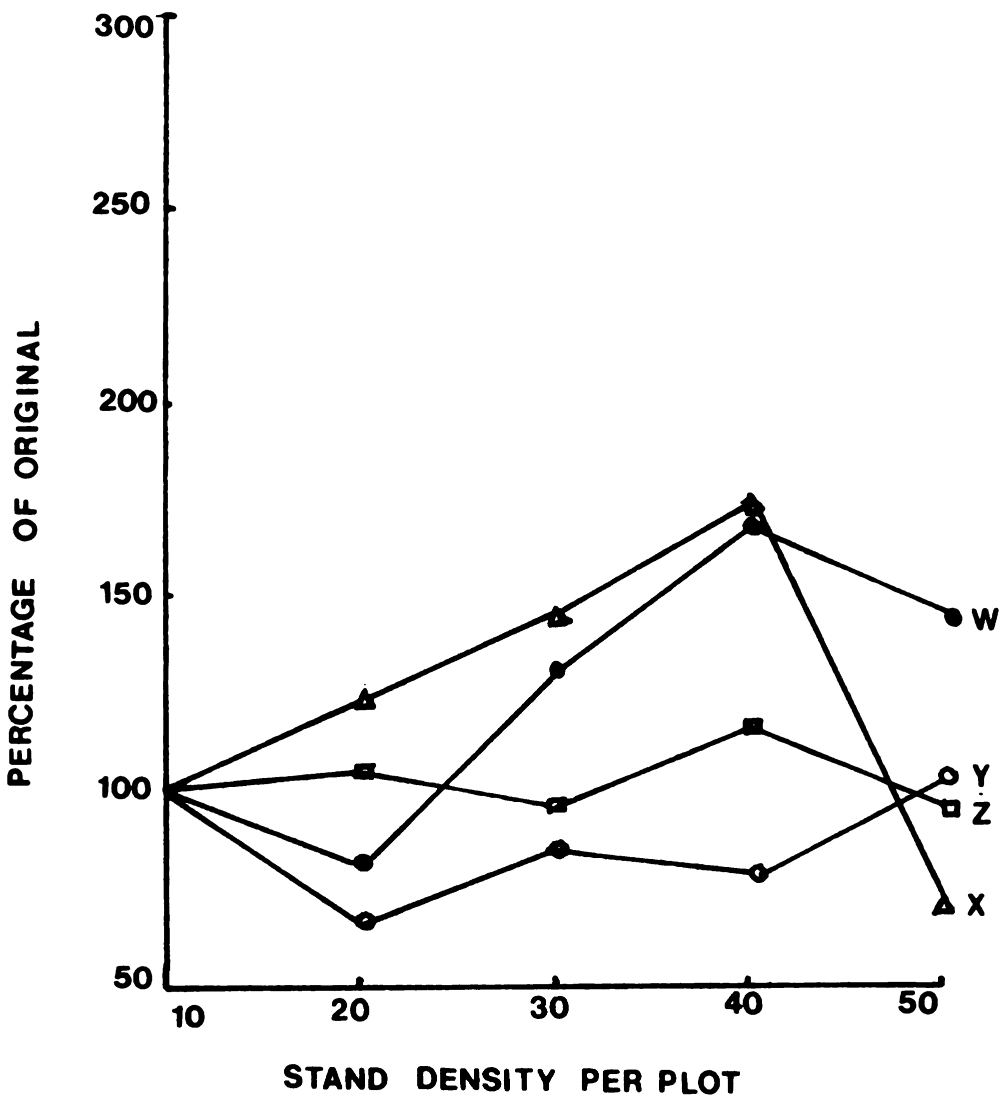

Figure 4. Yield and yield components as affected by stand density (Location 2).

** = P<.01

DISCUSSION

i) The relationship of yield to stand density

The response of grain yield and its components to a varying stand density was evaluated at two different locations in Michigan. Soil moisture during the growing period is believed to be an important factor in determining the influence of stand density on grain yield. It was observed that when yield was regressed on stand density (Tables 2 and 3), a significant relationship was observed in the drier location (Location 2) while no such relationship was evident at Location 1. It has been noted (Grimes and Musick 1960, Porter et al. 1960, Robinson et al. 1964) that when soil moisture is abundant, the performance of sorghum in terms of grain yield is not significantly affected by variation in plant population. The crop has a great capacity to adjust by tillering more profusely and developing bigger head size in poor stand density and reducing head size and "cancelling" the production of tillers on some plants in a densely populated environment. No significant relationship was observed at Location 1 but it is likely that a behavior similar to Location 2 may be in operation when stress occurs.

At Location 2 stand density appears to have an effect on grain yield. The significance of the quadratic relationship between grain yield and stand density implies that a certain environmental resource is limiting. Although sorghum is well known to be a drought-resistant crop, a limited amount of moisture in the soil during the critical stages of plant growth may ultimately determine the size of plant population that could be sustained.

When an essential input becomes limiting in an environment, individual plants which may previously be at ease with each other, will compete for that product. Two consequences ensue - firstly, the sharing of the limited input restricts the amount that would be available to each individual, thus retarding its growth; secondly, the "survival of the fittest" syndrome would result in the inhibition of the weaker competitors, thus reducing the number of potential individuals that could contribute to the overall performance of the crop population.

Plant competition in the words of F.E. Clements as quoted by Donalds (1963) is "Purely a physical process. With few exceptions, such as the crowding of tuberous plants when grown too closely, an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of the modified factors upon its competitors. In the exact sense, two plants no matter how close, do not compete with each other so long as the water content, the nutrient material, the light and the heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins."

Mather (1961) on the subject of competition (when individuals are mutually detrimental) and cooperation (when individuals are mutually beneficial) among plants, proposed that cooperation or neutrality will prevail when the relationship is density - independent; on the other hand, when it is density-dependent, cooperation only occurs at the low densities, followed by a neutral relationship and ultimately by active competition at the higher densities.

It is suggested here that soil moisture at the critical growth stages is the determinant factor which resulted in different responses of yield to stand density at the two locations.

At Location 1, with water and all other essential inputs assumed to be present in adequate amounts, the occurrence of interplant competition must be minimal and/or non significant. However, this does not mean that an increase in stand density would result in a corresponding increase in grain yield. Another form of competition, occurring at the intraplant level, would give rise to component compensatory reactions ensuring that yield is kept constant within a wide range of stand density. Hence, the density-independent relationship manifested at Location 1.

At Location 2, where water was believed to be limiting, yield became dependent on stand density.

Cooperation between plants intensified with increasing densities until an optimum was reached beyond which keen competition assumed its natural course.

The optimum population is here defined as that level of stand density in which an exhaustive exploitation of the limiting essential input (soil moisture in this case) is exerted by the individual plants as a group such that the maximum potential of the crop is realized at that particular environment.

The non-linearity of grain yield at the drier location also implied that interplant competition was a much stronger force than intraplant competition in determining yield. Indeed if competition between plants is very intense, the role of intraplant competition and hence yield component compensation may be of minor importance. As an illustration, assume that for a particular plant population a basic (minimum) requirement of essential inputs is needed for a certain level of production. If this minimum is not met, yield would be reduced. Any component compensation that follows would be mediated at a lower level of yield.

ii) Yield components in relation to yield

Traits and characters belonging to an organism can exhibit significant correlation between each other by the occurrence of genetic linkage, pleiotropy or the obligatory sharing of the same source of essential inputs required for their development.

With respect to yield components, Duarte (1966) and Adams (1967), have shown that in field beans these subtraits are indeed controlled by independent gene systems and that correlations between them are caused by the third possibility cited above.

Could this be true too in the sorghum plant? Table 6 provides the simple correlation coefficients among the traits and it is of interest to note the difference in magnitude of the correlations observed between the two locations. Except for r_{xz}, all the values at Location 2 are found to be of a larger magnitude than that at Location 1. If correlation is any indication of the influence exerted by environmental forces, then the explanation for the variation may be simply put forth. At Location 2, the sorghum plants were subjected to a more strenuous environment in the nature of limiting soil moisture. Consequently, intraplant competition involving the yield components were greatly amplified giving rise to larger values of r. On the contrary, the environs of plants at Location 1 were much more relaxed, with lesser demands being imposed on the compensatory mechanism of the yield components. As a result, intraplant competition was reduced and a lower r value was registered.

The preceding observations in sorghum appear to confirm what several workers have implied in other crops that the correlations among yield components are due not to linkage nor pleiotropy but due to the sharing of a common essential input needed for their development.

Figure 3 illustrates the nature of compensation among the yield components. X and Y were at odds with each other. Each of these two components also demonstrated quadratic relationships (Table 4) with stand density. However, since W is the product of XYZ (note: Z is found to be statistically constant across stand densities) the curvilinear effects of stand density on X (positive) and Y (negative) tend to cancel one another and results in the linearity of W.

As had been pointed out by earlier workers, yield component compensation is a property of good genotypes. It is an intraplant buffering complex which goes into operation in response to induced stress by limiting environmental resources. Attached to this concept is the underlying theory that yield components have a sequential pattern of development. The apportionment of a bigger amount of resources in producing high X for example, would result in a lesser amount available for producing a satisfactory level of Y or Z. However, it need not necessarily be true that the earliest formed component receives top priority at all times. In certain environments, adverse conditions at the time of formation of X may impede the actions of genes responsible for high X, thus drastically inhibiting the expression of the true genetic potential of this particular component. The environment might change for the better during the development of the next sequential character, Y and the Y-genes would be favored to exploit the now bigger share of resources. The strong positive correlation between W and Y in the present data suggests that they might fit in the scheme mentioned above. In other environments, Z genes might be favored, either in lieu of better performances from X and Y or concomitantly with either X or Y.

The contribution of the individual yield components to the ultimate complex trait, yield are examined, as summarized in Tables 9 and 10. Each of the components significantly contribute to the expression of W. (The beta weight, which is the standard partial regression coefficient, is highly significant for all three components). This is hardly surprising biologically since grain yield is the multiplicative expression of the three components. However it is interesting to note the importance attached to each of these components by the complex trait.

Seeds per head (Y), with the biggest magnitude in all statistics at both locations obviously has the greatest influence on yield. In order of reduced importance were X and Z respectively. Further evidence in the role of Y is furnished in table 13 which represents a grouping of the five highest entries. Plus values for X,Y,Z are prevalent on the top entries. However, the consistency of Y is noteworthy. Undoubtedly, any yield improvement for this environment have to take Y into prime consideration.

The influence of Z in both locations was the weakest among all the three components. Grafius and Thomas (1971) have shown in oats that the genetic control of sequential traits is to a great extent indirect through the determination of the initial traits in the series. Their concept of "oscillatory convergence" include the fact that the more remote a trait from the origin of sequence, the less the direct genetic control. An identical mechanism might indeed be existing in sorghum too and would explain why the relationship of average kernel weight and grain yield is minimal.

iii) Geometric Configuration

Let grain yield in sorghum (W) be represented by the volume of a parallelepiped with the number of heads per unit area (X), seeds per head (Y) and average seed weight (Z) as its edges.

The shape of this three-dimensional figure is determined by the individual lengths of its three edges (viz. X, Y and Z). These lengths are in turn subject to modification by the particular environment in which the plants are grown. Since X, Y and Z are sequential in development, it could be inferred that each is exposed to a different environmental pressure and consequently, the degree of change imposed on the length of each edge varies.

By convention, it is known that the volume of a rectangular parallelepiped is affected most by changes in the shortest edge and least by changes in its longest edge. For a genotype to be highly productive in a particular region and/or locality, it must have the ability to transform its geometric configuration in such a way that the variable most subject to change is its longest edge. This is crucial since in the event of an adverse situation, any reduction in the length of the longest edge would not result in a substantial loss of yield.

The top 5 varieties from both locations were examined with respect to optimum shape. The number of seeds per head (Y) was found to be the longest edge of the rectangular parallelepiped in this particular region in Michigan (Table 14). Among the 5 best varieties, i.e. Y = 113.41%; X = 99.22%; 2 = 97.42%. However, the geometric approach has rightly cautioned against overemphasizing the importance of one particular component (edge) while neglecting the other edges in the configuration. It is imperative that the "minor" components which help make up the complete structure of yield be placed in perspective too for each of these components is complimentary to each other. In Table 14, for example, 1015 BR has the longest Y edge, but without the proper balance in the other components (specifically - a very short Z edge), its volume is reduced considerably.

A suitable shape for this region would be one with Y as the longest edge (exceeding the population mean) and X and Y being of equivalent lengths and clustering around the population mean.

At Location 1 (Table 15), where growing conditions were more stable, the configuration was more or less identical with the general shape fitted for the region. On the other hand, when the environment was less favorable, as in Location 2, there was a tendency for shape modification. Almost invariably, the higher yielding varieties (NK 180 and 1015 BR - Table 16) had extremely long Y edges, at the expense of either X or Z. The ability to lengthen the edge of the component most strongly correlated with the complex trait seem to be indicative of a universal genotype and could be regarded as a stabilizing mechanism to maintain yield.

It is also interesting to observe the behavior of number of heads per unit area (X) under two different environments. As had been noted earlier (Table 5, Figure 4) the quadratic relationship evident at Location 2 between grain yield and stand density was essentially due to X; failure of the plants to tiller adequately (and consequently to produce heads) at the drier location resulted in the decline of W at higher densities. Tables 15 and 16 seemed to reaffirm those conclusions; the mean percentage of the top 5 varieties for X dipped from 101.37% (Location 1) to 91.82 (Location 2).

LITERATURE CITED

1. Adams, M.W. (1967). Basis of yield component compensation in crop plants with special reference to the field bean, P. vulgaris. Crop Sci. 7:505-510.

2. Bond, J.J., Army, T.J., and Lehman, O.R. (1964). Row spacing, Plant Populations and Moisture Supply as Factors in Dryland Grain Sorghum Production, Agron. J. 56:3-6.

3. Brown, P.L. and Shrader W.D. (1959). Grain yields, Evapotranspiration and Water use efficiency of Grain Sorghum under different cultural practices. Agron. J. 51:339-343.

4. Cohen, J. (1968). Multiple Regression as a General Data - analytic System. Psycho. Bulletin 70(6):426-443.

5. Donald, C.M. (1963). Competition among crop and pasture plants. Adv. Agron. 15:1-118.

6. Draper and Smith (1967). Applied Regression Analysis. J. Wiley, New York.

7. Duarte, R.A. (1966). Responses in yield and yield components from recurrent selection practiced in a bean hybrid population at 3 locations in North and South America. ph.D. Thesis, Mich. State Univ., E. Lansing.

8. Grafius, J.E. (1956). Components of yield in oats: A geometrical interpretation. Agron. J. 48:419-423.

9. ________ (1965). A geometry of plant breeding. MSU Agric. Exp. Sta. RB #7, 59p.

10. ________, R.L. Thomas (1971). The case for indirect genetic control of sequential traits and the strategy of deployment of environmental resources by the plant. Heredity 26(3):433-442.

11. Grimes, D.W. and Musick, J.T. (1960). Effect of plant spacing, fertility and irrigation management on grain sorghum production. Agron. J. 52:647-650.

12. Hutchinson, J.B. (1940). The application of genetics to plant breeding I. The genetic interpretation of plant breeding problems. J. of Genetics 40:271-282.

13. Karchi and Rudich (1966). Effects of row-width and seedling spacing on yield and its components in grain sorghum grown under dryland conditions. Agron. J. 58(6):602-604.

14. Maddur, A.B. (1972). Yield component compensation in mixtures of oats. M.S. Thesis. Mich. State U.

15. Mann, H.O. (1965). Effects of rates of seeding and row widths on grain sorghum grown under dryland conditions Agron. J. 57(2):173-176.

16. Mather, K. (1961). Competition and Cooperation. Symp. Soc. Exptl. Biol. 15:264-281.

17. Mathews, O.R. and Barnes, B.F. (1940). Dryland Crops at Dalhart (Texas) Field Sta. USDA Cir. 564.

18. Nelson, C.E. (1952). Effects of spacing and nitrogen applications on yield of grain sorghums under irrigation. Agron. J. 44:303-305.

19. Porter, K.B., Jensen, M.E. and Sletten, W.H. (1960). The effect of row spacing, fertilizer and planting rate on the yield and water use of irrigated grain sorghum. Agron. J. 52:431-434.

20. Robinson, R.G., Bennet, L.A., Nelson, W.W., Thompson, R.L. and Thompson, J.R. (1964). Row spacing and plant population for grain sorghum in the humid north. Agron. J. 56:189-191.

21. Suits, D. (1957). Use of dummy variables in regression equations. J. Am. Stat. Assoc. 52:548-551.

22. Stickler, F.C. and Wearden, S. (1965). Yield and yield components of grain sorghum as affected by row width and stand density. Agron. J. 57(6): 564-567.

23. Thomas- R.L., Grafius, J.E., Hahn, S.K. (1970a). Stress: an analysis of its source and influence. Heredity 26:423-432.

24. ________ (1970b). Genetic analysis of correlated sequential characters. Heredity 26:177-188.

25. Whitehouse, R.N.H., Thompson, J.B., Valle Ribeiro, M.A.M. (1958). Studies in the breeding of self-pollinating cereals. The use of diallel cross analysis in yield prediction, Euphytica 7:147-169.