YIELD COMPONENT COMPENSATION IN MIXTURES OF OATS (*Avena sativa* L.)

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ABSTRACT

YIELD COMPONENT COMPENSATION IN MIXTURES OF OATS (*Avena sativa L.)*

By

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Six oat varieties were compared with several mixtures of the same varieties for yield and yield components. The mixtures were found to have affected the yield additively and therefore no mixture yielded greater than the highest yielding variety in the mixture. A significant negative correlation was observed between the tiller number (X) and the kernel per tiller number (Y), and negative, though insignificant, correlation between the latter component and the kernel weight (Z). A remarkable disturbance in the tiller number has occurred in the mixtures which is believed to have resulted from some sort of competition between the mixed varieties. The disturbance in X components was not found to have any influence on the additive effect of the varieties on the mixtures' yield because Y and Z that follow X in development showed a great flexibility in adjusting in a compensatory manner to changes

in X in a way that maintains the yield linearity. It is believed that yield component compensation was caused by intraplant competition due to stress. A positive relation was detected between the varietal differences in X and the disturbance in X caused in their mixtures. A hypothesis relating the amount of disturbance in the tiller number in the mixture to the range of that component between the mixed varieties was proposed.

YIELD COMPONENT COMPENSATION

IN MIXTURES OF OATS

(Avena sativa L.)

By

Abubaker M. Maddur

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Cont.)

Table | Page

LIST OF TABLES (Cont.)

LIST OF FIGURES

LIST OF FIGURES (Cont.)

Figure

INTRODUCTION

The traditional pattern in varietal development in oats and similar crops is characterized by the release of varieties with a high degree of homogeneity, possessing a satisfactory adaptation to the predominant environmental conditions. Yield of seed in most crops, though genetically controlled, is a trait highly influenced by the environment, and subject to a wide variation when growth conditions change. Yield and its stability can thus be considered a measure of accommodation of the plant to the operating natural factors of growth.

Under given environmental conditions, different oat varieties may show remarkable differences in yield, probably as a result of their differences in needs for growth and development, or because of differences in capability of exploiting the available environmental resources.

It has been argued for a long time that heterogeneous populations might be superior to homogeneous varietal populations in their efficiency in exploiting these environmental resources, and consequently might yield more.

Yield in oats is a product of several components which are sequential in time, gene regulated, and highly influenced by growth conditions. Moreover these components are interdependent in their development, and known to function in a compensatory manner in expressing the ultimate grain yield.

The aim of this study is to determine whether varietal mixtures would have any superiority in yield over their component varieties, by observing the behavior of yield components in their interrelated function.

LITERATURE REVIEW

Varietal Mixtures Versus Pure Cultures

Jensen and Kent (1963) warned that the genetic homogeneity that characterizes major domestic varieties of crops may mask a disastrous agent that cannot be observed under some environmental conditions and therefore a superiority expressed by a given variety under some conditions may diminish when conditions change.

Their examples were the two major diseases in oats, stem rust and crown rust. With the great number of races and subraces the causal pathogens are able to produce through hybridization and mutation, it becomes very difficult to develop a single variety resistant to all those existing and to new developing races of the pathogens. A uniline variety with resistance to one or few races is apt to lose its resistance when new races are developed or are introduced into the area. The authors suggested multiline varieties built up of several lines that are similar in appearance but different in genetic structure to supplement the domestic varieties.

Flor (1956) similarly reported that many flax varieties, developed as rust resistant, frequently yield to new races, or to changes in the prevalence of races of the pathogen that attacks them. He suggested that this problem can be handled by developing several varieties, where each variety carries different sets of genes for resistance and then pooling these varieties into a composite variety.

Cournoyer, Browning and Jowett (1968) argued that oat mixtures supported less crown rust early in the season than did the pure line varieties and that the progress of the epiphytotic was much slower in the multiline variety.

In contrast Borlaug (1959) found that mixtures are not necessarily consistent in retarding the spread of diseases among populations.

From this point the argument of mixtures versus pure cultures was extended to investigation on other agronomic characters including lodging resistance, insect resistance and yield.

A plant population made up of several genotypes differing in their environmental needs and biological activities is believed to be more efficient than a pure culture in exploiting the available environmental resources to their maximum potential and therefore may produce a high and/or more consistent yield. The available information does not support absolute superiority of mixtures over the mean of pure cultures of their consitutent varieties under all circumstances, in either yielding ability or yield stability. Grafius (1966) mixed two oat varieties, "Simcoe" and "Rodney," with a third variety, "Garry" in 10% increments, and found that random mixtures are not expected to yield more than the mean yield of the varieties included in the mixtures. However, the superiority of the mixture 40:60% of "Rodney" and "Garry," in yield, lodging resistance, and test weight was observed. He suggested that the superiority of a multiline will depend on careful selection plus optimum proportions of the varieties, included in the mixture to take advantage of non-linear effects.

Jensen (1965) compared oat composites with the mean of their component lines over a period of 8 years. The mixtures exceeded the average yield of the pure stands by 3.2%, and a 5-line oat multiline yielded 7.3% greater than the average yield of its component lines. A study on 6 oat cultivars and 57 mixtures among them by Frey and Maldonado (1967) produced several mistures yielding more than the best cultivar and the mixtures were more stable in production and showed a remarkable increased superiority when the environment became more stressed. In the meantime no association was found in this study between the number of cultivars in the mixtures and the grain yield of the mixtures.

Patterson and co-workers (1963) compared for four years six varieties of oats and equal blends of the six in all combinations of two. Though the mixtures did not show any superiority in yield, they were superior in their standing ability. On the other hand some of the literature does not support the consistent superiority of mixtures in either yield or other agronomic characters. A report by Clay and Allard (1969) found that barley mixtures expressed small advantage over their component varieties. Moreover the mixtures were inferior in stability.

Varietal Interaction

Whenever a mixture of two or more lines shows a significant deviation from the sum of the proportional performances of the pure cultures of the lines included in the mixture, some sort of phenotypic interaction between the lines is assumed to be involved. This type of interaction was reported by Probst (1957). In a mixture of soybean varieties, Probst observed that the latest maturing variety in a mixture matured earlier than a pure stand of the same variety. Jensen and Federer (1964) working with population mixtures of tall and short varieties of wheat found that the taller varieties enhanced the yield by five bushels per acre while the shorter ones reduced the yield by only 2.3 bushels per acre. Obviously, the enhancing and depressing effects did not behave in a compensatory manner, though they were additive in effect. The results shown by Grafius (1966) and Jensen (1965), also support the possibility of this kind of phenotypic interaction.

Gustafsson (1953) compared the yield performance of three barley varieties, "Golden," "Maja," and "Bonus," with their paired mixtures under two levels of manuring and two sowing densities. When sowing was dense and manure application was low, the mixtures were superior to the mean of the component variety by 10%. When manure was increased, with the density level constant, the mixtures yield dropped 7% below the mean yield of its component varieties. When the density tension was relaxed and manure level was lowered the mixtures and the pure stands yielded the same. However, mixtures regained a remarkable superiority when the manure was increased even under sparse sowing conditions. Varietal mixtures reacted in a specific manner to the varied environments.

Co-operation and Competition

Whenever organisms grow in a limited space with limited environmental inputs, they may compete against each other in exploiting the environment or act in a co-operative pattern which leads to better use of the limited resources they share. Milthorpe (1961) referred to competition in plants as ". . . those events leading to the retardation in growth of a plant which arise from association with other plants." Milthorpe set two conditions to be satisfied in order for competition to operate. First, competing individuals should share similarity in needs and activities. Second, the summed needs of individuals must exceed the supply of these needs available to the individual plants, i.e. the supply of environmental inputs does not satisfy the demand for maximum level of biological activities.

Mather (1961) noticed that adjacent organisms may develop a co-operative relationship to retard the effect of a common adverse factor, while still competing for another factor. So plants may compete for one thing while co-operating for another. The net outcome of such adverse relationships depends on the importance of the factors they co-operate or compete for, the degree of co-operation and the severity of competition among them. Differences in competitive ability between organisms of different genera and among species of the same genus were reported by several researchers (De Wit, 1961; Mather, 1961; Sakai, 1961; and Sandfar, 1970). Sandfar (1970) in his report on competition stated that the selective value of a genotype is positively correlated to its performance in pure stands. He also expressed the view that generally the frequency of high-yielding genotypes in mixtures is expected to increase in the course of time but sometimes the results come out to prove the opposite. But the author obviously ignored the role of selection for seed size. Under natural selection in mixtures of annual seed bearing crops, weed-like types will produce relatively more seeds, and consequently more viable offspring.

Sakai (1961) found that competitive ability in plants is an inherited trait conditioned by polygenes and characterized by a very low heritability. Harper (1961), however believes that the success of one species in a mixture at the expense of other species may be a function of the differences in embryonic capital available in the seeds of the two species or due to other differences in agronomic features such as growth rate, growth form, or still to other differences that function in the life cycle of the species. Most if not all of these authors ignore the fact that weeds have small seeds and that natural selection will not produce high yields of seed in annual crops.

Intraplant Competition and Yield Component Compensation

Grafius (1965) explained that the grain yield per unit area in oats can be represented geometrically by a volume (W) of a rectangular parallelepiped with dimensions X, Y, and Z, representing the number of panicles per unit area, the average number of kernels per panicle, and the average kernel weight respectively, so that W = XYZ. In order to keep the yield stable, any change in one axis has to be counterbalanced by change in another. This is a general characteristic of well-adapted varieties which exhibit a nearly constant mean yield under the dominant environmental conditions in the area. The yield components were reported by several workers to exhibit a negative relationship among them (Adams 1967, Adams and Grafius 1971, Dewey and Lu 1959, Rasmusson and Cannell 1970).

In an experiment on soybean, an artificial decrease of component (X) was found by McAlister and Krober (1958) to result in increasing in component (Z). Adams (1967) in a review of yield component compensation in crop plants explained that these negative relationships among yield components are developmental in nature. Adams believes that under severe conditions of interplant competition, available essential resources becomes inadequate to support the needs of individual plants. In consequence, there ensues intraplant competition involving the fitness components for those environmental inputs essential in the development of reproductive structures which finally compel the yield components to vary in a compensatory manner.

MATERIALS AND METHODS

Six varieties of oats *(Avena sativa L.)* were selected for study in three experiments. In each experiment, four oat varieties and nine mixtures among them were tested in a randomized block design with six replications. The mistures were made by mechanical mixing of the number of seeds from each variety equivalent to its desired proportion in a specific mixture to form a total of 1000 seeds (or nearly 30 grams) per plot. The plots were four rows each. Rows were eight feet long and one foot apart. The middle two rows in every plot were used for data collection and the outer two rows served as borders.

Experiment 1

The four varieties included in this experiment were "Ausable" (A), "Garry" (G), "Coachman" (C), and "Mi.-60-106-78" (E). The mixtures among them were 70%A:30%G, 30%A:70%G, 70%G:30%C, 30%G:70%C, 70%C:30%E, 30%C:70%E; 25%A:25%G:25%C:25%E; 10%A:10%G:40%C:40%E; and 40%A:40%G:10%C:10%E.

Experiment 2

In this experiment, "Diana" (D), and "Clintland 64" (L) varieties in addition to "Coachman" (C) and "Mi.-60-106-78" (E) were studied with their following mixtures: 70%C:30%D; 30%C:70%D; 70%D:30%L; 30%D:70%L; 70%L:30%E; 30%L:70%E; 25%C:25%D:25%L:25%E; 10%C:10%D:40%L:40%E; and 40%C:40%D:10%L:10%E. Experiments 1 and 2 were carried out at the Michigan State University Crop Science Research Farm. The oats for both experiments were sown in the second week of April, 1971.

Experiment 3

This experiment was performed on a farm in Lenawee County, Michigan, and the seeds were sown 5 days earlier than experiments 1 and 2. The same varieties and mixtures tested in experiment 2 were tested in this experiment. However, because of an error during the time of sowing, data from Coachman plots in all replications were excluded. For that reason, this experiment was analyzed and handled separately.

The major interest of the study was the grain yield and its morphological components. Data on these characters were collected in a similar way in the three experiments as follows:

<u>Yield (W)</u>

The inner two rows in each plot were harvested the last week of July, and the seeds were dried and weighed and then the average yield per square foot was calculated.

<u>Yield Components (X,Y,Z)</u>

1. Number of tillers (X)

   Twelve days prior to harvesting the tillers in 30 inches from each of the two middle rows were counted and the average number of tillers per square foot was obtained.

2. Average Kernel Weight (Z)

   The number of grains contained in a random sample of three grams of grain was counted using an electrical counter and the average kernel weight calculated.

3. Number of Kernels per Tiller (Y)

   Kernels per tiller (Y) were calculated by dividing the average yield per square foot (W) by the product of the number of tillers per square foot (X) and the average kernel weight (Z).

RESULTS

The mean yield (W) and its components (X,Y,Z) of the thirteen entries included in each experiment are summarized in Tables 1, 2, and 3. The mean squares for the four varieties taken from analysis of variance tables are presented in Tables 4, 5, and 6. It is obvious from Tables 1, 2, and 3, that in no case did the yield of any mixture exceed the yield of its highest yielding component variety.

Sets of each two varieties with the two mixtures of each were separately tested for curvilinear regression for yield and its components (Tables 8 through 15). The pattern of yield and components were further traced graphically (Figures 1 through 8). Figures 9, 10, and 11 illustrate the responses of yield and components of those mixtures in each experiment where the four varieties were included. Tables 8 through 15 clearly show that only linear responses occurred for yield which demonstrates how the yield components have developed a compensatory adjustment to keep the linearity of yield.

TABLE 1.--Yield and yield component means of four oat varieties, Ausable (A), Garry (G), Coachman (C) and Mi.60-106-78 (E) and nine mixtures. (Exp. 1)

Entries	Yield Components			Average Yield (Grams per ft^2 (W)
	Average Number of Tillers per ft^2 (X)	Average Number of Kernels per Tiller (Y)	Average Kernel Weight in Grams (Z)	
100%A	32.63	40.98	.03142	41.76
70%A:30%G	29.03	49.66	.02969	42.23
30%A:70%G	32.07	46.68	.02978	44.27
100%G	33.50	44.99	.03011	45.27
70%G:30%C	31.70	45.80	.02916	41.78
30%G:70%C	32.67	37.59	.03256	39.56
100%C	33.50	31.85	.03370	35.62
70%C:30%E	36.90	33.17	.03140	38.06
30%C:70%E	31.47	42.81	.03065	40.96
100%E	31.77	49.53	.02816	43.42
25%A:25%G:25%C:25%E	39.23	34.45	.03182	41.77
10%A:10%G:40%C:40%E	34.20	41.25	.02965	41.59
40%A:40%G:10%C:10%E	30.87	44.86	.03092	42.33
Mean	33.04	41.82	.03069	41.43

TABLE 2.--Yield and yield component means of four oat varieties Coachman (C), Diana (D), Clintland 64 (L) and Mi. 60-106-78 (E) and nine mixtures. (Exp. 2)

Entries	Yield Components			Average Yield (Grams per ft^2) (W)
	Average Number of Tillers per ft^2 (X)	Average Number of Kernels per Tiller (Y)	Average Kernel Weight in Grams (Z)	
100%C	33.70	34.49	.03302	37.65
70%C:30%D	32.90	33.43	.03387	36.78
30%C:70%D	36.17	33.80	.03031	36.06
100%D	35.10	35.66	.03069	37.89
70%D:30%L	35.13	34.49	.03044	36.70
30%D:70%L	33.37	32.89	.02983	31.76
100%L	40.43	29.86	.02687	32.18
70%L:30%E	34.13	37.33	.02818	35.86
30%L:70%E	31.47	44.98	.02928	40.52
100%E	33.30	46.77	.02767	42.23
25%C:25%D:25%L:25%E	35.17	36.75	.02973	37.99
10%C:10%D:40%L:40%E	33.07	37.91	.02961	37.18
40%C:40%D:10%L:10%E	35.83	35.26	.03085	38.90
Mean	34.60	36.43	.03003	37.05

TABLE 3.--Yield and yield component means[1] of four oat varieties Coachman (C), Diana (D), Clintland 64 (L), and Mi.60-106-78 (E), and nine mixtures. (Exp. 3)

Entries	Yield Components			Average Yield (Grams per ft^2) (W)
	Average Number of Tillers per ft^2 (X)	Average Number of Kernels per Tiller (Y)	Average Kernel Weight in Grams (Z)	
100%C	-	-	-	-
70%C:30%D	34.33	37.18	.03048	38.66
30%C:70%D	35.83	34.74	.03044	37.77
100%D	36.63	37.97	.02761	38.03
70%D:30%L	36.80	36.07	.02826	37.27
30%D:70%L	34.63	39.31	.02738	36.76
100%L	36.56	37.64	.02681	36.54
70%L:30%E	33.59	42.55	.02624	36.61
30%L:70%E	32.26	47.70	.02590	39.68
100%E	31.93	50.81	.02606	41.54
25%C:25%D:25%L:25%E	33.13	42.14	.02776	38.54
10%C:10%D:40%L:40%E	35.89	40.68	.02680	38.70
40%C:40%D:10%L:10%E	36.29	38.64	.02854	39.73
Mean	34.77	40.56	.02769	38.36

[1]Adjusted least square means due to missing data.

TABLE 4.--Mean squares from analysis of variance tables for a randomized block design for yield (W) and its components (X, Y, Z) for the oat varieties and mixtures tested in experiment 1.

Source of Variation	D.F.	X M.S.	Y M.S.	Z M.S.	W M.S.
Replications	5	19.420	182.930**	.00000183	146.185**
Entries	12	41.474*	214.034*	.00001345**	38.734**
Remaining error	60	14.177	24.555	.00000252	5.477

*, ** = Significance at 5% and 1% level respectively.

TABLE 5.--Mean squares from analysis of variance tables for a randomized block design for yield (W) and its components (X, Y, Z) for the oat varieties and mixtures tested in experiment 2.

Source of Variation	D.F.	X M.S.	Y M.S.	Z M.S.	W M.S.
Replications	5	33.714	267.957**	.00000269	198.767**
Entries	12	29.078	132.162**	.00002245**	49.265**
Remaining error	60	25.776	20.584	.00000271	15.374

** = Significance at 1% level.

TABLE 6.--Mean squares[1] from analysis of variance tables for randomized block design for yield (W) and its components (X, Y, & Z) for the oat varieties and mixtures tested in experiment 3.

Source of Variation	D.F.	X M.S.	Y M.S.	Z M.S.	W M.S.
Replications	5	54.083**	322.353**	.00000379	162.415**
Entries	11	17.865**	132.505**	.00001412**	12.920
Remaining error	53	6.355	20.730	.00000197	7.545

** = Significance at 1% level.

[1]Note that in an unbalanced experiment the adjusted source sums of squares will not, in general, add to give exactly the (unadjusted) total sums of squares.

TABLE 7.--Means of yield and yield components of mixtures (M) compared with those of pure stands (P) in the three experiments.

Experiment	Number of Tillers (X)		Number of Kernels/Tiller (Y)		Kernel Weight (Z)		Yield (W)	
	P	M	P	M	P	M	P	M
Exp. 1	32.85	33.13	41.84	41.81	.03085	.03062	41.52	41.40
Exp. 2	35.63	34.14	36.69	36.32	.02956	.03024	37.48	36.86
Exp. 3	35.04	34.68	42.14	40.03	.02682	.02798**	38.70	38.24

** = Pure Stands and mixtures are significantly different at 1% level.

TABLE 8.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of "Ausable" (A) and "Garry" (G) varieties and mixtures. (Exp. 1, graphed in Fig. 1)

Source of Variation	D.F.	Components			W
		X M.S.	Y M.S.	Z M.S.	M.S.
Replications	5	8.042	63.813*	.00000121	34.907**
Trends	3	22.619	78.753*	.00000387	16.633
Linear	1	11.189	20.504	.00000420	48.424*
Quadratic	1	38.001*	161.244*	.00000643	.423
Cubic	1	18.668	54.512	.00000097	1.051
Error	15	8.201	20.663	.00000196	7.190

*, ** = Significance at 5% and 1% level respectively.

TABLE 9.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of "Garry" (G) and "Coachman" (C) varieties and mixtures. (Exp. 1, graphed in Fig. 2)

Source of Variation	D.F.	Components			W
		X M.S.	Y M.S.	Z M.S.	M.S.
Replications	5	19.946	30.826	.00000017	69.624**
Trends	3	4.402	261.726**	.00002660**	98.271**
Linear	1	.387	698.183**	.00006319**	287.510**
Quadratic	1	10.401	64.478	.00000656	.315
Cubic	1	2.417	22.517	.00001005	6.988
Error	15	21.663	21.575	.00000269	2.591

** = Significance at 1% level.

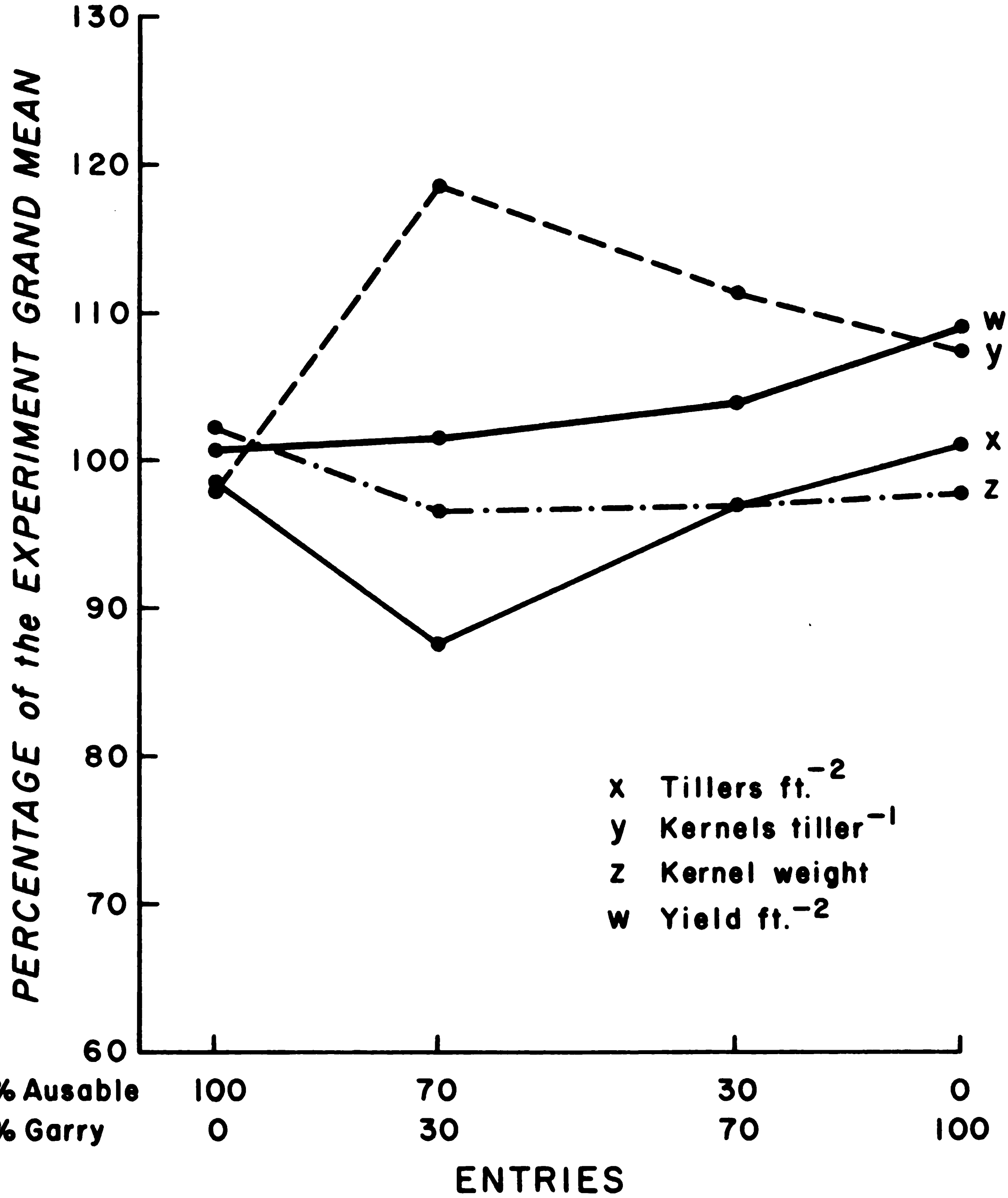

FIG. 1.--Component compensation and its effect on yield of "Ausable" and "Garry" oat varieties and two mixtures among them. (Exp. 1)

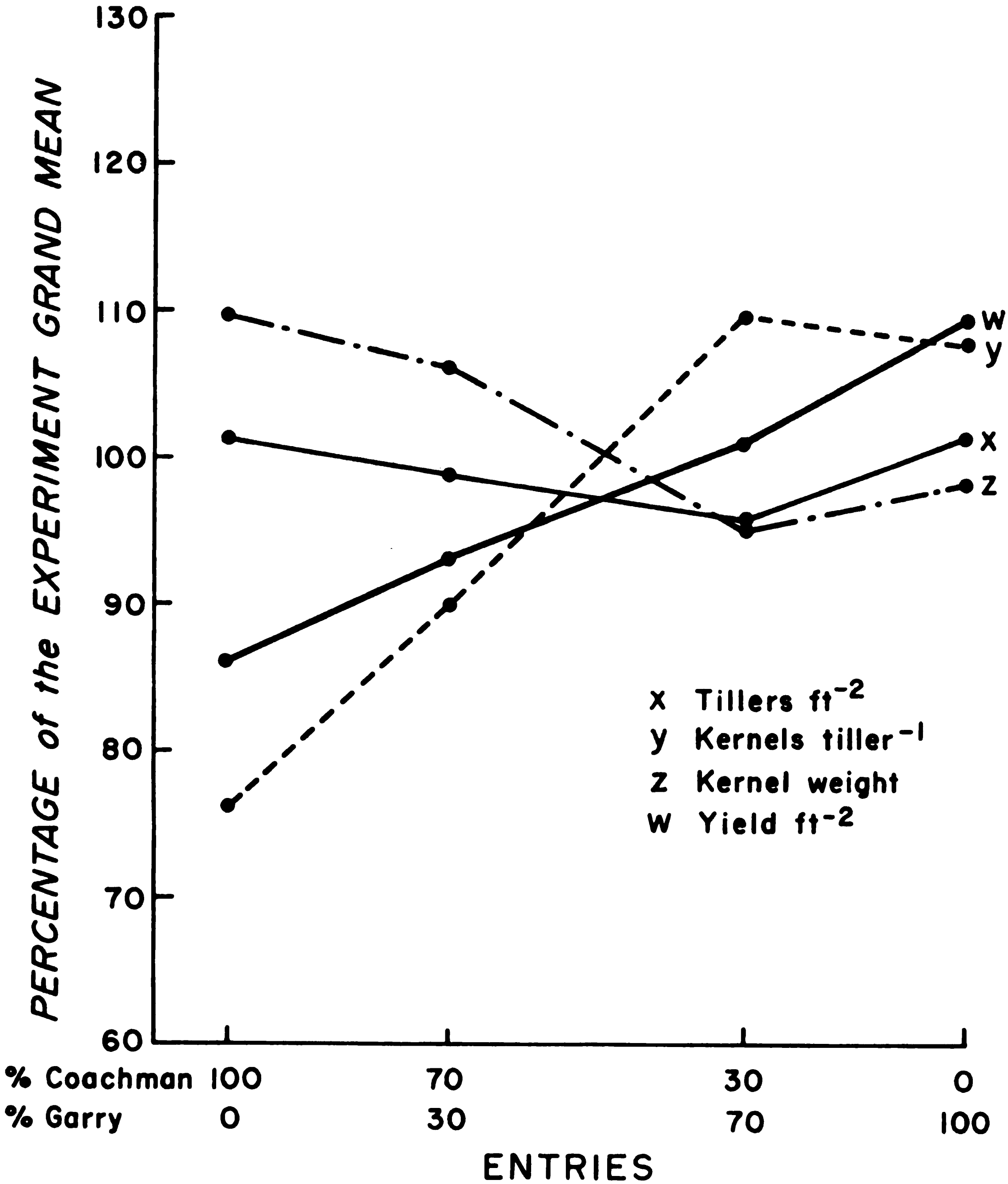

FIG. 2.--Component compensation and its effect on yield of "Coachman" and "Garry" oat varieties and two mixtures. (Exp. 1)

TABLE 10.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of Coachman (C) and Mi.60-106-78 (E) varieties and mixtures. (Exp. 1, graphed in Fig. 3)

Source of Variation	D.F.	Components			W M.S.
		X M.S.	Y M.S.	Z M.S.	
Replications	5	17.158	165.041**	.00000106	75.307**
Trends	3	37.331*	419.973**	.00003123**	69.258**
Linear	1	39.471	1199.327**	.00008807**	207.644**
Quadratic	1	14.415	43.585	.00000006	.000
Cubic	1	58.106*	17.008	.00000555	.131
Error	15	11.308	14.394	.00000167	5.756

*, ** = Significance at 5% and 1% level respectively.

TABLE 11.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of Coachman (C) and "Diana" (D) varieties and mixtures. (Exp. 2, graphed in Fig. 4)

Source of Variation	D.F.	Components			W M.S.
		X M.S.	Y M.S.	Z M.S.	
Replications	5	30.031	146.916**	.00000455	123.812**
Trends	3	12.667	5.775	.00001823*	4.185
Linear	1	18.947	4.493	.00003642*	.006
Quadratic	1	.106	12.808	.00000035	10.834
Cubic	1	18.947	0.025	.00001792	1.716
Error	15	24.884	24.970	.00000539	11.499

*, ** = Significance at 5% and 1% level respectively.

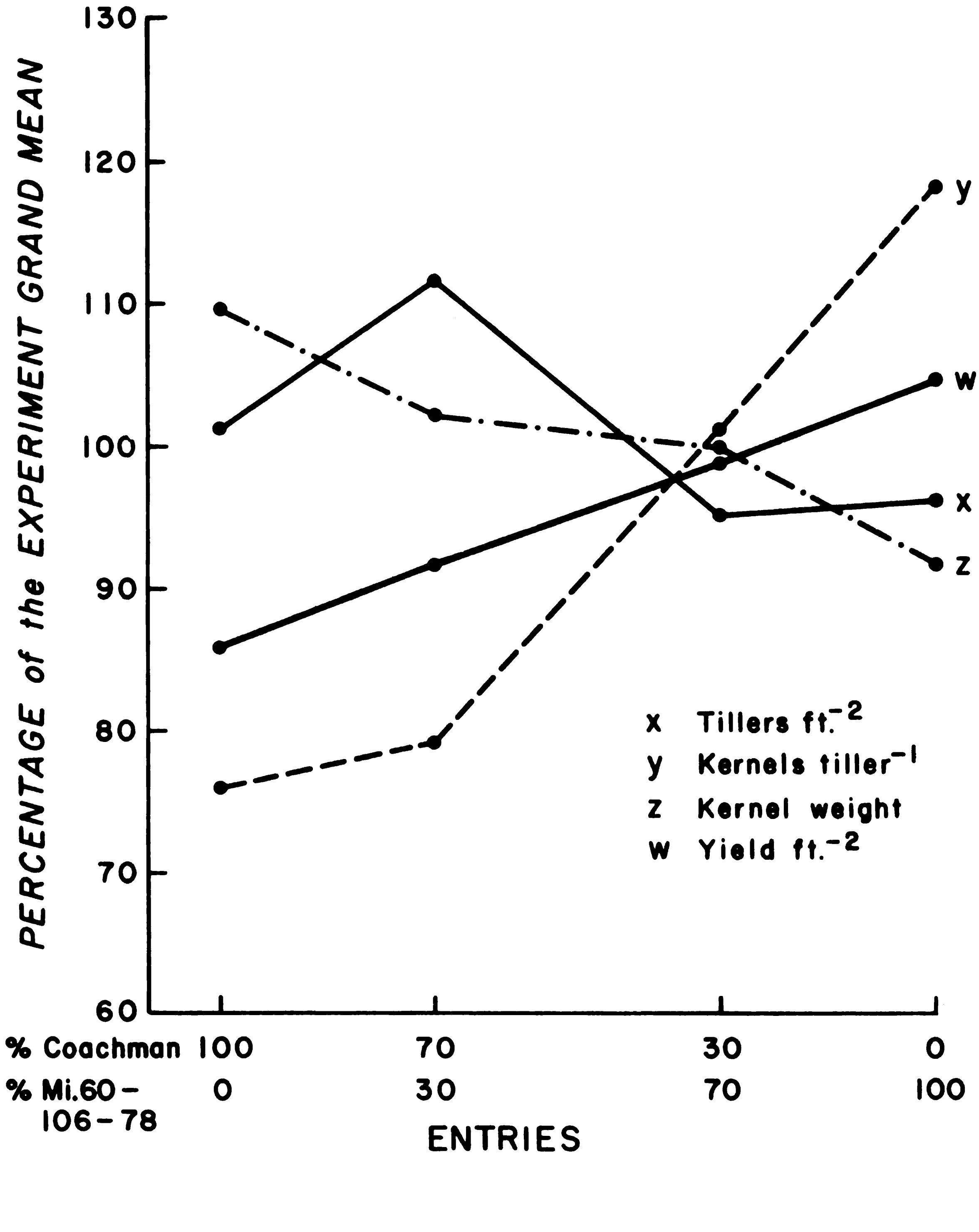

FIG. 3.--Component compensation and its effect on yield of "Coachman" and "Mi.60-106-78" oat varieties and two mixtures. (Exp. 1)

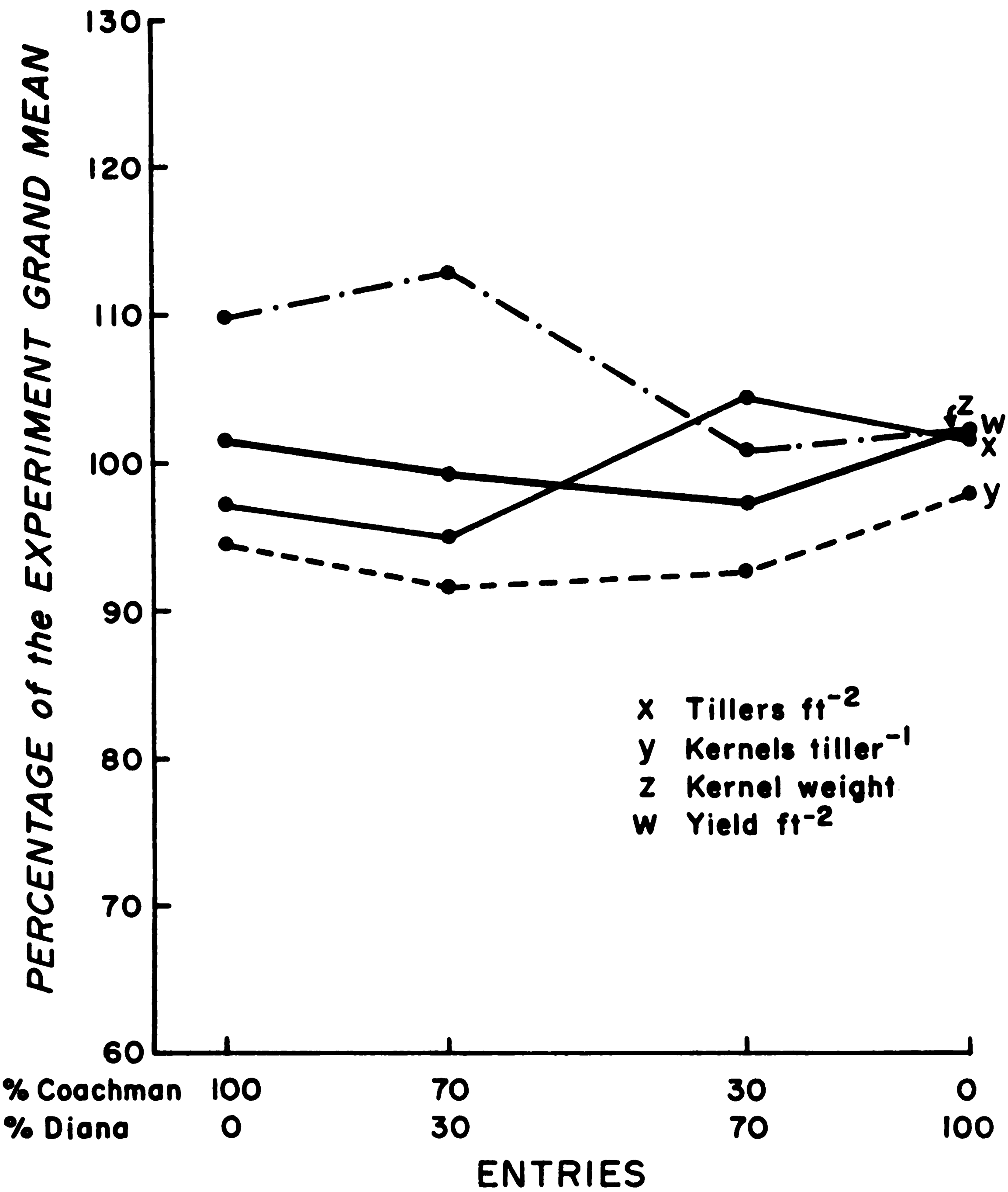

FIG. 4.--Component compensation and its effect on yield of "Coachman" and "Diana" oat varieties and two mixtures. (Exp. 2)

TABLE 12.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of "Diana" (D) and "Clintland 64" (L) varieties and mixtures. (Exp. 2, graphed in Fig. 5)

Source of Variation	D.F.	Components X M.S.	Components Y M.S.	Components Z M.S.	W M.S.
Replications	5	34.822	79.918**	.00000263	76.246**
Trends	3	56.299	37.930	.00001860**	58.251**
Linear	1	55.360	107.218*	.00004264**	152.673**
Quadratic	1	74.202	5.229	.00001100*	3.860
Cubic	1	39.336	1.343	.00000217	18.219
Error	15	39.221	14.771	.00000210	9.782

*, ** = Significance at 5% and 1% level respectively.

TABLE 13.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of "Clintland 64" (L) and "Mi.60-106-78" (E) and mixtures. (Exp. 2, graphed in Fig. 6)

Source of Variation	D.F.	Components X M.S.	Components Y M.S.	Components Z M.S.	W M.S.
Replications	5	26.535	71.707	.00000093	25.085
Trends	3	91.071	360.705**	.00000611**	124.684**
Linear	1	173.896*	1031.581**	.00000397	367.131**
Quadratic	1	99.226	48.496	.00001276*	5.876
Cubic	1	0.091	2.038	.00000160	1.044
Error	15	41.280	25.556	.00000180	23.956

*, ** = Significance at 5% and 1% level respectively.

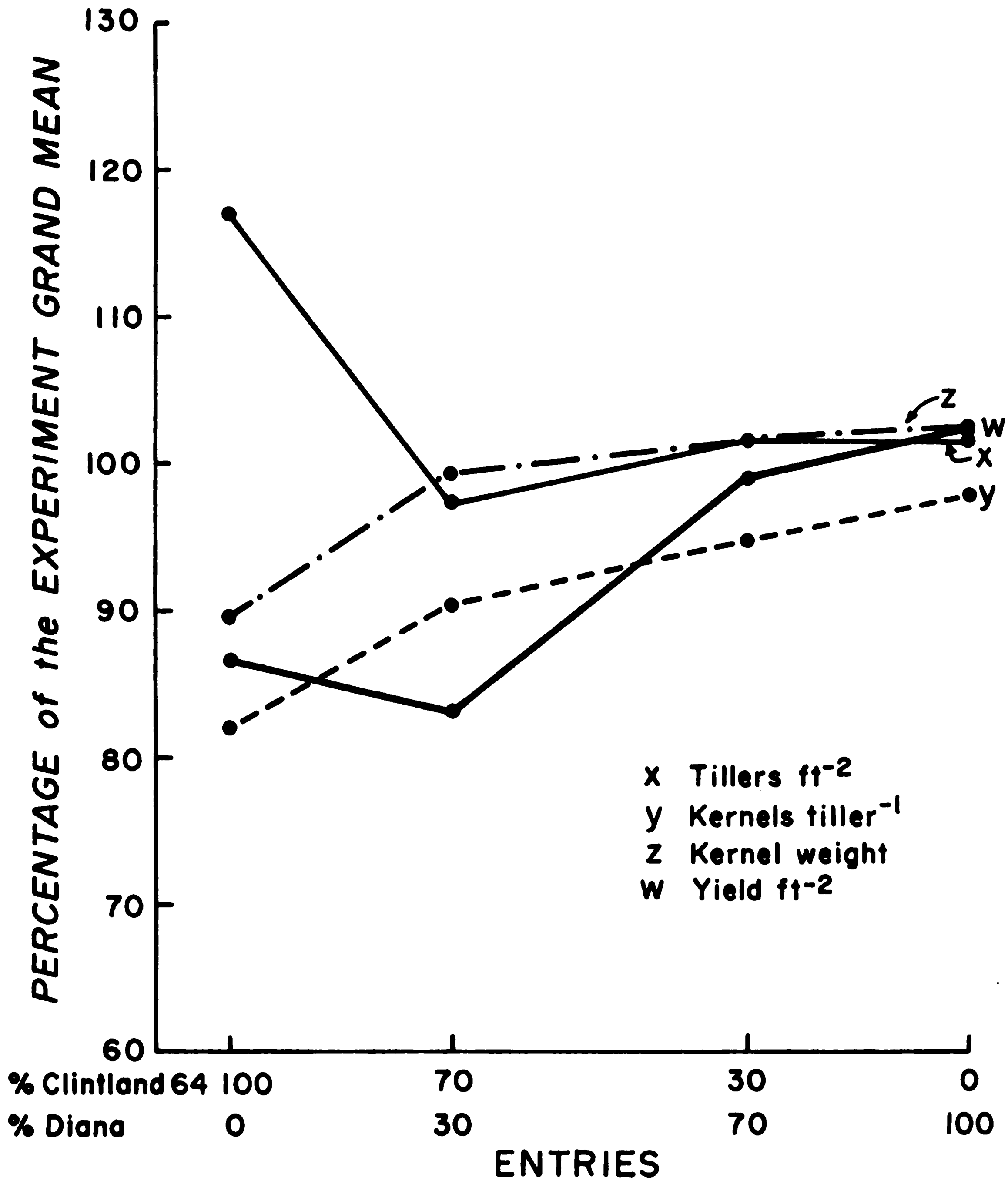

FIG. 5.--Component compensation and its effect on yield of "Clintland 64" and "Diana" oat varieties and two mixtures. (Exp. 2)

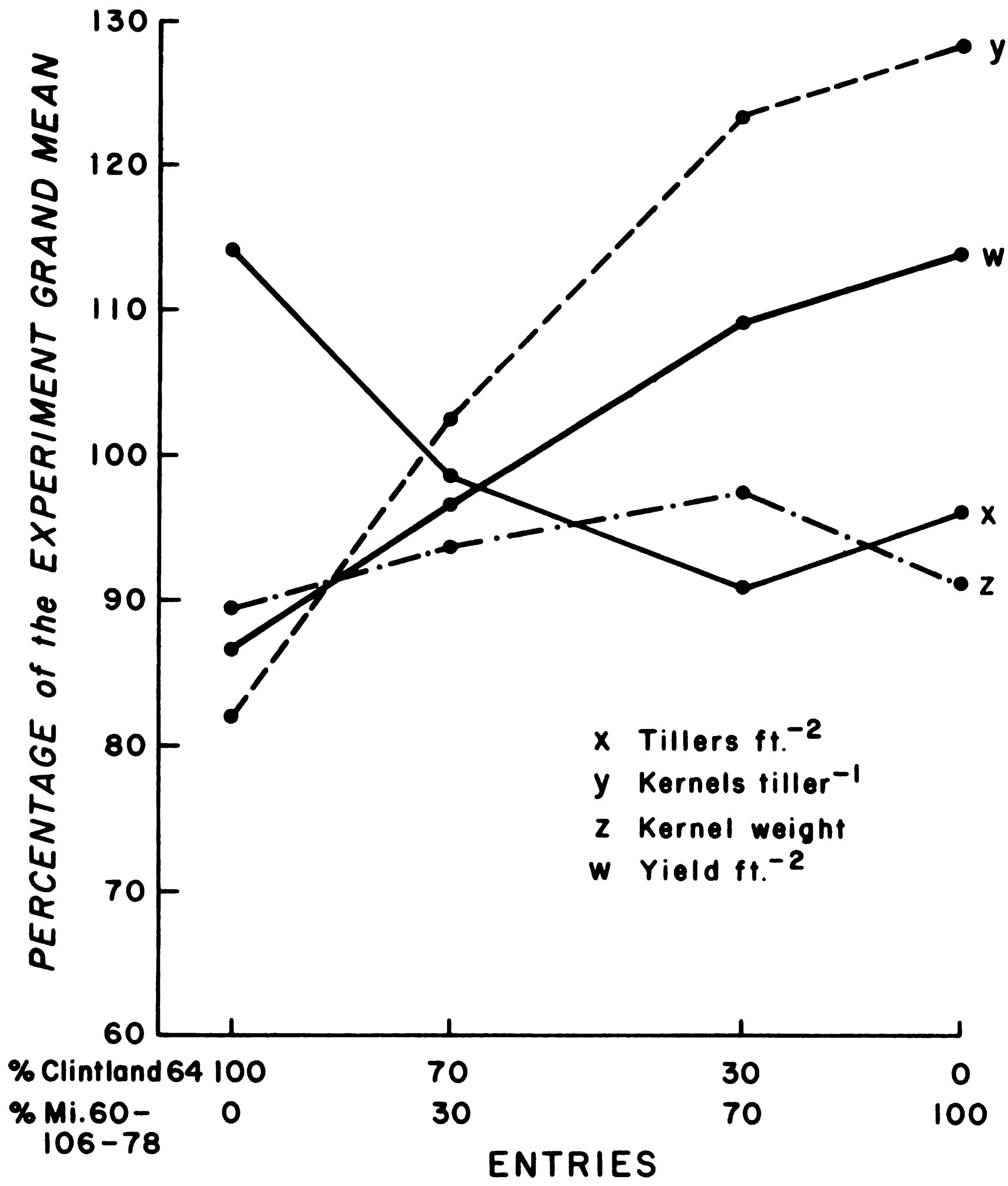

FIG. 6.--Component compensation and its effect on yield of "Clintland 64" and "Mi.60-106-78" oat varieties and two mixtures. (Exp. 2)

TABLE 14.--Testing for curvilinear regression for yield (W) and yield components (X, Y, Z) of "Diana" (D) and "Clintland 64" (L) varieties and mixtures. (Exp. 3, graphed in Fig. 7)

Source of Variation	D.F.	Components X M.S.	Y M.S.	Z M.S.	W M.S.
Replications	5	22.375	82.113*	.00000246	53.074**
Trends	3	6.529	10.187	.00000182	2.354
Linear	1	2.475	2.208	.00000257	6.655
Quadratic	1	4.743	.008	.00000195	.407
Cubic	1	12.368	28.345	.00000095	.000
Error	13	10.160	23.780	.00000189	7.550

*, ** = Significance at 5% and 1% level respectively.

TABLE 15.--Testing for Curvilinear regression for yield (W) and yield components (X, Y, Z) of "Clintland 64" (L) and "Mi.60-106-78" (E) varieties for mixtures. (Exp. 3, graphed in Fig. 8)

Source of Variation	D.F.	Components X M.S.	Y M.S.	Z M.S.	W M.S.
Replications	5	16.081*	190.915**	.00000331	69.686**
Trends	3	22.059*	170.408**	.00000046	33.522**
Linear	1	56.497**	508.440**	.00000090	92.745**
Quadratic	1	9.068	2.782	.00000036	4.689
Cubic	1	.611	.003	.00000004	3.131
Error	14	5.279	33.331	.00000320	5.921

*, ** = Significance at 5% and 1% level respectively.

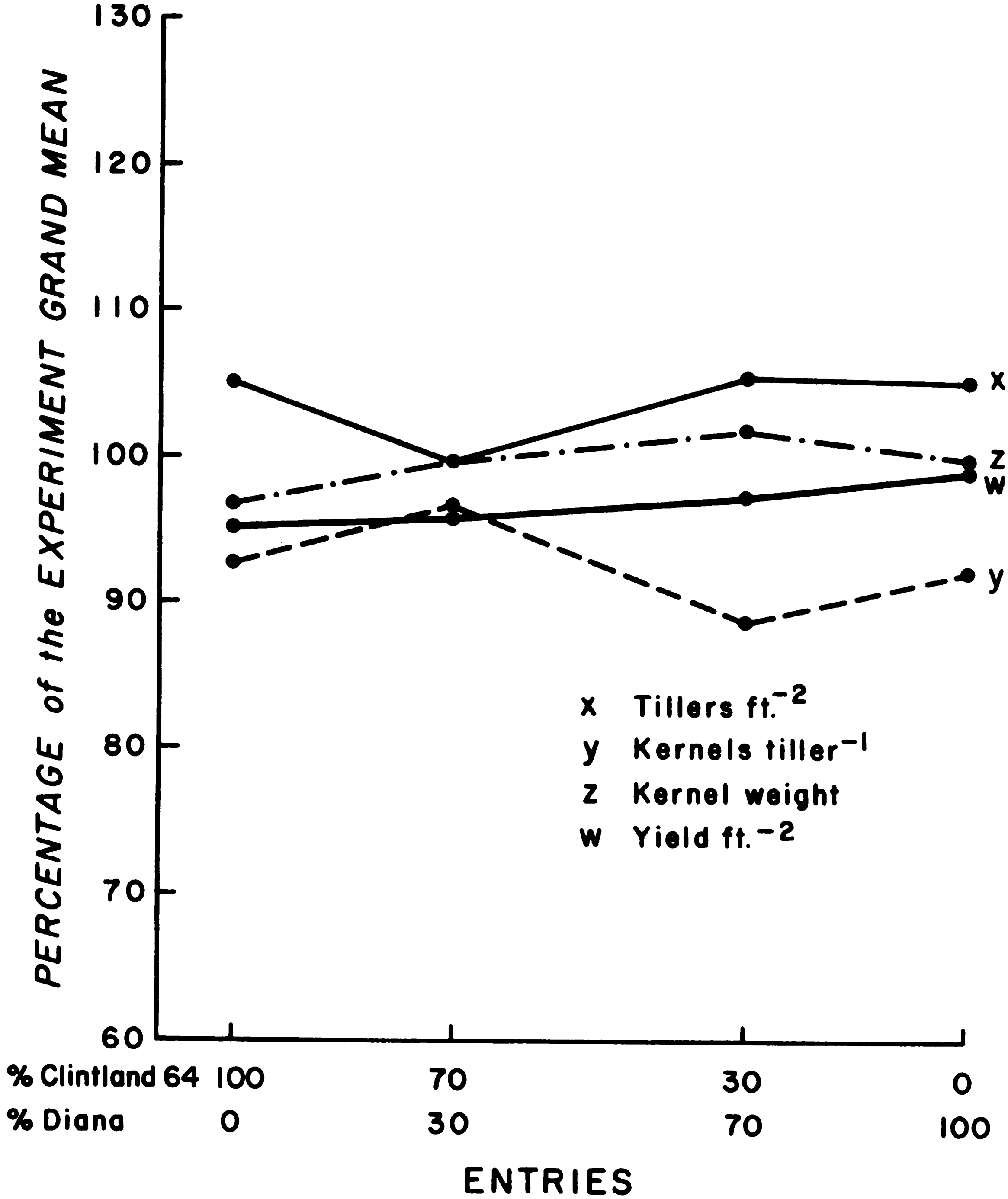

FIG. 7.--Component compensation and its effect on yield of "Clintland 64" and "Diana" oat varieties and two mixtures. (Exp. 3)

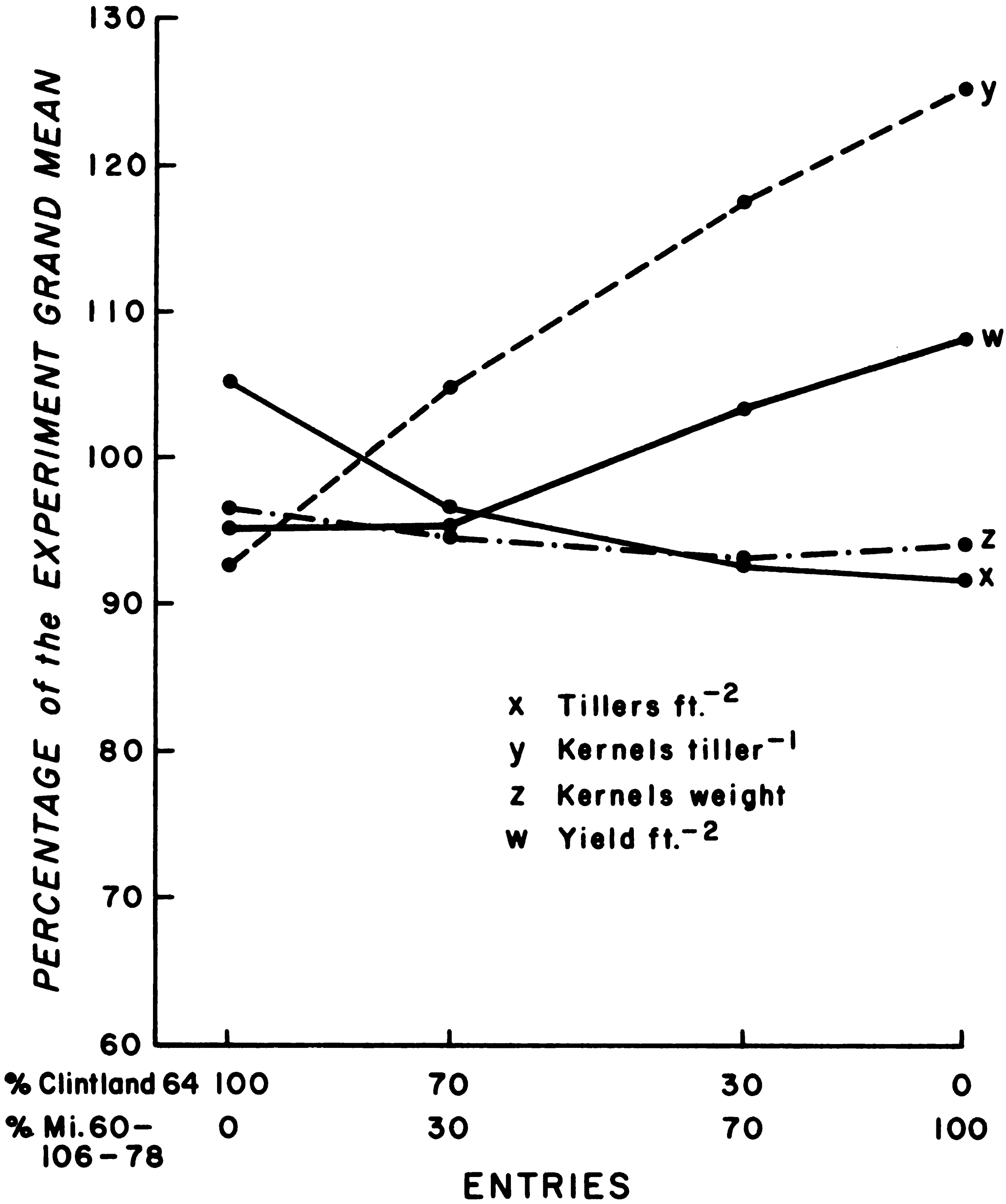

FIG. 8.--Component compensation and its effect on yield of "Clintland 64" and "Mi.60-106-78" oat varieties and two mixtures. (Exp. 3)

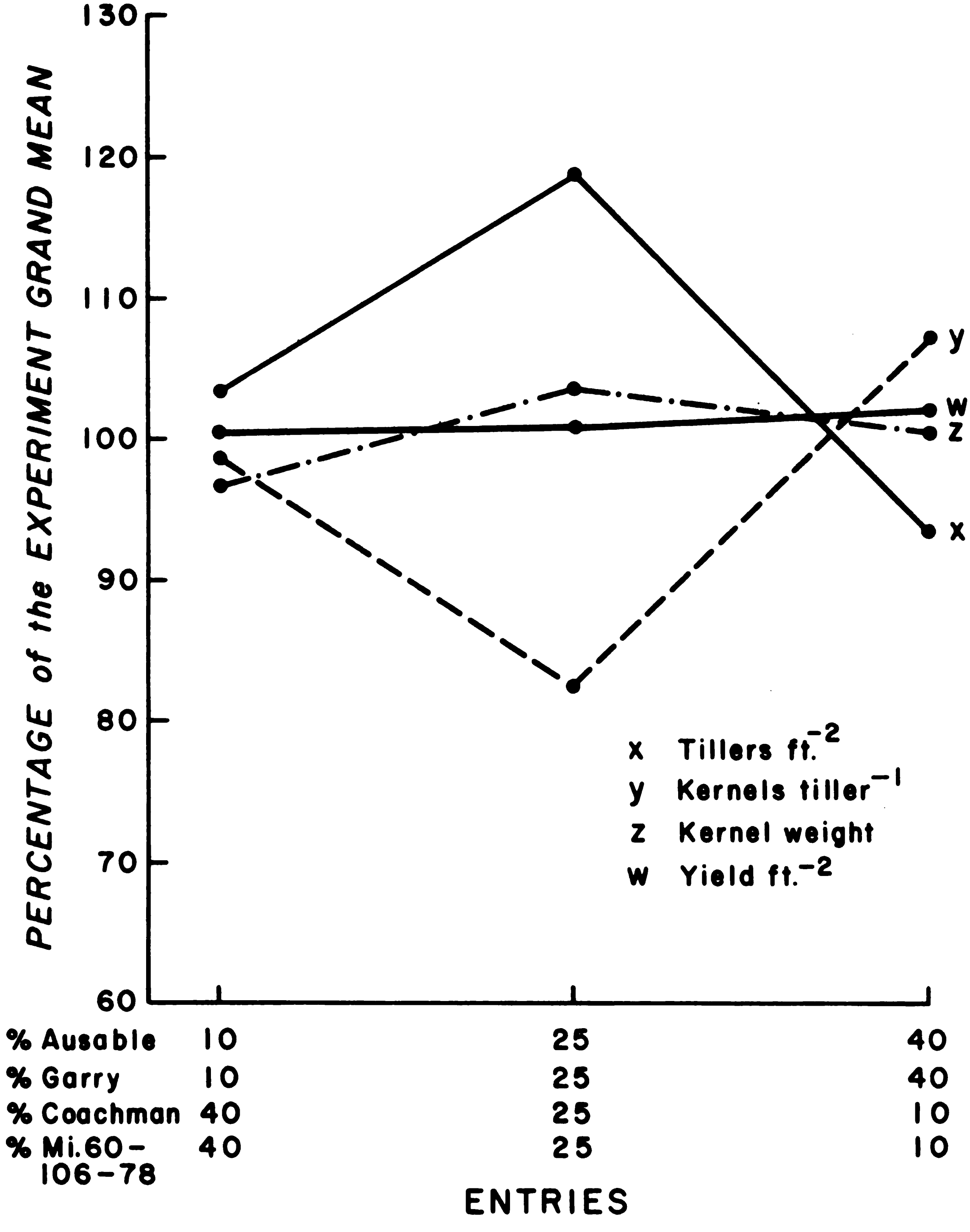

FIG. 9.--Component compensation and its effect on yield of the three 4-varietal mixtures tested in experiment 1.

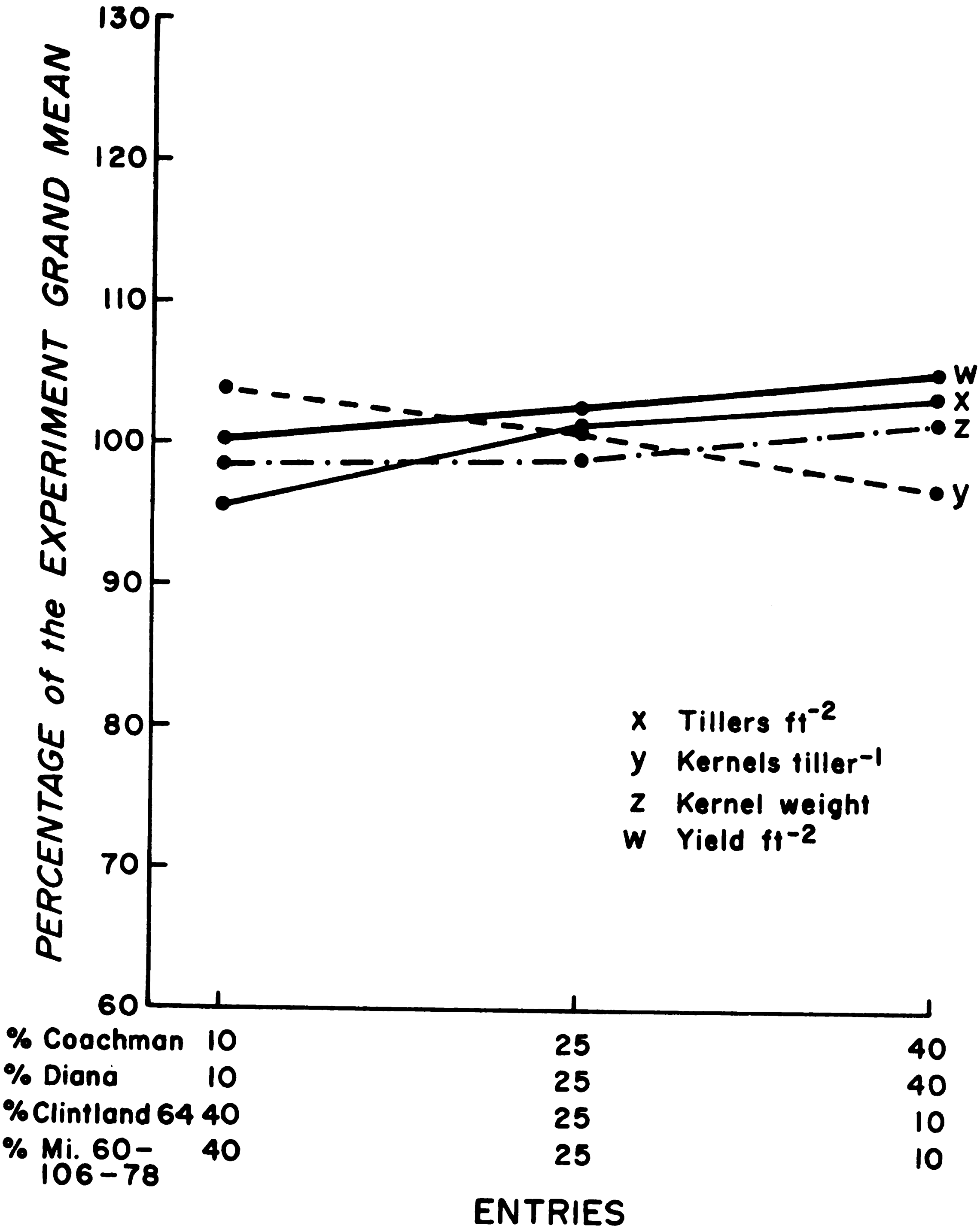

FIG. 10.--Component compensation and its effect on yield of the three 4-varietal mixtures tested in experiment 2.

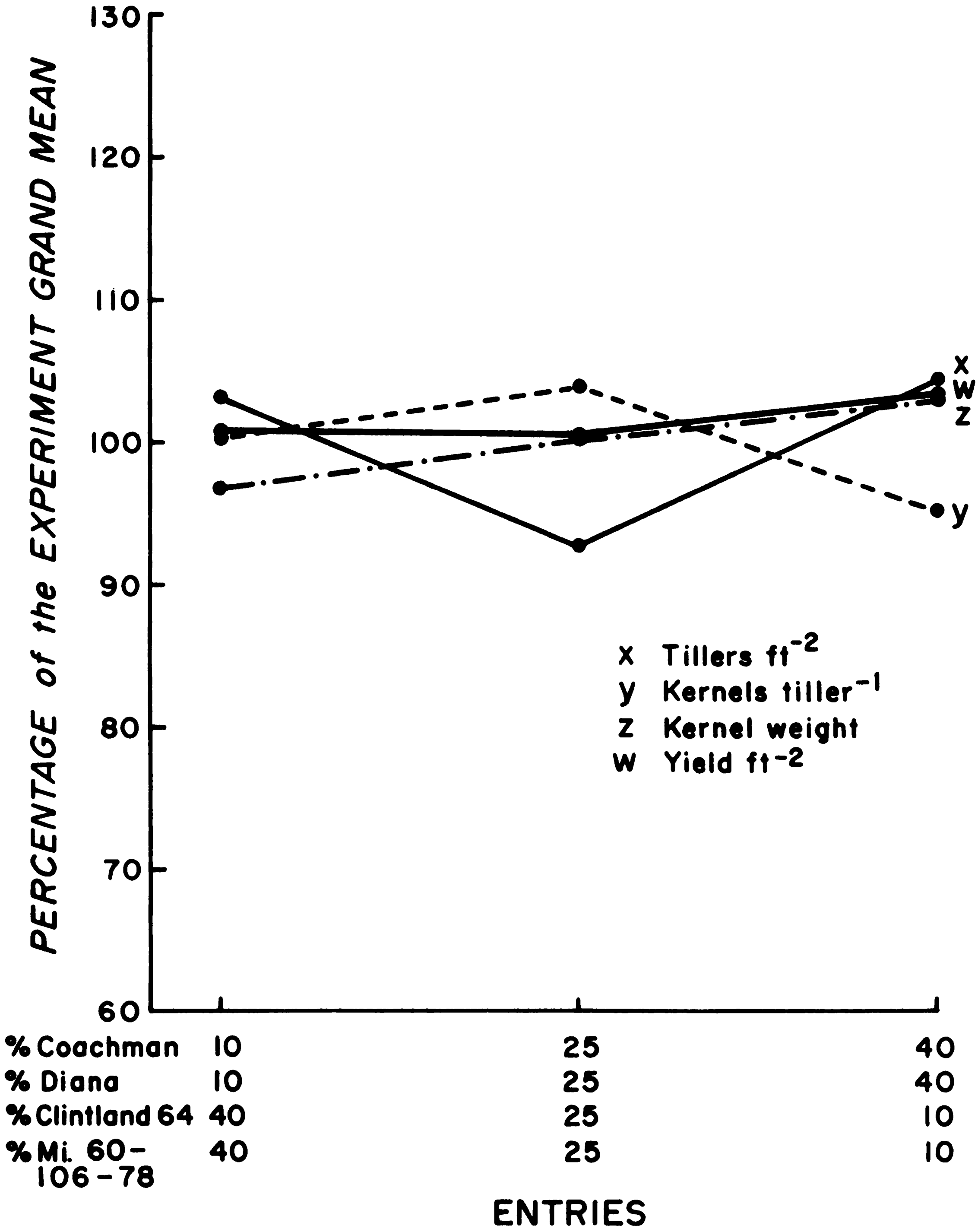

FIG. 11.--Component compensation and its effect on yield of the three 4-varietal mixtures tested in experiment 3.

For further exploration of possible varietal interaction relationship among the mixed varieties, two equations were applied to approximate the expected yield of each mixture using the data provided from pure stands of the mixed varieties.

1. In the absence of interaction between varieties, the yield that is expected from a mixture can be estimated from the information on yield of its constituent varieties in pure stand as follows:

$$W_{AB\cdots N} = aW_A + bW_B + \ldots + nW_N \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

Where $W_{AB\cdots N}$ is the yield of a mixture where varieties A,B...N were mixed in proportions a, b, & n respectively. W_A, W_B, and W_N are the yield in pure stands of the varieties A, B, and N respectively.

2. Information on the yield components from pure stand conditions can also be used to estimate the yield expected, assuming that the varieties in a mixture behave in an additive manner without any varietal interaction.

$$X_{AB\cdots N} = aX_A + bX_B + \ldots + nX_N \quad \ldots\ldots \quad (a)$$

$$Y_{AB\cdots N} = aY_A + bY_B + \ldots + nY_N \quad \ldots\ldots \quad (b)$$

$$Z_{AB\cdots N} = aZ_A + bZ_B + \ldots + nZ_N \quad \ldots\ldots \quad (c)$$

Where $X_{AB\cdots N}$, $Y_{AB\cdots N}$, and $Z_{AB\cdots N}$ are the expected number of tillers per unit area, number of kernels per tiller and average kernel weight respectively of a mixture where varieties A, B, ... N were mixed in a, b, ... n proportions. X_A, Y_A, Z_A are the number of tillers per unit area, number of kernels per tillers, and average kernel weight of the variety A respectively estimated from pure culture.

Knowing W = XYZ,

$$W_{AB\cdots N} \simeq (aX_A + bX_B + \ldots nX_N)\ (aY_A + bY_B + \ldots + nY_N)\ (aZ_A + bZ_B + \ldots nZ_N) \qquad (2)$$

Yield of mixtures of the three experiments calculated by equation (1) along with the observed yield of those mixtures are provided in Tables 16, 17, and 18. Tables 19, 20, and 21 provide a similar comparison of the mixtures' yield and yield calculated by equation (2). Though both equations provided a close estimation of the actual yield, equation (2) gave estimations which predominantly fell slightly below the observed yield and were generally less accurate than equation (1) in estimating the yield.

TABLE 16.--Comparison between observed yield of mixtures and their calculated yield from the yield of their constituent varieties (Exp. 1).

Mixtures	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%A:30%G	42.23	42.81	-.58
30%A:70%G	44.27	44.22	.05
70%G:30%C	41.78	42.37	-.59
30%G:70%C	39.56	38.51	1.05
70%C:30%E	38.06	37.96	.10
30%C:70%E	40.96	41.08	-.12
25%A:25%G:25%C:25%E	41.77	41.52	.25
10%A:10%G:40%C:40%E	41.59	40.32	1.27
40%A:40%G:10%C:10%E	42.33	42.72	-.39

† $t = .5228$ N.S.

TABLE 17.--Comparison between observed yield of mixtures and their calculated yield from the yield of their constituent varieties (Exp. 2).

Mixtures	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%C:30%D	36.78	37.72	-.94
30%C:70%D	36.06	37.81	-1.75
70%D:30%L	36.70	36.17	.53
30%D:70%L	31.76	33.89	-2.13
70%L:30%E	35.86	35.19	.67
30%L:70%E	40.52	39.21	1.31
25%C:25%D:25%L:25%E	37.99	37.48	.51
10%C:10%D:40%L:40%E	37.18	37.32	-.14
40%C:40%D:10%L:10%E	38.90	37.65	1.25

† t = .1829 N.S.

TABLE 18.--Comparison between observed yield of mixtures and the calculated yield from the yield of their constituent varieties (Exp. 3).

Mixtures[1]	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%D:30%L	37.27	37.58	-.31
30%D:70%L	36.76	36.99	-.23
70%L:30%E	36.61	38.04	-1.43
30%L:70%E	39.68	40.04	-.36

[1]Note that the Wc of the rest of the mixtures cannot be calculated because of lack of data on "Coachman" (C).

† t = 2.0525 N.S.

TABLE 19.--Comparison between observed yield of mixtures and the calculated yield from the yield components of their constituent varieties (Exp. 1).

Mixtures	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%A:30%G	42.23	43.05	-.82
30%A:70%G	44.27	44.40	-.13
70%G:30%C	41.78	42.88	-1.10
30%G:70%C	39.56	39.11	.45
70%C:30%E	38.06	39.25	-1.19
30%C:70%E	40.96	42.58	-1.62
25%A:25%G:25%C:25%E	41.77	42.39	-.62
10%A:10%G:40%C:40%E	41.59	41.60	-.01
40%A:40%G:10%C:10%E	42.33	43.19	-.86

† $t = 3.0184$ *, significant at 5% level.

TABLE 20.--Comparison between observed yield of mixtures and the calculated yield from the yield components of their constituent varieties (Exp. 2).

Mixtures	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%C:30%D	36.78	38.42	-1.64
30%C:70%D	36.06	38.43	-2.37
70%D:30%L	36.70	36.78	-.08
30%D:70%L	31.76	34.38	-2.62
70%L:30%E	35.86	36.26	-.40
30%L:70%E	40.52	40.53	-.01
25%C:25%D:25%L:25%E	37.99	38.65	-.66
10%C:10%D:40%L:40%E	37.18	38.62	-1.44
40%C:40%D:10%L:10%E	38.90	38.56	.34

† t = 2.760 *, significant at 5% level.

TABLE 21.--Comparison between observed yield of mixtures and the calculated yield from the yield components of their constituent varieties (Exp. 3).

Mixtures[1]	Observed yield Wo	Calculated yield Wc	Difference† Wo-Wc
70%D:30%L	37.27	37.94	-.67
30%D:70%L	36.76	37.34	-.54
70%L:30%E	36.61	38.88	-2.27
30%L:70%E	39.68	41.03	-1.35

[1]Note that the Wc of the rest of the mistures cannot be calculated because of lack of data on "Coachman" (C).

† t = 3.0477 N.S.

From Tables 22 and 23, X and Y components are tied with a negative relationship in the three experiments, although the relationship is not significant in experiment 2. Negative, though not significant association obtains between Y and Z components in all experiments. With the Y component being positively correlated with W ($r_{YW} = .67$), it appears that the number of kernels per head was more important than any other component in determining the yield.

TABLE 22.--Phenotypic correlations between yield and yield components in the three experiments for the varieties and the mixtures tested.

Experiment	r_{XY}	r_{XZ}	r_{XW}	r_{YZ}	r_{YW}	r_{ZW}
Exp. 1	-.6978**	.1166	-.0447	-.5469	.6395*	-.2286
Exp. 2	-.4760	-.2613	.1767	-.2769	.6587*	-.0452
Exp. 3	-.7381**	.1977	-.2280	-.4224	.6987*	.1208
Average	-.647*	.011	-.024	-.422	.666*	-.058

*, ** = Significance at 5% and 1% level respectively.

TABLE 23.--Correlation between the logarithms of yield and yield components for the varieties and mixtures in the three experiments.

Experiment	r_{XY}	r_{XZ}	r_{XW}	r_{YZ}	r_{YW}	r_{ZW}
Exp. 1	-.7079**	.1262	-.0457	-.5396	.6622*	-.2319
Exp. 2	-.4841	-.2522	.1449	-.2496	.7089**	-.0395
Exp. 3	-.7547**	.2010	-.2524	-.4221	.7116**	.1133
Average	-.660*	.020	-.045	-.410	.694**	-.060

*, ** = Significance at 5% and 1% levels respectively.

DISCUSSION

The mixtures failed to yield more than their constituent varieties in any experiment. Instead the yield of mixtures was proportional to the yield and relative frequencies with which the varieties were mixed (Tables 16, 17, & 18). Differences between yield of mixtures and their yield calculated from the yield of the pure cultures of their constituent varieties were not significant, statistically or biologically; however, when the yield of mixtures was calculated using yield components based on pure culture values, the differences between the actual and the approximated yield values were almost unidirectional. In nearly every case the calculated was less than the observed. These differences when tested were significant. The reason for this difference is both biologic and geometric. The failure of yield components to approximate the yield can be related to the interaction between competitive varieties. Under varietal interaction which the present data suggest $\frac{1}{n}\sum_{1}^{n}(aX_A + bX_B)$ will not be equal to the calculated X_{AB}. With negative correlation between X and Y, also $\frac{1}{n}\Sigma(aY_A + bY_B)$ will not be equal to Y_{AB}.

However with the results showing that the disturbance in one component due to varietal interaction was counterbalanced by the other component(s), therefore varietal interaction alone does not explain the cause of the deviation of the observed yield of mixtures and their calculated yield from the yield components of their constituent varieties. In the two dimentional relation between X and Y, $\sum_{1}^{n} XY$ equals to $\frac{1}{n}\sum_{1}^{n} X \sum_{1}^{n}$ if and only if r_{XY} equals zero. Also since the present study shows that X and Y are negatively correlated, ΣXY will not equal $\frac{1}{n}\sum_{1}^{n} X \sum_{1}^{n} Y$. Similarly, $\sum_{1}^{n}(aX_A + bX_B)\ (aY_A + bY_B)$ will not equal

$$\frac{1}{n}\sum_{1}^{n} (aX_A + bX_B) \sum_{1}^{n} (aY_A + bY_B).$$

The same argument applies to Y and Z; therefore,

$$W_{AB\ldots N} \neq (aX_A + bX_B + \ldots + nX_N)\ (aY_A + bY_B + \ldots + nY_N)$$
$$(aZ_A + bZ_B + \ldots + nZ_N).$$

When those mistures made up of two varieties were studied separately, the compensatory trends among yield components became apparent. Figures 1 through 8 where those relations were graphically illustrated are self-explanatory. Also the 4-variety mixtures in Figures 9, 10, & 11 show the compensatory pattern of yield components. The oscillatory nature of the components X, Y, & Z maintained the linearity of yield. This situation was further confirmed in Tables 8 through 15, where in not one case did yield follow a non-linear course while the components were non-linear in several cases.

The compensatory counterbalance relationship between components is undoubtedly related to both the genotypes and to the sequential nature of development of yield components. A well adapted good yielding variety of a grain crop with high tiller number usually tends to be early, have shorter stalks, smaller Y and larger Z, while a good yielding variety with low tiller number usually tends to be late, have tall stalks, large Y and medium Z. The effects in these character combinations are determined by both genotypes of the plants and the operating growth conditions. The compensatory requirements in the present situation are established by the gene pool and the Michigan environment which enhanced stress. Since yield components known to be independently inherited, they are expected to be also biologically independent in function and magnitude. Their sequential development which seem to determine the interdependent relationships among them suggests that the compensatory pattern that the components follow to determine the yield is unlikely to occur in the absence of intraplant competition due to stress factors. Under stress, mixtures are then likely to tend to modify the stress pattern of a variety by introducing competition of another variety. The degree and the sign of a component modification depends on what signal it receives from the preceding component in the sequence. The original signal is perhaps mainly genetic but the influence of genotype on a trait diminishes as its position in the developmental sequence approaches the end of the sequence (Thomas, Grafius, and Hahn 1971). Tiller number (X), being the first component to be determined in the developmentary sequence, frequently sets the stage for the behavior of the varieties in the mixtures, and any varietal interference in this stage will direct the following components' behavior according to the outcome of such interference. Component X seemed to have followed three distinct patterns in the mixtures (Figures 1 through 8). In two cases X dropped below either variety in the mixtures (Figures 1 and 2). In two cases, one mixture produced more tillers and the other mixture produced less tillers than either one of their constituent varieties (Figures 3 and 4). The third pattern was represented in Figures 6 and 8 which show a linear response in regard to the X component. The X curve in either Figures 5 or 7 was difficult to categorize in any of the previous groups. The linearity of the X component in Figures 6 and 8 indicate that intervarietal competition is not evident. The number of tillers increased as the proportion of the high tillering variety (Clintland 64) increased and decreased as the low tillering companion (Mi.60-106-78) increased in the mixture. Figure 3 indicates that some sort of varietal interference occurred among the varieties forming that set.

In Figure 3 the mixture with a high frequency of Coachman--the highest tillering variety in this set--increased the tiller number of the mixed population. In the other mixture where Mi.60-106-78 was the dominant variety the tiller number fell behind. Since Coachman matures earlier than its companion variety, it is reasonable to assume that Coachman in a mixture will tend to determine its tiller number in a shorter time than its companion variety. This would give Coachman the advantage of an earlier start and development at the expense of the neighboring variety. As Coachman approaches heading stage and maturity, the stress of competition relaxes and conditions become more favorable for the Mi.60-106-78 variety to produce a large number of tillers under less competitive conditions. This would increase the total tiller number of the mixed population. Because this increase in tillers occurs late in the season, most of the tillers of the depressed variety that were produced later will not have enough time and favorable conditions to form enough kernels. So these tillers will tend to bear few panicles, or panicles with a large portion of florets unable to set seeds. This may also explain why kernel number (Y) was low in that mixture where tiller number was high.

However, it is difficult to say very much about those mixtures where four varieties were involved (Figures 9, 10 & 11). The relationship among varieties in those mixtures is expected to reflect more complex interrelations than those operating among two varieties.

A further attempt was made to explore the disturbances in component X resulting from the varietal interaction in the light of the difference between the interacting varieties. This was done by comparing the range between competing varieties and the deviation in the X variable of the mixtures from what was expected if the varieties are not competitive (Table 24, Figure 12). The regression analysis applied to the data shows that the relationship between the varietal difference in X and disturbance in this component when varieties grow in a mixture can be represented by a linear model (Table 25) and the fluctuation in mixtures increases as the range between the mixed varieties increases (Figure 12).

TABLE 24.--Disturbance in mixtures' X component (calculated as the mean of mixture's absolute deviation of observed from calculated in the absence of varietal interaction) as related to the range in X component between the varieties. Both variables are expressed as the percentage of the experimental grand mean.

	Varieties	X range in X between varieties	Mean deviation of mixtures in X
Exp. 1	Ausable Garry	2.63	7.63
	Coachman Garry	.00	4.00
	Coachman Mi.60-106-78	5.24	7.17
Exp. 2	Coachman Diana	4.05	3.93
	Clintland 64 Diana	15.40	10.17
	Clintland 64 Mi.60-106-78	20.61	11.73
Exp. 3	Clintland 64 Diana	.20	3.08
	Clintland 64 Mi.60-106-78	13.32	3.80

TABLE 25.--Analysis of variance of the relationship between varietal range in X and the deviation in X of the mixtures.

Source of variation	D.F.	S.S.	M.S.	F
Explained--due to linear regression	1	38.8748	38.8748	6.9324*
Unexplained--error around regression line	6	35.4841	5.9140	
Total	7	74.3589		

*Significance at 5% level.

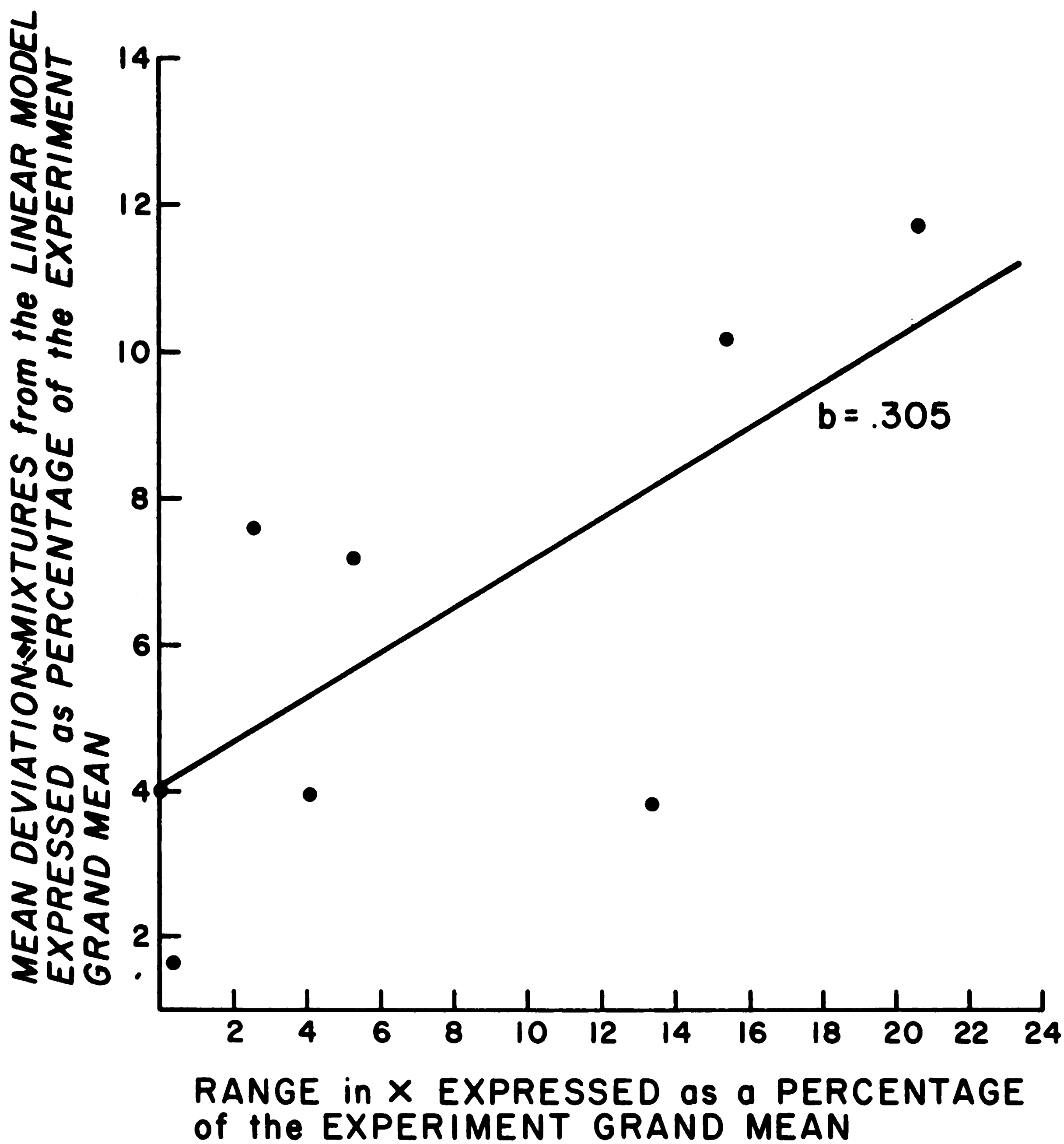

FIG. 12.--The effect of differences in the X component between oat varieties on the disturbance in the X component of mixtures.

Varietal difference in X reflects genetical difference for this trait. If any deviation in X is assumed to be caused by varietal interaction due to competition, it is possible to conclude that competition for X resources--under the present growth conditions will be most keen where X is genetically different in the competitive varieties. A hypothesis that relates the deviation in the X component of mixtures to the range of their constituent varieties may be proposed as follows: "In a mechanical mixture, the probability of disturbance in Component X is greater when the constituent varietal range in X is greater. Y and Z, that follow X in the sequence, will adjust in a compensatory manner." However, this should not be understood to mean that stress conditions will necessarily function in the tillering stage. If the competing varieties started with the same tiller number (Thomas, Grafius, and Hahn 1971), or conditions for any reason tend to provoke stress in the later stages, say in the seed setting stage for example, this will eliminate X as a factor that determines the magnitude and the direction of the compensatory pattern.

The failure of the mixtures to yield greater than the pure cultures of the varieties should not close the door to further investigations on the subject. Under conditions resulting in the highest yielding variety being more susceptible to a given stress such as disease or lodging, mixtures may yield greater than the highest yielding variety.

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