STABILITY, COMPENSATION AND HERITABILITY OF

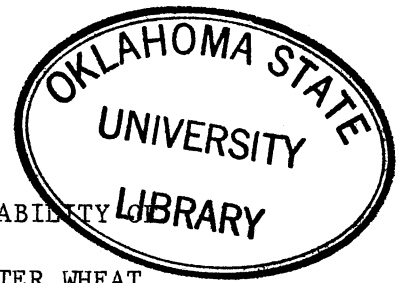YIELD AND YIELD COMPONENTS IN WINTER WHEAT

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STABILITY, COMPENSATION AND HERITABILITY OF

YIELD AND YIELD COMPONENTS IN WINTER WHEAT

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The first three chapters of this dissertation are separate and complete manuscripts to be submitted to Crop Science for publication. The format of each manuscript conforms to the style of Crop Science.

PART I

HERITABILITIES AND INTERRELATIONSHIPS OF

KERNEL WEIGHT AND OTHER YIELD

COMPONENTS IN WINTER WHEAT

Heritabilities and Interrelationships of

Kernel Weight and Other Yield

Components in Winter Wheat[1]

ABSTRACT

Two winter wheat populations derived from crosses between 'C.I. 17851' and 'Vona' (Pop. 1) and between 'Sadovo 1' and Vona (Pop. 2) were evaluated for kernel weight, grain yield, tiller number and kernels/spike. Measurements were made on space planted P_1, P_2, F_1, F_2, BC_1, and BC_2 plants. Additive, dominance and environmental variances were calculated as well as broad and narrow-sense heritabilities. Mid-parent heterosis was calculated for the F_1. Phenotypic and genotypic correlation coefficients as well as path coefficients were also calculated.

Parental means for kernel weight and other characters differed greatly for both populations. Zero or near zero variances and heritabilities were recorded for all traits except kernel weight in Population 2. In Population 1, additive variance was more important than dominance or environmental variance for kernel weight and kernels/spike. Additive and environmental variances were of similar magnitude for tiller number and grain yield. Kernel weight had the largest broad-sense heritability estimate (.76). The narrow-sense heritability estimate for kernel weight was .45. All other yield components as well as yield itself had intermediate narrow-sense heritability estimates. Tiller number had the largest phenotypic

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correlation with yield (.68) while kernel weight had the largest genotypic correlation with yield (.51). With the exception of kernels/spike and tiller number, all correlations among yield components were low to intermediate in magnitude and negative in sign. Based on phenotypic path analysis, tiller number had the largest direct effect on yield. Kernel weight had the largest direct genotypic effect on yield.

Additional index words: Triticum aestivum L.em Thell, Path coefficients, Correlations, Grain yield, Tiller number, Kernels/spike.

INTRODUCTION

Plant breeders are continually interested in improving the yield potential of crop plants. The complex nature of yield and the degree of environmental influence on yield makes direct selection for increased yield potential difficult. Indirect selection for yield based on yield components offers a possible alternative to selection for yield per se. Yield components must have moderate heritabilities, be positively correlated with yield and show a minimum of negative association among themselves for yield component selection to be effective.

The importance of kernel weight as a component of yield in wheat has been demonstrated in several studies (2,7,8,11). Amonsilpa (2) and Sidwell et al. (11) found kernel weight to contribute substantially to grain yield and that kernel weight would be the easiest component to improve by direct selection. They also concluded that selection for kernel weight would be more effective in increasing yield than selection for yield per se. Knott and Talukdar (7) selected for kernel weight in the progeny of a cross between two spring wheat cultivars, one with low kernel weight and good yield, the other with large kernels and low yield. Lines with large kernels were obtained that were superior in yield to either parent.

Heritability estimates for yield and yield components depend on the material being studied, the method used to estimate heritability and the environments sampled during the estimation. Ketata et al. (6) and Sidwell et al. (11) reported moderate narrow-sense heritabilities of 65 and 37%, respectively, for kernel weight in studies with hard red

winter wheat populations. Johnson et al. (5), working with winter wheats, and Sun et al. (14), working with spring wheats, also reported moderate to high heritabilities for kernel weight with values ranging from 51 to 85%. Sharma and Knott (10) and Reddi and Heyne (9) reported low to moderate heritabilities for kernel weight and concluded that this trait was controlled by four or fewer genes.

Heritabilities for yield, tiller number and number of kernels/spike have also been reported in wheat (4,6,8). In general, yield components had higher heritability values than yield itself. Most were intermediate to high in magnitude and ranged from a low of 7% to a high of 89%. Heritabilities for yield ranged from near zero in a study by Johnson et al. (5) to 50% as reported by Fonseca and Patterson (4).

Interrelationships among components have been studied using correlations and path coefficient analysis. Kernel weight has been reported to have a positive correlation with yield with values ranging from low to intermediate in magnitude (4,8,11). Positive correlations between tiller number and yield have also been reported. These ranged from low to high in magnitude and in general were slightly larger than correlations between kernel weight and yield (4,11). Path coefficients also indicate that tiller number has a large direct effect on yield followed by kernel weight which has an intermediate direct effect on yield (11). Adams (1) reported that the development of yield components in many crops is sequential in time. He suggested that yield components are genetically independent but are often negatively associated. These negative relationships are largely due to competition for growth substances by sequentially developing characters.

While negative correlations are reported among yield components, selection based on yield components may still be effective provided compensation among components is not complete.

The objectives of this study were to estimate heritabilities for kernel weight, yield and other yield components and to study interrelationships among yield and yield components using correlations and path coefficient analysis.

MATERIALS AND METHODS

Two winter wheat populations were used in this study. Population 1 was derived from a cross between 'C.I. 17851' and 'Vona'. C.I. 17851 was recently released from Oklahoma State University as a large-seeded germplasm line (12). The line was selected from a cross between 'Lovrin 6', a large-seeded genotype from Romania and 'TAM W-101,' a cultivar released from the Texas Agricultural Experiment Station. C.I. 17851 is characterized by medium maturity, increased kernel weight and plant height of approximately 80 cm. Vona, the other parent in the cross, was released from Colorado State University in 1976 and is a semi-dwarf cultivar of early maturity, relatively small kernels and good yield potential.

Population 2 involved a cross between 'Sadovo 1' and Vona. Sadovo 1 originated in Bulgaria but is fairly well adapted to the Southern Great Plains. It is characterized by medium to early maturity, large kernels and is approximately 85 cm tall. Parents involved in both populations had previously been evaluated in replicated nurseries for grain yield and yield components. Populations consisted of P_1, P_2, F_1, F_2, BC_1, and BC_2 plants.

The experiment was grown as space plants on the Oklahoma Agricultural Experiment Station at Stillwater, Oklahoma during the 1979-80 growing season. Seeds were germinated in flats in the greenhouse and seedlings transplanted to rows 31 cm apart in the field. Each row consisted of 20 plants that were spaced 15 cm apart within the row. The experimental design was a randomized complete-block design with three replications. Each replication consisted of eleven rows.

Of these eleven rows, one row was planted to each of the parents and the F_1, four rows consisted of F_2 plants and two rows were grown for each of the backcross generations. Kernel weight, tiller number, kernels/spike and grain yield were measured on each plant. Seventeen healthy bordered plants were used from each row for statistical analysis.

Additive, dominance and environmental variances were calculated for each of three replications for all traits. Values reported represent means of three replications. A negative variance estimate was replaced by zero and included in the calculation of the mean. The following formulas were used to calculate environmental additive and dominance variances (11):

$$\sigma^2_E(x) = [Var(x)_{P_1} + Var(x)_{P_2} + Var(x)_{F_1}]/3$$
$$\sigma^2_A(x) = 2Var(x)_{F_2} - [Var(x)_{BC_1} + Var(x)_{BC_2}]$$
$$\sigma^2_D(x) = Var(x)_{F_2} - [\sigma^2_A + \sigma^2_E]$$

Standard deviations of the mean were also calculated for each estimate based on values from three replications (13).

Broad and narrow-sense heritability estimates were obtained for yield and the components of yield. Broad-sense heritabilities were estimated as the ratio of additive plus dominance variance to the sum of additive, dominance and environmental variance (11). Narrow-sense

$$h^2_{bs} = \frac{\sigma^2_A(x) + \sigma^2_D(x)}{\sigma^2_A(x) + \sigma^2_D(x) + \sigma^2_E(x)}$$

heritability estimates were calculated as the ratio of additive variance to total variance:

$$h^2_{ns} = \frac{\sigma^2_A(x)}{\sigma^2_A(x) + \sigma^2_D(x) + \sigma^2_E(x)}$$

Heritability values for individual replications that were greater than one or less than zero were equated to one and zero, respectively, and then used in calculating the mean. Standard deviations were also calculated for heritabilities. Phenotypic correlations were calculated using F_2 data. Genotypic correlations were obtained in a similar manner to phenotypic correlations but used genetic covariances calculated from BC data. Path coefficients were also calculated (3,13).

RESULTS AND DISCUSSION

Means and standard deviations for both parents and the F_1 for

Population 1 are presented in Table 1. Large differences were observed

between P_1 and P_2 for kernel weight, kernels/spike and grain yield.

The difference between P_1 and P_2 for kernel weight was 16.7 grams per

1000 kernels, which represents 72% of the mean of the low parent, P_2.

C.I. 17851 was characterized by increased kernel weight but reduced

kernels/spike while Vona had a large value for kernels/spike but

reduced kernel weight. F_1 - mid-parent deviations, also presented in

Table 1, are estimates of mid-parent heterosis. Grain yield showed

significant heterosis at the 0.01 level and kernel weight and

kernels/spike showed significant heterosis at the 0.05 level. All

characters showed large differences in expression between parents in

Population 2 (Table 2). Kernel weight differed by 6.6 grams per 1000

kernels which represents 30% of the mean of the low parent, P_2.

Parents also differed for tiller number in Population 2 in contrast to

Population 1. Kernels/spike was the only character in Population 2 to

show significant mid-parent heterosis.

Heritabilities were calculated for both Population 1 and

Population 2. Unexpected results were obtained from Population 2. A

predominance of very small or negative variance estimates resulted in

both broad and narrow-sense heritability estimates at or near zero for

all traits except kernel weight. Broad and narrow-sense heritabilities

for kernel weight were .569 and .222, respectively. Several possible

explanations exist for the observed results in Population 2. A lack of

genetic variance within the population could have resulted in zero

heritabilities. A second alternative could be that the assumption of equal variances among generations was not met. This would result in improper estimations of additive and non-additive variances. In any case, no further analysis was conducted on Population 2.

Additive, dominance and environmental variance as well as broad and narrow-sense heritabilities for Population 1 are presented in Table 3. Additive variance was more important than either dominance or environmental variance for kernel weight and kernels/spike. A fairly large dominance variance was also observed for kernel weight. Kernels/spike, on the other hand, had a large environmental variance relative to dominance variance. Additive and environmental variance were of similar magnitude for tiller number and grain yield. Dominance variance for these traits was zero or close to zero.

Kernel weight had the largest broad-sense heritability estimate (.763), followed by grain yield and kernels/spike. Grain yield, however, had the largest narrow-sense heritability estimate (.504), followed by tiller number (.492) and kernel weight (.452). Heritabililty estimates for kernel weight are in agreement with other reports which indicate moderate heritabilities for kernel weight (4,5,6). Intermediate heritabilities for tiller number and kernels/spike have also been reported but low values are usually reported for grain yield. Grain yield had unusually high heritability estimates in Population 1.

Phenotypic and genotypic correlations among yield and yield components are presented in Table 4 for Population 1. Tiller number had the highest phenotypic correlation with yield (.676), followed by yield vs kernel weight (.457) and yield vs kernels/spike (.414). All

phenotypic correlations with yield vs the yield components were significant at the 0.01 level. Phenotypic correlations for tiller number vs kernel weight and for kernel weight vs kernels/spike were low and negative. An intermediate positive correlation was observed between tiller number and kernels/spike.

Genotypic correlations were similar to phenotypic correlations. Several differences did exist, however. Kernel weight was the component with the highest genotypic correlation with yield followed by yield vs kernels/spike and yield vs tiller number. Rather large differences in magnitude were noted between phenotypic and genotypic correlations for yield vs tiller number, kernel weight vs tiller number and kernels/spike vs tiller number. No tests for statistical significance were conducted on genotypic correlations.

Phenotypic and genotypic path analyses are presented in Table 5 and Table 6, respectively. Based on phenotypic path analysis (Table 5), tiller number had the largest direct effect on yield (.627). The direct phenotypic effect of kernel weight on yield was of similar magnitude (.590), followed by kernels/spike (.290). The genotypic path analysis was very similar to the phenotypic analysis, the major difference being that kernel weight had the largest direct genotypic effect on yield whereas tiller number had the largest direct phenotypic effect on yield. Kernels/spike had a considerably smaller direct effect on yield than either kernel weight or tiller number by either analysis.

Figures 1 and 2 are graphic representations of phenotypic and genotypic path analyses. The direct effect of the component on yield is indicated by the pathway, P. Correlations among components are

denoted by the coefficient, r. The residual effect is denoted by the pathway, P_{X4}, and is considered to be independent of the other components. This factor measures the failure of the components to completely account for grain yield. Increased values for the residual path result when yield components are not meaured with sufficient precision. Based on estimates of residual paths, the phenotypic analysis was better than the genotypic analysis for predicting yield as the direct result of yield components. The phenotypic analysis accounted for 81% of yield while genotypic analysis only accounted for 63%. Indirect effects reported in Tables 5 and 6 are a result of the product of the correlation among two components, r, and the direct effect of the alternate path, P.

In summary, based on the results from Population 1, additive variance was found to be important for both kernel weight and kernels/spike. This suggests that improvement can be made on these components using traditional breeding methods for self-pollinated crops. Narrow-sense heritability estimates for all yield components as well as for yield itself were found to be intermediate in magnitude ranging from 40 to 50%. Heritabilities of this magnitude indicate reasonable genetic gains can be expected if selection is practiced in this population. The unusually high heritability estimate for yield also indicates that selection for yield itself may be effective in Population 1. Correlations among yield and the components of yield were all positive in sign and intermediate in magnitude with tiller number being most highly correlated with yield. The positive association among tiller number and kernels/spike as well as the correlation between yield and tiller number suggests that selection for

tiller number may result in larger yield increases than selection for one of the other yield components. Phenotypic path analysis also supports the importance of tiller number to grain yield. Genotypic analysis, however, indicates the importance of kernel weight as a contributing factor to yield.

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    kernel weight in six spring wheat crosses. Crop Sci. 12:1-5.

LIST OF TABLES AND FIGURES

Table 1. Means and standard deviations for both
parents and the F_1 plus mid-parent deviations
for Population 1.

Character	P_1 (C.I. 17851)	P_2 (Vona)	F_1 (P_1xP_2)	F_1-MP Deviations
Kernel Weight (g/1000)	39.9 ± 3.7	23.2 ± 1.7	36.8 ± 2.9	5.2*
Tiller Number (per plant)	11.2 ± 2.4	12.0 ± 2.5	13.2 ± 2.1	1.6*
Kernels/Spike	33.9 ± 4.7	47.3 ± 4.8	39.7 ± 3.2	-0.9
Grain Yield (g/plant)	11.9 ± 3.4	9.1 ± 2.4	14.3 ± 2.9	3.8**

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 2. Means and standard deviations for both parents
and the F_1 plus mid-parent deviations for Population 2.

Character	P_1 (Sadovo 1)	P_2 (Vona)	F_1 (P_1xP_2)	F_1-MP Deviations
Kernel Weight (g/1000)	28.8 $\pm$ 3.9	22.2 $\pm$ 2.5	25.9 $\pm$ 2.5	0.4
Tiller Number (per plant)	6.4 $\pm$ 1.4	12.6 $\pm$ 2.4	11.2 $\pm$ 2.7	1.7
Kernels/Spike	36.2 $\pm$ 4.4	46.6 $\pm$ 4.9	47.6 $\pm$ 5.1	6.2*
Grain Yield (g/plant)	5.4 $\pm$ 1.6	8.4 $\pm$ 2.2	9.6 $\pm$ 2.7	2.7

* Significant at the 0.05 level.

Table 3. Heritability and variance estimates
for Population 1.

Character	Additive Variance	Dominance Variance	Environmental Variance	h^2 Broad-Sense	h^2 Narrow-Sense
Kernel Weight	18.04 + 10.79	10.11 + 7.22	8.36 + 0.18	.763 + .032	.452 + .239
Tiller Number	5.30 + 1.37	0.00 + 0.00†	5.37 + 1.05	.492 + .105	.492 + .105
Kernels/ Spike	26.88 + 19.31	5.91 + 5.91	18.69 + 2.25	.578 + .109	.400 + .227
Grain Yield	10.29 + 1.77	1.29 + 1.29	8.55 + 1.35	.579 + .043	.504 + .040

† Negative estimates in each replication converted to zero.

Table 4. Phenotypic and genotypic correlations among
yield and yield components for Population 1.

Character	Tiller Number	Kernel Weight	Kernels/ Spike
Grain Yield †	.676**	.457**	.414**
‡	.313	.514	.329
Tiller Number		-.114	.399**
		-.430	.622
Kernel Weight			-.214**
			-.220

*, ** Significant at the 0.05 and 0.01 levels,
     respectively.

†   Upper values denote phenotypic correlations and
      statistical significance for those values.

‡   Lower values represent genotypic correlations.

Table 5. Phenotypic path analysis for Population 1.

Pathway	Direct Effect	Indirect Effect	Correlation Coefficient
Yield vs Tiller Number	.627		
via Kernel Weight		−.067	
via Kernels/Spike		.116	
Total			.676
Yield vs Kernel Weight	.590	−.071	
via Tiller Number		−.062	
via Kernels/Spike			
Total			.457
Yield vs Kernels/Spike	.290		
via Tiller Number		.250	
via Kernel Weight		−.127	
Total			.414

Table 6. Genotypic path analysis for Population 1.

Pathway	Direct Effect	Indirect Effect	Correlation Coefficient
Yield vs <u>Tiller Number</u>	.554		
via Kernel Weight		-.338	
via Kernels/Spike		.099	
Total			.313
Yield vs <u>Kernel Weight</u>	.786		
via Tiller Number		-.238	
via Kernels/Spike		-.035	
Total			.513
Yield vs <u>Kernels/Spike</u>	.157		
via Tiller Number		.345	
via Kernel Weight		-.173	
Total			.329
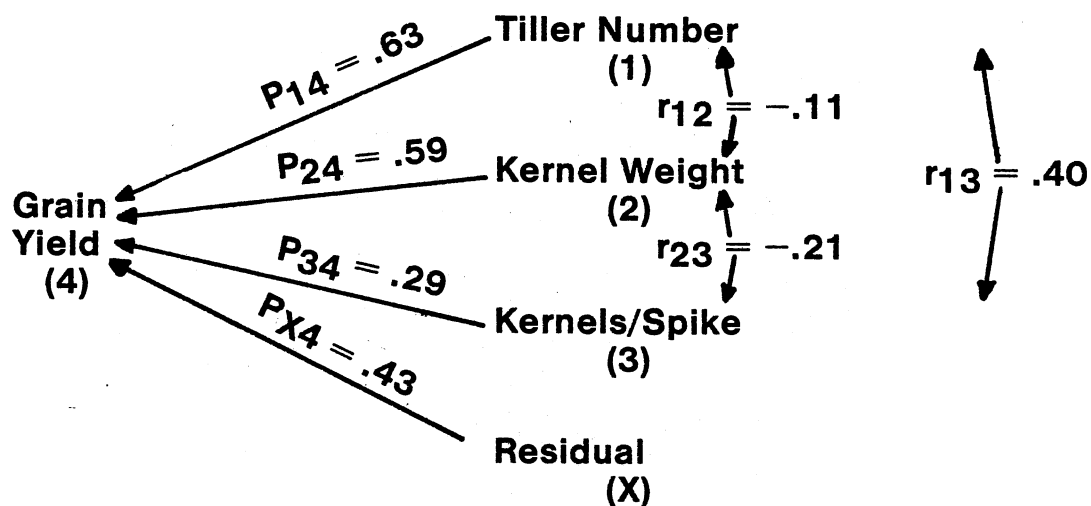
Fig. 1. Phenotypic path diagram for Population 1.
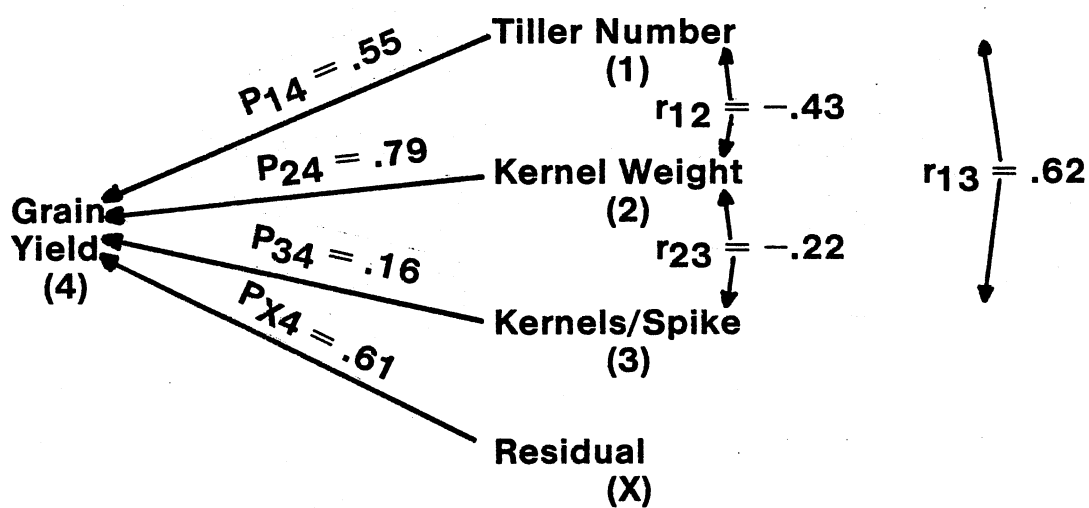
Fig. 2. Genotypic path diagram for Population 1.

PART II

YIELD AND YIELD COMPONENT STABILITY FOR

TEN WINTER WHEAT GENOTYPES

Yield and Yield Component Stability for

Ten Winter Wheat Genotypes[1]

ABSTRACT

Ten winter wheat genotypes with a range of expression for yield
and the components of yield were grown for two years at each of four
locations in Oklahoma. Grain yield, tiller number, kernel weight and
kernels/spike were measured on each genotype. Analysis of variance and
regression techniques were applied to the data to measure yield and
yield component stability.

Analysis of variance detected significant differences among
genotypes for all characters. Significant genotype-environment
interactions were noted for all traits for year by genotype and
location by genotype interactions. The three-way interaction estimate,
(years by location by genotype) was significant for all traits except
tiller number. Regression analysis indicated that genotypes assorted
into three distinct groups for all traits (below average, average, and
above average stability). Higher yield appeared to be associated with
a trend toward instability. Four genotypes having yields above the
nursery mean had below average stability and exhibited specific
adaptation to favorable environments. Genotypes with extreme
expression for any one of the components of yield generally had
regression coefficients quite different from the value of one for that
trait. No one genotype was found with average stability for yield and
all yield components. The highest yielding genotype had the closest

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[1]To be submitted for publication in <u>Crop Science</u>.

approximation to average stability for all traits. This indicates that stability of components may be more important than absolute expression of yield components for high yield in a specific environment.

Additional index words: <u>Triticum aestivum</u> L. em Thell, Genotype-environment interaction, Tiller number, Kernel weight, Kernels/spike.

INTRODUCTION

The development of superior, high yielding cultivars continues to be a major objective of most breeding programs. Identification of superior genotypes is often complicated by genotype-environment interactions. Hill (7) states that genotype-environment interactions result in inconsistent performance of genotypes when measured over a series of environments. This inconsistency is expressed as either differences in ordering among genotypes or as changes in absolute differences among genotypes when order remains unchanged. Eberhart and Russell (4) described two methods of overcoming genotype-environment interactions. The first method uses stratification of environments to reduce genotype-environment interaction. Using this approach, locations are divided into groups, each group being similar with respect to macro-environmental differences such as soil type, rainfall or temperature. Within groups, however, genotype interactions with locations or interactions with years at the same location may still exist. A second approach to the problem would be to develop more stable genotypes. The model proposed by Eberhart and Russell (4) to measure genotype stability will be examined in more detail later.

Johnson et al. (8) and Smith (10) both emphasized the need for genotype stability in wheat cultivars grown under the extreme environmental conditions encountered in the Southern Great Plains. Johnson et al. (8) found newer hard red winter wheat cultivars to be superior in both stability of yield and actual yield potential when compared with a long-term check cultivar. In considering a plant architecture approach to wheat breeding in the Great Plains, Smith (10)

stated that environmental influences on yield-related traits must be understood if a plant architecture approach is to be successful. He also expressed concern that selection for yield per se may reduce the stability of yield.

Several methods have been proposed to study genotype-environment interactions and to measure genotype stability. Comstock and Moll (2) outlined a model using variance components to separate genotype-environment effects from genetic variance. Finlay and Wilkinson (5) regressed genotype means on an environmental index to measure stability. They described genotypes with average stability as having a regression coefficient (b) approximately equal to 1.0. Genotypes with average stability (b = 1.0) can have actual performance levels consistently above or below the environmental mean. Performance consistently above the environmental mean indicates good adaptability to all environments while performance below the mean indicates poor adaptability to all environments. Regression coefficients greater than 1.0 (below average stability) indicate specific adaptation to environments favoring high production. Regression coefficients less than 1.0 denote above average stability with specific adaptation to poor environments.

Eberhart and Russell (4) expanded the regression model to include two stability components. The first component (b_i) is the regression of individual genotypes on an environmental index. This component measures the responses of a genotype to varying environmental indexes. The second component ($s^2 d_i$), the deviation component, is a measure of the unexplained deviation from the regression on the environmental

index. Eberhart and Russell (4) described desirable genotypes as having $b_i = 1.0$, a high mean performance, and $s^2d_i = 0$.

Several studies have been conducted to compare methods of measuring genotype-environment interaction and stability (3,7,9,11). Easton and Clements (3) found that certain wheat genotypes failed to show a linear response to nitrogen application. Regression techniques alone did not distinguish genotypes with a non-linear response. It was concluded that methods outlined by Plaisted and Peterson, Wricke, and Eberhart and Russell as described by Easton and Clements (3) would best identify genotypes with non-linear behavior. Hill (7) stated that linear regression would continue to be a valuable tool in the study of genotype-environemnt interactions. Multivariat analysis may also be helpful in situations where linear regression fails to give sufficient information (7). Based on a study of rye hybrids, mean squares for deviations from regression were found by Becker et al. (1) to be the most appropriate criterion for measuring phenotypic stability in an agronomic sense. Tai (11) found that path coefficient analysis as well as regression procedures were useful in measuring stability of potato yields and the effects of yield components on genotype-environment interactions for yield.

Ghaderi et al. (6) used cluster analysis as well as regression techniques to classify and group environments and genotypes. They found that genotypes of similar geographic origin or similar parentage fell into the same groups. Finlay and Wilkinson (5) also found genotypes to be grouped according to their geographic origins.

There is still some question as to the correlation between high yield potential and acceptable yield stability. Finlay and Wilkinson (5), Eberhart and Russell (4), and Kaltsikes and Larter (9) indicated that high yielding genotypes of barley, corn and wheat can be identified that also possess acceptable stability. Kaltsikes and Larter (9) found no correlation between yield and the stability of yield and concluded that stability need not be sacrificed for high yields. Tai (11), however, noted that high yielding potato genotypes tended toward instability.

The objectives of this study were to examine ten wheat genotypes for genotype-environment interactions for yield and the components of yield and to calculate and interpret stability estimates for this set of genotypes.

MATERIALS AND METHODS

Ten winter wheat genotypes were grown in a randomized complete-block experiment at each of four locations in Oklahoma during the 1980 and 1981 growing seasons. The genotypes were chosen on the basis of range of expression for grain yield, tiller number, kernels/spike and 1000 kernel weight. Five of the ten genotypes were Great Plains cultivars of commercial importance in the region. The remaining five were cultivars or germplasm lines from Eastern Europe. These genotypes are currently being used in the Oklahoma wheat breeding program. The ten genotypes examined in this study and their respective country or region of origin were as follows: 'Burgas 2', Bulgaria; 'F23-71', Romania; 'Lovrin 6', Romania; 'Newton', Kansas; 'NR391-76', Austria; 'Partizanka', Yugoslavia; 'Scout 66', Nebraska; 'Triumph 64', Oklahoma; 'TAM W-101', Texas; and 'Vona', Colorado.

The locations used for the study were chosen to represent a range of soil types and environmental conditions. The locations selected were, Altus in southwestern Oklahoma, Goodwell in the Oklahoma panhandle (furrow irrigation), Lahoma in North Central Oklahoma, and Stillwater on the eastern edge of the wheat belt in Oklahoma. Soil type, precipitation and temperature data for each location are presented in Table 1. Mean annual precipitation ranged from 456 mm at Goodwell to 811 mm at Stillwater. Altus had the highest mean annual temperature (17.2°C) while Goodwell had the lowest mean annual temperature (13.0°C).

The experiment was planted as a randomized complete-block experiment with three replications. Approximately 1000 seed

(equivalent to 67 kg/ha) were sown in plots 1.2 m by 3.1 m. Plots consisted of either four or five rows spaced 31 or 24 cm apart. Grain yield was measured on the entire plot at all locations except Stillwater where a 4.9 m sample was taken from the two center rows. Tiller number was determined by counting the number of fertile culms in two 31 cm sections of row for each plot. It was recorded as the average of the two measurements. Six heads were taken from each plot just prior to harvest. Kernels from these heads were counted and weighed to determine kernels/spike and 1000 kernel weight.

Analysis of variance procedures described by Comstock and Moll (2) were conducted on yield and each of the components of yield. An F test was used to test for significant differences among years, locations and genotypes as well as the interactions. The replication (years by locations) mean square from the analysis of variance was used to test differences among years and locations as well as the year by location interaction. All other tests for significance were made using the residual mean square as the error term.

Individual genotype means were regressed on an environmental index (mean of all genotypes in that environment) to provide estimates of genotypic stability for yield and its components. The model proposed by Eberhart and Russell (4) was employed. The model is defined as: $Y_{ij} = \mu i + \beta_i I_j + \delta_{ij}$, where Y_{ij} is the ith genotype mean in the jth environment, μi is the mean of the ith genotype averaged over all environments, β_i is the regression coefficient for the ith genotype, I_j is the environmental index for the jth environment and δ_{ij} is the deviation from the regression line. The Eberhart and Russell model allows genotype by environment interaction to be divided into two parts.

The first part represents the response of a genotype to different environments and is measured as the sum of squares due to regression. The second part measures the unexplained deviations from the regression on different environments. For the present study, regression coefficients were arbitrarily classified as less than one ($\bar{b} < .90$), equal to one ($.90 \leq \bar{b} \leq 1.1$) or greater than one ($1.1 < \bar{b}$).

RESULTS AND DISCUSSION

Analyses of variance conducted for yield and the components of yield are presented in Table 2. Year differences were found to be significant for all components of yield but not for yield itself. Significant differences among locations and genotypes were found for all four traits. Year by location and year by location by genotype interactions were significant for yield, kernels/spike and kernel weight but not for tiller number. All characters had highly significant year by genotype and location by genotype interactions. The presence of significant genotype-environment interactions for yield and the components of yield warrants further investigation of specific genotype response to varied environments.

Means, ranks, regression coefficients and deviations from regression are presented in Table 3 and Table 4 for yield and the components of yield. From Table 3, five genotypes (Burgas 2, Newton, NR391-76, Partizanka, TAM W-101) had mean yield greater than the overall mean. As previously defined, four of these five genotypes had regression coefficients greater than one, while the remaining genotype (NR391-76) had a regression coefficient equal to one. This is in agreement with Tai (11) who reported a trend toward instability for high yielding potato genotypes. The regression coefficient for Triumph 64 which ranked seventh for yield was very low and not statistically different from zero. Two other genotypes in the low yielding group had regression coefficients of less than one and ranked eighth and tenth for yield, indicating that above average stability may be associated with low yield. All genotypes had significant deviations

regression for yield. NR391-76 and Newton, both in the high yielding group, had relatively small deviations, while Scout 66, in the low-yielding group, also had a relatively small deviation.

A graphic representation of yield, the regression coefficient for yield and the deviation from regression is presented in Figure 1. An "ideal" genotype would be located on the right side of the graph, have a regression coefficient approximately equal to one and be close to the plane. None of the ten genotypes measured fit all three criteria for an ideal genotype for yield. Genotypes did, however, fall into three general groups: group one having high yields and below average stability (Burgas 2, TAM W-101, Partizanka, Newton), group two having intermediate yields and average stability (F23-71, NR391-76, Vona), and group three having below average yield but above average stability (Lovrin 6, Scout 66, Triumph 64). These groups did not correspond to groups based on geographic origin.

Means, regression coefficients and deviations from regression for tiller number are presented in Table 3. Of the ten genotypes studied, three had regression values equal to one, three had values greater than one and four had values less than one. All four genotypes having regression coefficients less than one ranked low (7th through 10th) for mean tiller number and all were of Eastern European origin. All Great Plains cultivars had tiller number means greater than the overall mean and regression coefficients equal to or greater than one. Finlay and Wilkinson (5) and Ghaderi et al. (6) measuring regression coefficients for yield and test weight, respectively, also found genotypes to fall into groups based on common geographic origin or common parentage. None of the deviations from regression were statistically significant

for tiller number. A graphic illustration of tiller number and the two stability components for the ten genotypes is presented in Figure 2. TAM W-101 could be considered to have near ideal expression for tiller number if high tillering is desirable in Great Plains wheats (high mean, $\bar{b} \approx 1$, $\bar{s}^2d \approx 0$). F23-71, Lovrin 6, Burgas 2 and NR391-76 all had negative deviations from regression and are represented as points on the graph. These negative deviations resulted from the pooled error variance for tiller number among the ten genotypes being larger than the regression mean square error for F23-71, Lovrin 6, Burgas 2 and NR391-76.

Kernels/spike data for the ten genotypes are presented in Table 4. All genotypes except Newton had regression coefficients that were significantly different from zero. Four genotypes had $\bar{b}$ values equal to one, three genotypes had values less than one, and three genotypes had values greater than one. F23-71 had the highest kernels/spike mean as well as the highest regression coefficient. Three genotypes, Vona, Burgas 2 and TAM W-101, had non-significant deviations from regression and ranked fourth, fifth, and tenth, respectively, for mean number of kernels/spike. A graphic illustration of kernels/spike means and the two stability components is presented in Figure 3. No association was evident between high kernels/spike means and relative instability ($\bar{b} > 1$). Vona and F23-71 both have high values for kernels/spike and $\bar{b}$ values greater than one. Burgas 2 and Newton, on the other hand, have high values for kernels/spike but $\bar{b}$ values less than one. As a point of interest, F23-71 and TAM W-101 had the extreme high and low mean values for kernels/spike respectively. These two genotypes also had the

highest and lowest regression coefficients and deviations from
regression for kernels/spike. In spite of a significant deviation from
regression, NR391-76 could be considered to have near ideal expression
for kernels/spike if high kernels/spike values are desirable (high
mean, $\bar{b} \approx 1$).

Means, ranks, regression coefficients and deviations from
regression for kernel weight are presented in Table 4. With the
exception of Lovrin 6, all genotypes had regression coefficients
significantly different from zero. Lovrin 6 had the highest kernel
weight mean as well as the largest deviation from regression. Five
genotypes had regression coefficients greater than one, three genotypes
had values less than one and two genotypes had values equal to one,
denoting average stability. Burgas 2 and TAM W-101 both had
non-significant deviations from regression. A three dimensional
representation of kernel weight means, regression coefficients and
deviations from regression is given in Figure 4. There appears to be
no trend toward instability as kernel weight increases. Lovrin 6 and
Triumph 64 both had kernel weight means above the overall mean but had
much greater than average stability for kernel weight ($\bar{b} < 1$).
On the other hand, Burgas 2, NR391-76 and TAM W-101 had kernel weight
means above the overall mean but also showed adaptability to favorable
environments ($\bar{b} > 1$). If high kernel weight was a desirable
characteristic, TAM W-101 would have the most desirable combination of
stability traits ($\bar{b}$ slightly > 1, $\bar{s}^2 d \approx 0$ and high kernel
weight mean).

The simultaneous interpretation of yield and yield component means
as well as stability estimates for the ten genotypes studied herein is

at best difficult. Some general observations can be made, however. As stated earlier, increased yield appears to be associated with a trend toward instability. Of the five genotypes with yield means above the overall mean, all but one showed a trend toward instability or specific adaptation to favorable environments. Genotypes with extreme expression for any one of the components of yield generally had regression coefficients that were quite different from one for that trait. F23-71 and Lovrin 6 illustrate this point. F23-71 had the highest kernels/spike mean and also had a regression coefficient of 1.8. On the other hand, Lovrin 6 had the highest kernel weight mean but had a regression coefficient of 0.55. It may be of interest to note that the five genotypes in the high yield group had $\bar{b}$ values less than one for kernels/spike and $\bar{b}$ values greater than one for kernel weight, but no pattern was observed for tiller number. Also, the two highest yielding genotypes, TAM W-101 and Burgas 2, had non-significant deviations from regression for kernels/spike and kernel weight.

The optimum expression of each yield component needed to maximize yield has yet to be established. Problems encountered in obtaining non-biased measurements of yield components may result in plant breeders' inability to establish optimums for yield component expression. It is clear, however, that the stability of yield components should be of concern to plant breeders. From this study, it was noted that no one genotype exhibited average stability ($\bar{b} = 1$) for yield and all of the components of yield. TAM W-101, the highest yielding genotype exhibited the closest approximation to average stability for all traits. Regression

coefficients for TAM W-101 were 1.22, 1.07, 0.62, and 1.12 for yield, tiller number, kernels/spike and kernel weight, respectively. Perhaps more important than the absolute expression of yield components in high yielding genotypes is the stability of those components over a range of environments.

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LIST OF TABLES AND FIGURES

Table 1. Soil type, mean annual precipitation and
mean annual temperature for four
locations in Oklahoma.

Location	Soil Type	Mean Annual Precip.	Mean Annual Temp.
		mm	C
Altus	Hollister and Tillman clay loam complex (Pachaic and Typic Paleustoll, fine, mixed, thermic)	615	17.2
Goodwell	Richfield clay loam (Aridic Argiustoll, fine, montmorillonitic, mesic)	456	13.9
Lahoma	Pond Creek silt loam (Pachaic Argiustoll, fine-silty, mixed thermic)	770	15.6
Stillwater	Kirkland silt loam (Udertic Paleustoll, fine, mixed thermic)	811	15.6

Table 2. Analyses of variance for yield and
yield components at four locations in two years.

Source	df	Mean Squares Yield (x1000)	Tiller Number	Kernels/ Spike	Kernel Weight
		kg/ha			g/1000
Year	1	22	4,352**	462.0**	1,559.1**
Location	3	58,349**	18,561**	83.0*	288.1**
Yr * Loc	3	7,950**	170	502.2**	416.3**
Rep (Yr * Loc) †	16	308	138	22.2	7.4
Genotype	9	3,138**	2,441**	1,450.8**	952.8**
Yr * Genotype	9	1,238**	95**	37.3**	54.9**
Loc * Genotype	27	660**	188**	20.1**	15.9**
Yr * Loc * Genotype	27	1,158**	55	15.5**	11.4**
Error	144	86	39	7.6	2.7

*, ** Significant at the 0.05 and 0.01 levels, respectively.

† Mean square for Rep (Yr * Loc) was used to test years, locations and Yr * Loc
interaction.

Table 3. Yield and tiller number means, ranks, regression coefficients and deviations from regression for ten genotypes.

Genotype	Origin	Yield Mean/Rank	Yield Regression Coefficient ($\bar{b}$)	Yield Deviation ($\bar{s}^2d$) (x100)	Tiller Number Mean/Rank	Tiller Number Regression Coefficient ($\bar{b}$)	Tiller Number Deviation ($\bar{s}^2d$)
		kg/ha					
Burgas 2	Bulgaria	3629 (2)	1.28**	3476**	39 (7)	0.75**	-4.26
F23-71	Romania	2824 (9)	1.08**	2257**	33 (10)	0.62**	-6.61
Lovrin 6	Romania	2720 (10)	0.76*	5598**	37 (8)	0.73**	-0.84
Newton	Kansas	3343 (5)	1.18**	992**	52 (5)	1.10**	7.26
NR391-76	Austria	3498 (4)	1.01**	564**	37 (9)	0.68**	-7.02
Partizanka	Yugoslavia	3513 (3)	1.23**	2100**	47 (6)	1.00**	5.88
Scout 66	Nebraska	3109 (8)	0.75**	965**	58 (3)	1.24**	8.09
Triumph 64	Oklahoma	3257 (7)	0.52	3939**	56 (4)	1.32**	5.22
TAM W-101	Texas	3917 (1)	1.22**	1931**	58 (2)	1.07**	1.53
Vona	Colorado	3286 (6)	0.97**	2555**	58 (1)	1.49**	4.96
Mean/St. Dev.		3310/293			47/6		

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Table 4. Kernels/spike and kernel weight means, ranks, regression
coefficients and deviations from regression for ten genotypes.

	Kernels/Spike			Kernel Weight		
Genotype	Mean/Rank	Regression Coefficient ($\bar{b}$)	Deviation ($\bar{s}^2 d$)	Mean/Rank	Regression Coefficient ($\bar{b}$)	Deviation ($\bar{s}^2 d$)
				g/1000		
Burgas 2	39 (5)	0.64**	0.03	36.2 (5)	1.16**	0.65
F23-71	50 (1)	1.81**	7.87**	33.9 (6)	1.11**	7.13**
Lovrin 6	29 (8)	1.03**	3.07*	50.4 (1)	0.55	22.77**
Newton	42 (3)	0.62	4.69**	27.7 (10)	1.06**	3.38**
NR391-76	45 (2)	0.95*	3.67*	37.5 (3)	1.30**	1.01*
Partizanka	36 (6)	0.96*	5.38**	33.7 (7)	1.37**	2.23**
Scout 66	30 (7)	1.10**	2.85*	33.7 (8)	0.84**	2.64**
Triumph 64	29 (9)	1.05**	3.63*	36.3 (4)	0.56**	1.82**
TAM W-101	28 (10)	0.62*	0.79	39.0 (2)	1.12**	0.18
Vona	42 (4)	1.22**	0.82	28.4 (9)	0.93**	3.18**
Mean/St. Dev.	37/3			35.7/1.6		

*, ** Significant at the 0.05 and 0.01 levels, respectively.

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Fig. 1.   Three dimensional representation of yield means, regression coefficients and deviations from regression for ten genotypes.

*, ** indicate significant deviations at the 0.05 and 0.01 levels, respectively.
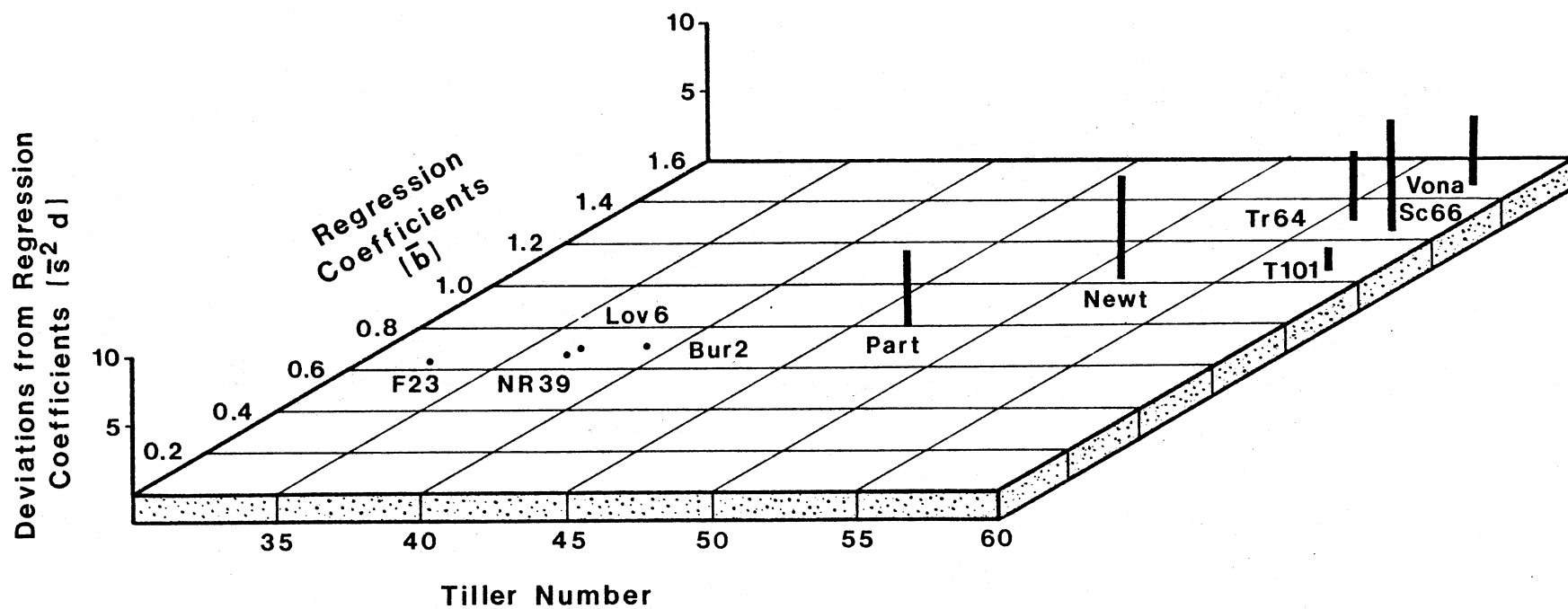
Fig. 2. Three dimensional representation of tiller number means, regression coefficients and deviations from regression for ten genotypes.

*, ** indicate significant deviations at the 0.05 and 0.01 levels, respectively.

Fig. 3. Three dimensional representation of kernels/spike means, regression coefficients and deviations from regression for ten genotypes.

*, ** indicate significant deviations at the 0.05 and 0.01 levels, respectively.
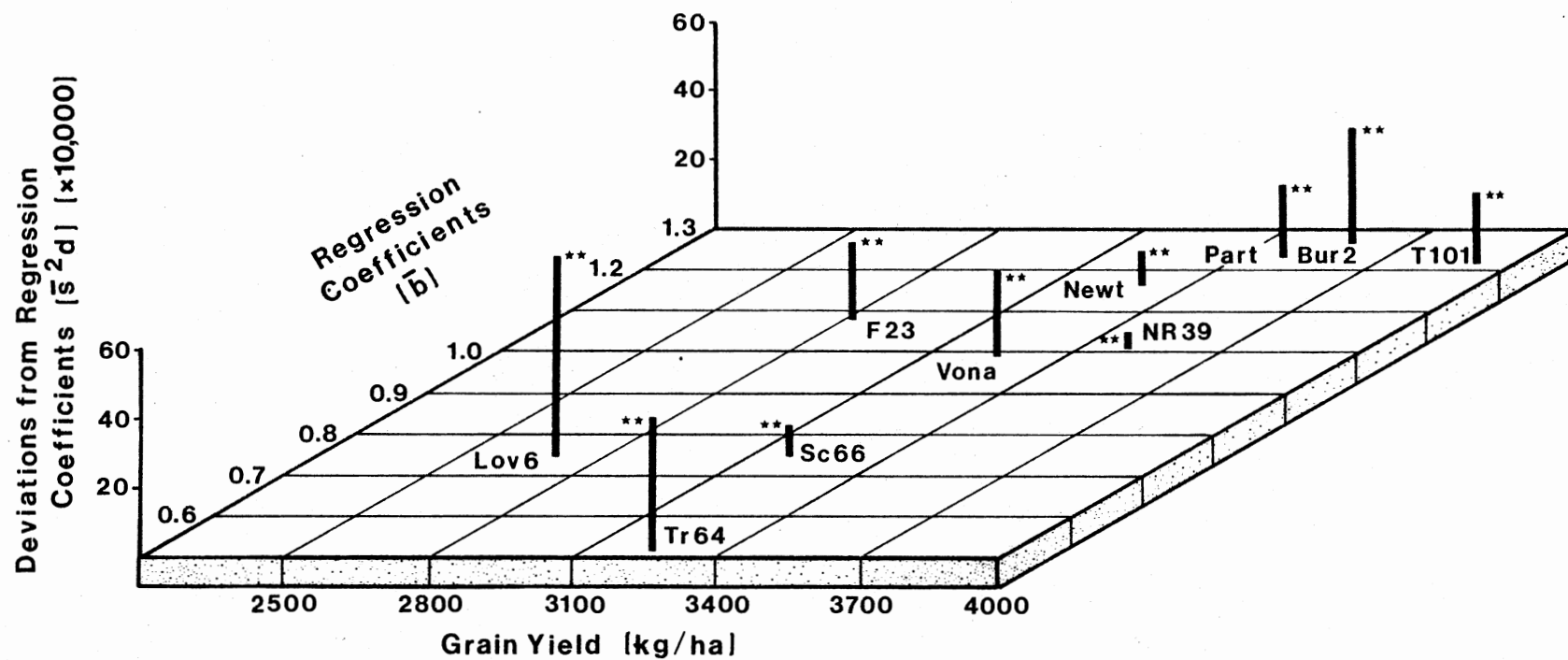
Fig. 4. Three dimensional representation of kernel weight means, regression coefficients and deviations from regression for ten genotypes.

*, ** indicate significant deviations at the 0.05 and 0.01 levels, respectively.
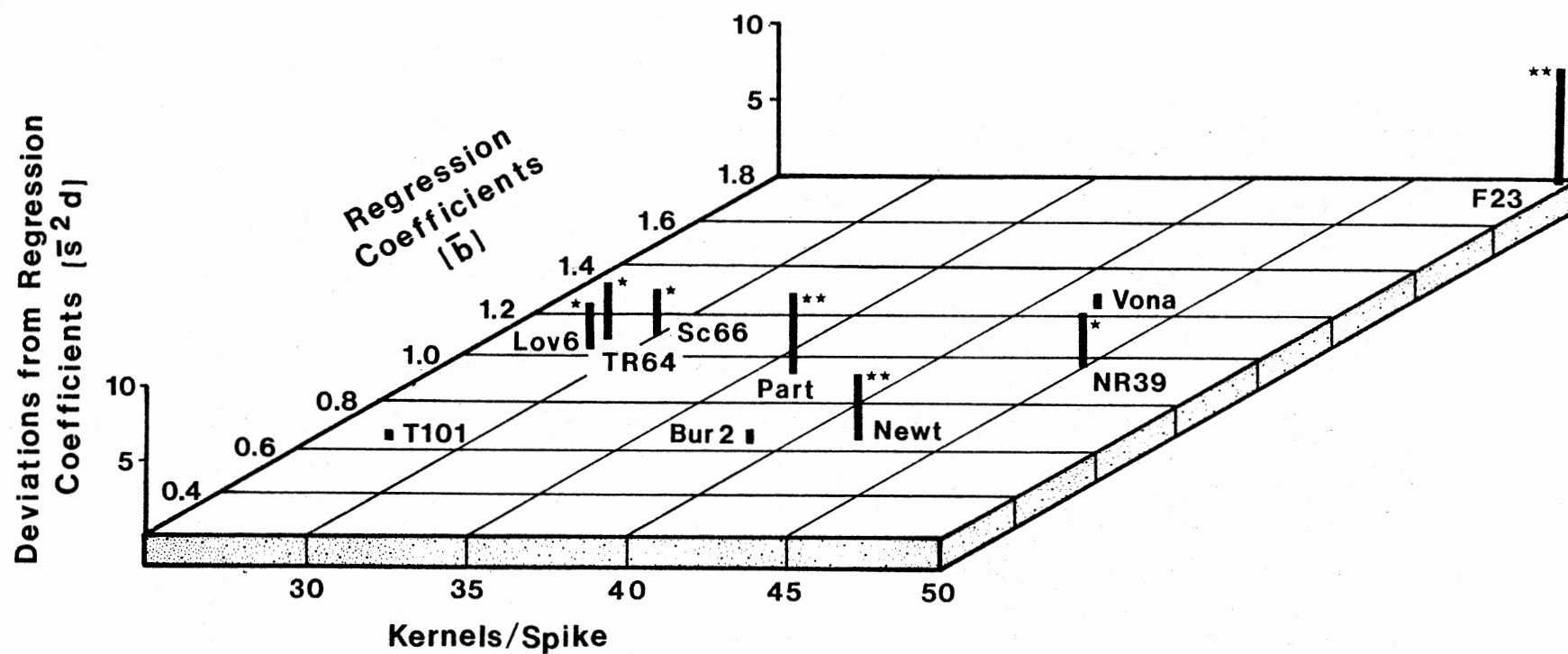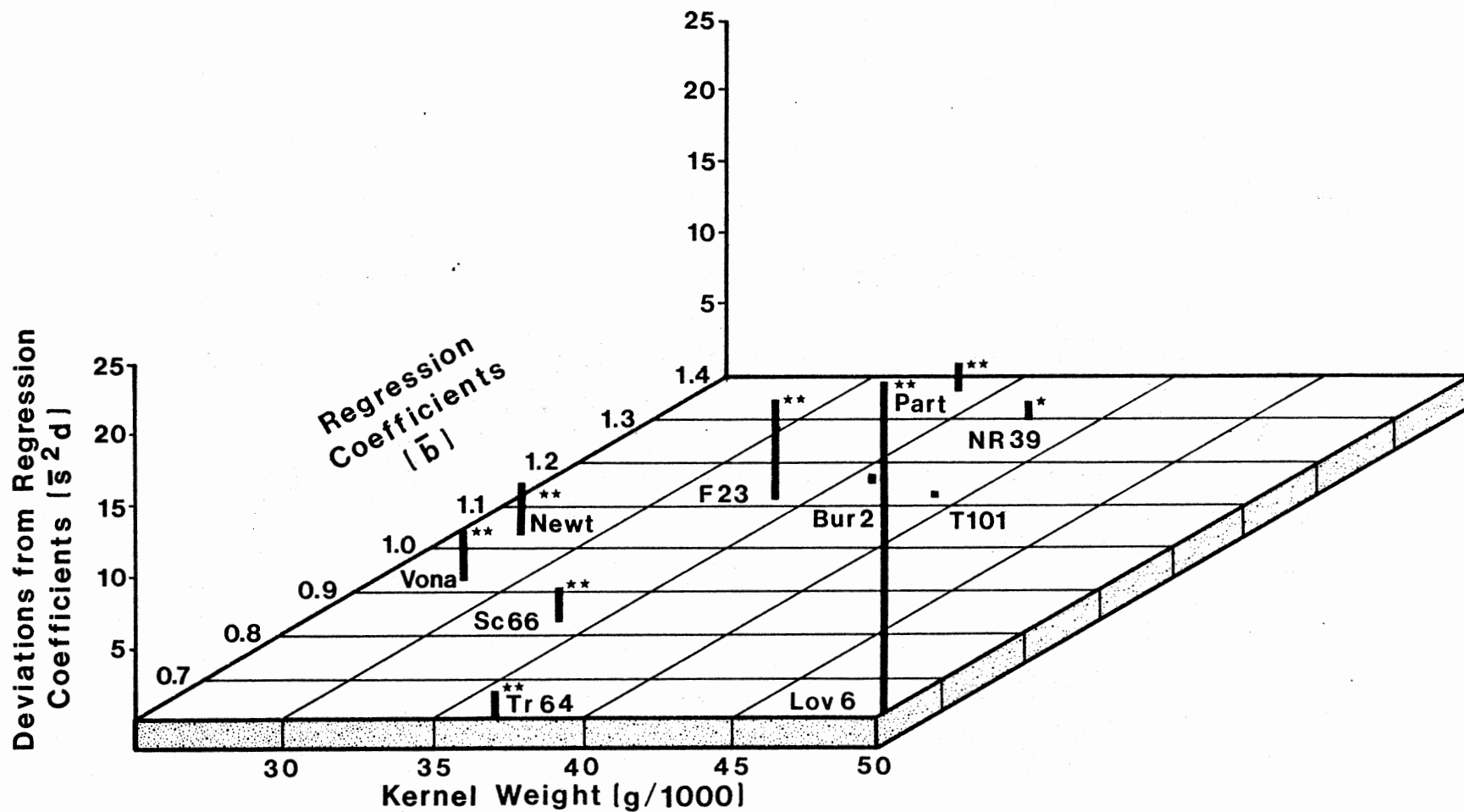
PART III

YIELD COMPONENT COMPENSATION

IN WINTER WHEAT

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Yield Component Compensation

in Winter Wheat[1]

ABSTRACT

Indirect selection for yield based on yield components offers an alternative to selection for yield per se. Selection based on yield components will be effective in increasing yield only when compensation among components is incomplete. Ten winter wheat genotypes with varied expression for yield and the components of yield were grown at each of four field locations and one greenhouse location during two crop seasons. Grain yield, tiller number, kernel weight, and kernels/spike were measured on each genotype. Analysis of variance, comparisons among means and correlation coefficients were used to study compensation among components.

Analysis of variance for all .traits indicated significant genotype-environment interactions for field data. Significant genotype by year interactions were recorded for all traits using greenhouse data. Several environments showed compensation among components based on examination of correlation data. One environment resulted in additivity among components. Genotype means plotted against environments were needed to detect compensation in some environments. Genotypes tended to exhibit greater compensation among yield components in either high or low production environments than in intermediate environments. In general, high yielding genotyes had high levels of expression for two of the three components and a correspondingly low

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expression for the third component. Each genotype arrived at yield through a unique balance of components. No one component or level of expression for all components could be described to maximize yield.

Additional index words: Triticum aestivum, L. em Thell, Genotype-environment interaction, Grain yield, Correlations among yield components.

INTRODUCTION

The use of yield components as an alternative method of selection for yield continues to be of interest to plant breeders. Thurling (15) stated, however, that the inability of breeders to achieve yield gains through yield component selection is a result of compensation among components. Several reports have indicated the presence of yield component compensation in a variety of crop plants (1,3,9,10,12,15). Adams (1) and Adams and Grafius (2) described yield components as sequential traits which develop over time. These traits share in sequence a pool of limited resources. Each trait may also draw from resources specific for that trait (8). Competition among plants and among components within the same plant for these limited resources results in yield component compensation.

Component compensation has been described as negative correlations among yield components (1,13). Adams (1) suggested that these negative correlations among components were a result of environmental influences and not genetic factors. Rasmusson and Cannell (13) suggested that gene linkage may also contribute to correlations among components. Thomas et al. (14) attributed most of the correlation among yield components to genotype-environment interaction.

As stated previously, correlations have been used by several workers to study component compensation. Hardwick and Andrews (11) expanded the use of correlations and developed a term ω, which quantified compensation. Values of ω range from zero to one. A value of 1.0 indicates complete additivity of components and results when correlations are large and positive. Independence among components is defined by ω values of 0.5 and results when correlations are zero or

have canceling effects. Large negative correlations among components result in $\omega = 0.0$ and implies component compensation. Path coefficient analysis has also been used to study yield component compensation (15). With this type of analysis, it can be shown that correlations among components sometimes mask the direct effect of a component on yield. Thurling (15) noted that the magnitude of direct effects tended to decrease with each successively developed component.

In spite of yield component compensation, optimum expression of each component in a given environment should maximize yield. Determining the optimum expression of each component, however, may be the breeder's most difficult task. Frey and Huang (7) found a curvilinear relationship between seed weight and grain yield in oats. This relationship suggested an optimum value for seed weight in oats. Seed weights above this optimum resulted in yield reduction. Rasmusson and Cannell (13), on the other hand, suggested maximizing the genetic ceiling for kernel weight in barley while restricting the genetic ceiling for heads per area and kernels per head. Studies involving source-sink relationships in wheat produced conflicting results (5,6,12). In some instances sink capacity was found to be the limiting factor in yield. This suggests a need to increase genetic ceilings for the components of yield, particularly kernels per area. In other cases, however, inputs were found to be limiting, especially for kernel weight, suggesting genetic ceilings for components are adequate for maximum yields.

Brinkman and Frey (3) concluded that selection for yield based on yield components would be successful provided that component compensation is not complete. They also found that no single yield

component increased yield consistently, indicating that a balance of
component expression is necessary. The objectives of this study were
to examine yield component compensation in a set of winter wheat
genotypes as it relates to varied environments and to define optimum
expression for each component.

MATERIALS AND METHODS

Ten winter wheat genotypes were grown in a randomized complete-block experiment at each of four field locations and one greenhouse location during the 1980 and 1981 growing seasons. The genotypes were chosen on the basis of varied expression for grain yield, tiller number, kernels/spike, and 1000 kernel weight. Five of the ten genotypes were U.S. Southern Great Plains cultivars; the remaining five were cultivars or germplasm lines from Eastern Europe, all of which are currently being utilized in the Oklahoma Agricultural Experiment Station wheat breeding program. These genotypes, the country or region of origin and the means and ranks for yield and the components of yield are presented in Table 1.

The locations utilized in this study were chosen to represent a range of soil types and environmental conditions. The locations selected were Altus in southwestern Oklahoma, Goodwell in the Oklahoma panhandle (furrow irrigation) and Lahoma and Stillwater, both in north central Oklahoma. As mentioned previously, the study was also grown in the greenhouse on the Oklahoma Agricultural Experiment Station at Stillwater. The greenhouse planting was used to approximate a non-stress environment. A range of soil type, mean annual precipitation, and mean annual temperature was encountered at the four trial locations. Mean annual precipitation ranged from 456 mm at Goodwell to 811 mm at Stillwater. Altus had the highest mean temperature, 17.2° C, while Goodwell had the lowest mean temperature, 13.9° C.

The field experiment was planted as a randomized complete-block trial with three replications. Approximately 1000 seed (equivalent to 67 kg/ha) were sown in plots 1.2 m by 3.1 m. Plots consisted of either four or five rows spaced 31 cm or 24 cm apart. Grain yield was measured on the entire plot at all locations except Stillwater where a 4.9 m length of row was taken from the two center rows. Tiller number was determined by counting the number of fertile culms in two 31 cm sections of row for each plot. It was recorded as the average of the two measurements. Six heads were taken from each plot just prior to harvest. Kernels from these heads were counted and weighed to determine kernels/spike and 1000 kernel weight.

The greenhouse experiment was also arranged as a randomized complete-block with three replications. Plants were germinated and vernalized in flats and then transplanted into rows in a greenhouse bed. Each row was 1.2 m long, consisted of 13 plants and constituted a plot. Spacing between rows was 31 cm. At maturity, individual plants were pulled and the two border plants discarded. Grain yield, tiller number, kernels/spike and kernel weight measurements were taken on individual plants. Prior to statistical analysis, one plant was discarded at random from each plot to make a total of ten test plants per plot.

Analyses of variance procedures described by Comstock and Moll (4) were conducted on yield and each of the components of yield for the eight field tests. A separate analysis was conducted on the greenhouse study. No attempt was made to merge the field and greenhouse data. An F test was used to test for significant difference among years, locations and genotypes as well as the interactions. Correlation

coefficients were calculated for all possible two-way comparisons among traits. Correlations were calculated for each of the eight field environments, the combined field environments and the combined greenhouse environments.

RESULTS AND DISCUSSION

Analysis of variance (data not shown) conducted for yield and the components of yield for the eight field environments indicated significant differences among years for all yield components but not for yield itself. Significant differences were also found among genotypes and locations for all traits. Year by location and year by location by genotype interactions were significant for yield, kernels/spike and kernel weight but not for tiller number. All characters had highly significant year by genotype and location by genotype interactions. Analysis of variance for greenhouse data indicated significant differences among genotypes for all traits. Kernel weight was the only character to show significant differences among years. With the exception of tiller number, all characters showed significant genotype by year interaction.

Means and ranks for the ten genotypes averaged over eight field environments and two greenhouse years are presented in Table 1. Genotypes are listed according to yield rank based on field means. Greenhouse values are included for each character so that comparisons might be made. Based on field data, five gentoypes had mean yields above the overall mean. Of these five genotypes, each achieved its yield value through a different expression of yield components. 'TAM W-101', the highest yielding genotype, had above average values for tiller number and kernel weight but a below average value for kernels/spike relative to the overall mean. 'Burgas 2', on the other hand, had above average expression for kernels/spike and kernel weight but was below the overall mean for tiller number. Of the remaining genotypes with above average yields, 'NR391-76' and 'Newton' both had

above average expression for two of the three yield components but were below average for the third component. 'Partizanka', which ranked third for overall yield, was the only genotype that exhibited average expression for all components. This is in agreement with Brinkman and Frey (3) who found that no single yield component was consistently responsible for yield increases.

In general, genotypes with yields below the overall mean had above average expression for only one of the components and intermediate or below average expression for the remaining two components. 'F23-71' and 'Lovrin 6' had extreme expression for kernels/spike and kernel weight, respectively. These genotypes compensated, however, with very low values for one or both of the other components. Yields for these two genotypes were also considerably below the overall mean for field data. For all traits measured, five genotypes fell above the overall mean and five fell below the mean, but no single genotype was above the overall mean for all components.

A comparison of field and greenhouse means and ranks for each genotype indicates that the relative distribution of genotypes with regard to yield was inconsistent. For example, TAM W-101 ranked first for yield in field observations but ranked sixth in the greenhouse. F23-71, on the other hand, ranked ninth for yield in the field but ranked first in the greenhouse. This type of inconsistency was not observed, however, among the yield components. In general, genotypes maintained their relative rank with respect to each other when yield components were considered.

Greenhouse means for kernel weight were consistently greater than field values. This indicates that the genetic potential for

kernel weight is seldom achieved under field conditions. This is in agreement with Fischer and HilleRisLambers (6) who found kernel weight to be limited by photosynthetic inputs under field conditions. Kernels/spike values for several genotypes (Burgas 2, Partizanka, 'Vona' and Lovrin 6) did not differ appreciably between field and greenhouse plantings. This suggests that some genotypes are able to express their genetic potential for kernels/spike under field conditions, assuming the greenhouse situation in this study represents a non-stress environment.

Environmental means for each of the eight field environments as well as two greenhouse years are presented in Table 2. Field environments tended to assort into three distinct groups based on mean yields. Two environments were classified as high yielding (Goodwell 1980 and 1981), three environments were classified as intermediate (Altus 1980, Altus 1981 and Stillwater 1980) and three were classified as low yielding (Lahoma 1980, Lahoma 1981 and Stillwater 1981). High yielding environments were characterized by a very high expression for tiller number and a range of expression for kernels/spike and kernel weight. All genotypes appeared to compensate for excessive tillering at Goodwell in 1980 by a reduction in kernel weight. Intermediate environments did not show consistent patterns of expression for yield components. The three low yielding environments were characterized by low tillering and a wide range of values for kernels/spike and kernel weight. The extreme low and high mean values for kernels/spike and the extreme low mean value for kernel weight were recorded in the low yielding environments.

Phenotypic correlation coefficients were calculated for all two-way comparisons among traits for the combined field environments (Table 3). Tiller number was most highly correlated with yield (r = .627) followed by kernel weight (r = .321). Kernels/spike had a small, negative and non-significant correlation with yield. With the exception of the correlation between kernels/spike and kernel weight (r = -.408), all other correlations among components were of low magnitude and non-significant. The negative correlation between kernel weight and kernels/spike implies compensation among these two components if all environments are considered together.

Greenhouse correlations (Table 4) again show tiller number to be the component most highly correlated with yield (r = .841). Kernels/spike had a correlation coefficient with yield that was intermediate in magnitude and positive in sign. This is not in agreement with correlations from field data. Kernel weight again had a low but positive correlation with yield. Correlations among components were near zero with the exception of the correlation between kernels/spike and tiller number (r = .315). This is in partial agreement with Adams (1) who concluded that correlations among components should be zero in a non-stress environment. The positive association between kernels/spike and tiller number as well as significant genotype by year interactions for all components indicates that greenhouse environments in this study may not represent a "true" non-stress environment.

Correlations among yield and the components of yield for each environment are presented in Table 5. With the exception of one environment, correlations among tiller number and yield were low to

intermediate in magnitude and positive in sign. The two high yielding environments (Goodwell 1980 and 1981) that also had high values for tiller number had surprisingly low correlations between tiller number and yield. Correlations between kernel weight and yield were all low in magnitude, positive in sign and not significant. A range of values was observed for correlations between kernels/spike and yield. No apparent trends were noted for these values.

Examination of correlations among yield components at individual environments should help clarify yield component compensation. None of the environments studied showed consistently large positive or large negative correlations among the three components. Most correlations were near zero or had canceling effects (Table 5). Based on Hardwick and Andrews (11) interpretation, yield components tended toward independence. Two environments, Altus 1980 and Goodwell 1980, had a tendency to show yield component compensation based on negative correlations. One environment, Goodwell 1981, had a tendency to exhibit additivity among components based on positive correlations among components. None of these positive correlations, however, were statistically significant. A strong negative association among components was not observed in environments with extreme expressions for one yield component. Negative correlations among components were not found to increase as yield levels increased as reported by Grafius et al. (9).

In order to examine compensation among components for individual genotypes, yield and the components of yield were plotted against environments for six genotypes. Two genotypes were chosen from the high yielding group (TAM W-101 and Burgas 2), two old Great Plains

genotypes were chosen from the low yielding group ('Triumph 64' and 'Scout 66') and two genotypes were chosen because of extreme expression for one of the yield components (F23-71 and Lovrin 6). Environments were ordered from low to high based on environmental mean yields. Relative units are the same for each genotype and represent kg/ha x 0.015 for yield, actual tiller number divided by two for tiller number and the observed values for kernels/spike and kernel weight.

Yield and yield component information for TAM W-101 and Burgas 2 is presented in Figures 1 and 2, respectively. Two environments show distinct compensation among yield components for both genotypes. The Lahoma location in 1980 showed an increase in kernels/spike for both genotypes that was accompanied by a reduction in kernel weight. Burgas 2 showed a larger degree of compensation than TAM W-101 for these two components. Large values for tiller number were recorded at the 1980 Goodwell environment for both genotypes. Increased tillering for both genotypes was accompanied by a reduction in kernel weight. The reduction in kernel weight was not, however, large enough to offset the increase in fertile spikes. Consequently, a high yield value resulted.

Compensation between kernels/spike and kernel weight was again noted for Scout 66 and Triumph 64 (Figures 3 and 4) at the Lahoma location in 1980. Again, high tillering at Goodwell in 1980 was accompanied by a reduction in both kernels/spike and kernel weight for Scout 66 and Triumph 64. In general, these four genotypes (TAM W-101, Burgas 2, Scout 66 and Triumph 64) showed similar trends for compensation over all eight environments.

Yield and yield component information for F23-71 and Lovrin 6 is presented in Figures 5 and 6. F23-71 and Lovrin 6 had extreme expression for kernels/spike and kernel weight, respectively. These two genotypes did not show compensation patterns similar to other genotypes. The previous four genotypes showed compensation between kernels/spike and kernel weight at the 1980 Lahoma environment. F23-71 did show compensation for these two traits but Lovrin 6 did not. Lovrin 6 did show an increase in tiller number at Goodwell in 1980 as did TAM W-101, Scout 66 and Triumph 64, but did not show a compensating reduction in kernel weight and kernels/spike similar to the three previous genotypes. F23-71 showed no compensation among components at this environment and exhibited a reduction in tiller number as well as the other two components. In general, fluctuations in yield and yield components were greater for F23-71 and Lovrin 6 than for the previously mentioned genotypes. Genotypes with extreme expression for one of the yield components may be useful as germplasm sources, but plant breeders may wish to avoid these genotypes as potential cultivars.

In summary, yield component compensation was observed for the ten genotypes studied. In some cases correlations among components revealed compensation, but in other cases examination of genotype response to individual environments was needed to detect compensation. The diversity among genotypes for component expression may explain the failure of correlations to detect compensation. Genotypes tended to exhibit more compensation among components in low or high yielding environments than in intermediate environments. With the exception of Partizanka, high yielding genotypes tended to have high levels of expression for two of the three components and a correspondingly low

expression for the third component. Each genotype accomplished yield by a unique balance between the three components of yield. Adams and Grafius (2) denoted this type of component complimentation as compensatory oscillation. No specific optimum values for each component can be determined by this study. It appears, however, that genotypes with extreme expression for kernels/spike and kernel weight tend to be less stable for yield and yield components than genotypes with less extreme values for these traits.

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LIST OF TABLES AND FIGURES

Table 1. Means and ranks for ten genotypes averaged over
eight field environments and two greenhouse years.

Genotype	Origin	Yield	Tiller Number		Kernels/ Spike		Kernel Weight	
		kg/ha					g/1000	
TAM W-101	Texas	†3917 (1)	58	(2)	28	(10)	39.0	(2)
		‡14.9 (6)	10.2	(5)	35	(9)	49.0	(2)
Burgas 2	Bulgaria	3629 (2)	39	(7)	39	(5)	36.2	(5)
		13.4 (8)	9.2	(7)	41	(6)	41.5	(8)
Partizanka	Yugoslavia	3513 (3)	47	(6)	36	(6)	· 33.7	(7)
		12.4 (10)	9.2	(6)	36	(8)	42.8	(7)
NR391-76	Austria	3498 (4)	37	(9)	45	(2)	37.5	(3)
		16.6 (4)	7.4	(10)	56	(3)	45.2	(5)
Newton	Kansas	3343 (5)	52	(5)	42	(3)	27.7	(10)
		20.3 (3)	10.8	(4)	57	(2)	41.0	(9)
Vona	Colorado	3286 (6)	58	(1)	42	(4)	28.4	(9)
		12.4 (9)	11.2	(3)	43	(5)	31.4	(10)
Triumph 64	Oklahoma	3257 (7)	56	(4)	29	(9)	36.3	(4)
		16.4 (5)	11.5	(1)	39	(7)	45.2	(6)
Scout 66	Nebraska	3109 (8)	58	(3)	30	(7)	33.7	(8)
		22.2 (2)	11.4	(2)	51	(4)	45.3	(4)
F23-71	Romania	2824 (9)	33	(10)	50	(1)	33.9	(6)
		23.5 (1)	9.1	(8)	66	(1)	46.3	(3)
Lovrin 6	Romania	2720 (10)	37	(8)	29	(8)	50.4	(1)
		14.0 (7)	8.5	(9)	32	(10)	65.5	(1)
Overall Mean:								
Field		3310	47		37		35.7	
Greenhouse		16.6	9.8		46		45.3	
Standard Deviation:								
Field		293	6		3		1.6	
Greenhouse		6.5	3.0		7		5.6	

† Upper values represent field means.

‡ Lower values represent greenhouse means. Greenhouse yield measured
in grams/plant. Tiller number for field data represents tillers per
31 cm of row. Greenhouse values represent tillers per plant.

Table 2. Environmental means for ten
genotypes at eight field environments
and two greenhouse environments.

Environment	N	Yield	Tiller Number	Kernels/ Spike	Kernel Weight
		kg/ha			g/1000
High					
1981 Goodwell	30	4624	68	38	39.3
1980 Goodwell	30	4576	79	36	32.2
Intermediate					
1980 Stillwater	30	3489	50	39	35.5
1980 Altus	30	3433	40	37	37.9
1981 Altus	30	3308	32	35	38.3
Low					
1981 Lahoma	30	2667	35	31	38.6
1981 Stillwater	30	2602	39	39	36.8
1980 Lahoma	30	1780	39	42	27.0
Combined Environments	240	3310	47	37	35.7
1980 Greenhouse	300	17.0	9.6†	46	47.7
1981 Greenhouse	300	16.2	10.0‡	45	43.0
Combined Greenhouse	600	16.6	9.8‡	46	45.3

† Yield in grams per plant.
‡ Tiller number as tillers per plant.

Table 3. Correlation coefficients for all two-way
comparisons between yield and yield components (field).

DF = 227	Tiller Number	Kernels/ Spike	Kernel Weight
Yield (kg/ha)	0.627**	−0.100	0.321**
Tiller Number		0.021	−0.100
Kernels/ Spike			−0.408**

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Correlations calculated on the basis of 8 environments
(4 locations in 2 years).

Table 4. Correlation coefficients for all two-way
comparisons between yield and yield components (greenhouse).

DF = 587	Tiller Number	Kernels/ Spike	Kernel Weight
Yield (gms/plt)	0.841**	0.590**	0.271**
Tiller Number		0.315**	0.089*
Kernels/ Spike			-0.036

*, ** Significant at the 0.05 and 0.01 levels, respectively.

Correlations calculated on the basis of two years greenhouse data.

Table 5. Correlation coefficients for all two-way comparisons between yield and yield components for ten genotypes in in eight environments.

	Year	Tiller Number Locations				Kernels/Spike Locations				Kernel Weight Locations			
		AL	GD	LA	ST	AL	GD	LA	ST	AL	GD	LA	ST
Yield	80	-.34	.08	.49*	.34	-.04	-.60**	.29	.44	.05	.18	.08	.08
(kg/ha)	81	.22	.21	.29	.14	-.03	.31	.54*	.12	.15	.19	.24	.20
Tiller Number	80					-.49*	-.17	.25	.08	-.06	-.08	-.27	-.07
	81					.22	.44	.29	-.52*	.02	.08	-.26	-.18
Kernels/	80									.07	-.40	.25	-.09
Spike	81									-.48*	.39	-.04	.44

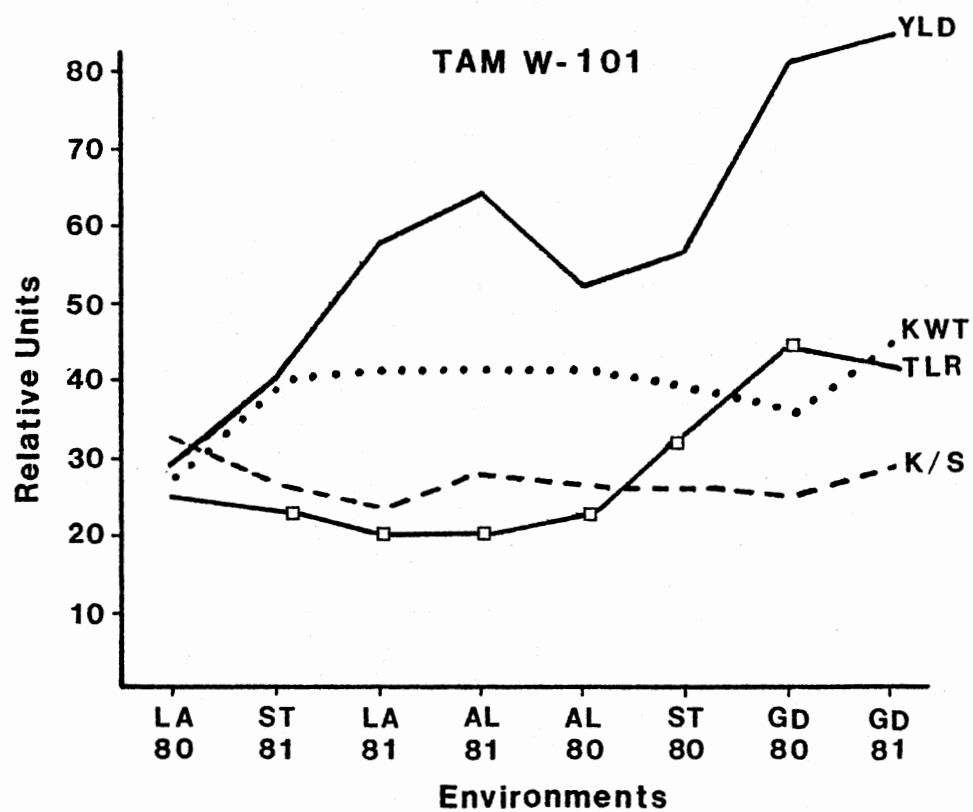*, ** Significant at the 0.05 and 0.01 levels, respectively.

Fig. 1. Yield and yield components plotted against environments
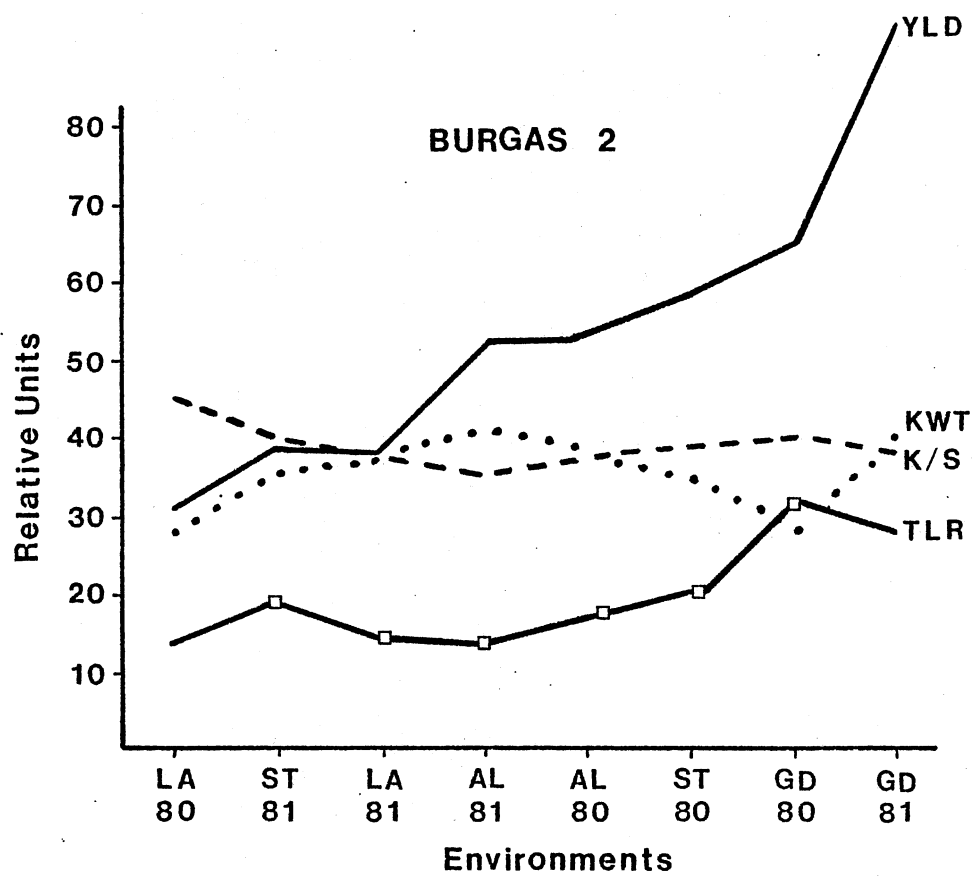   for TAM W-101.

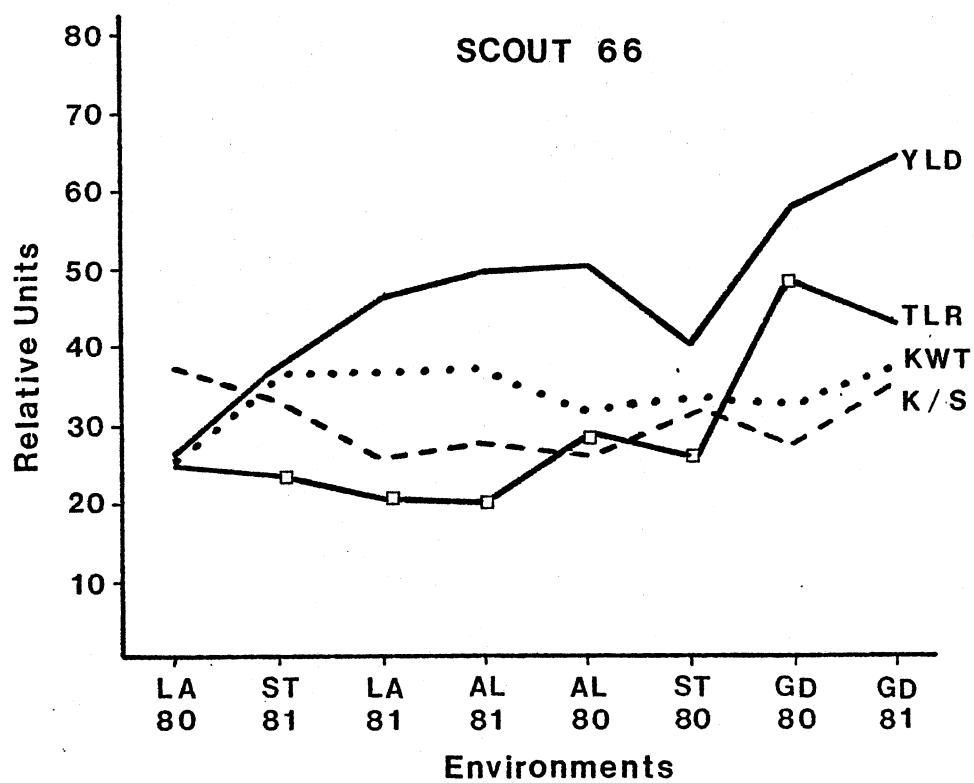Fig. 2. Yield and yield components plotted against environments for Burgas 2.

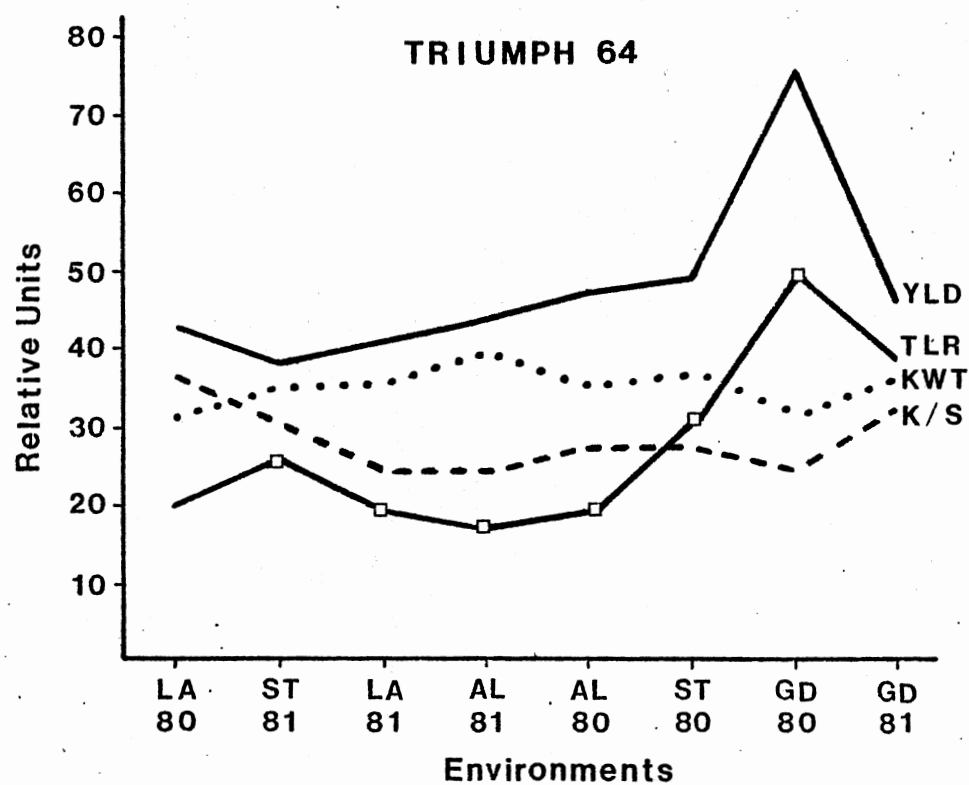Fig. 3. Yield and yield components plotted against environments for Scout 66.

Fig. 4.   Yield and yield components plotted against environments
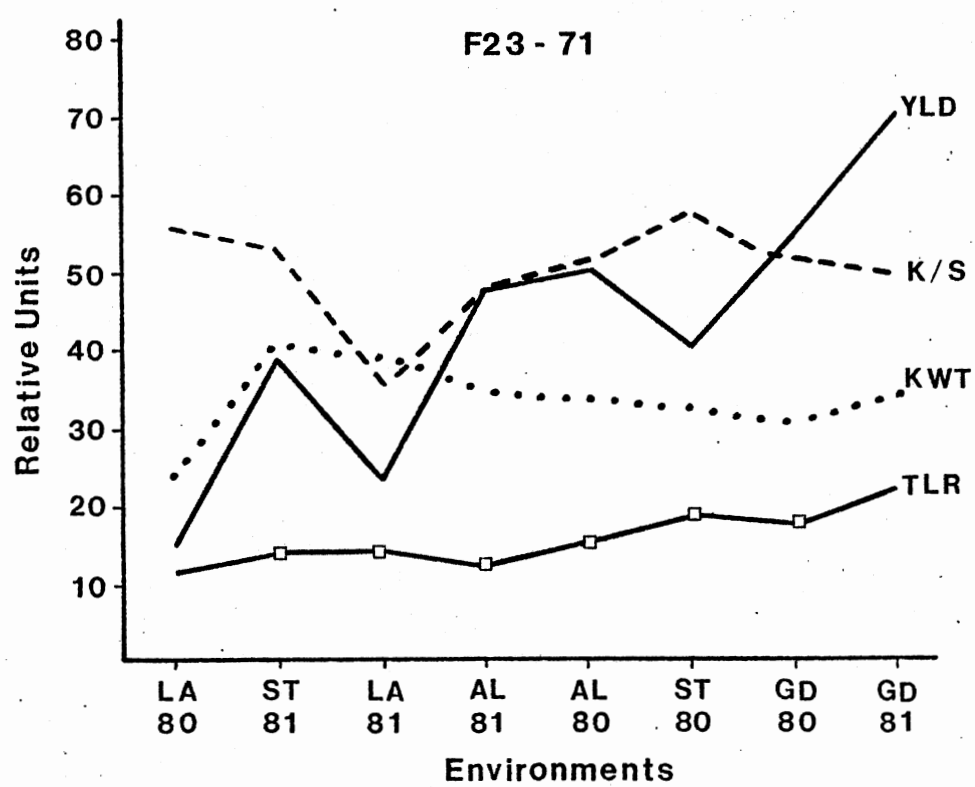for Triumph 64.

Fig. 5. Yield and yield components plotted against environments
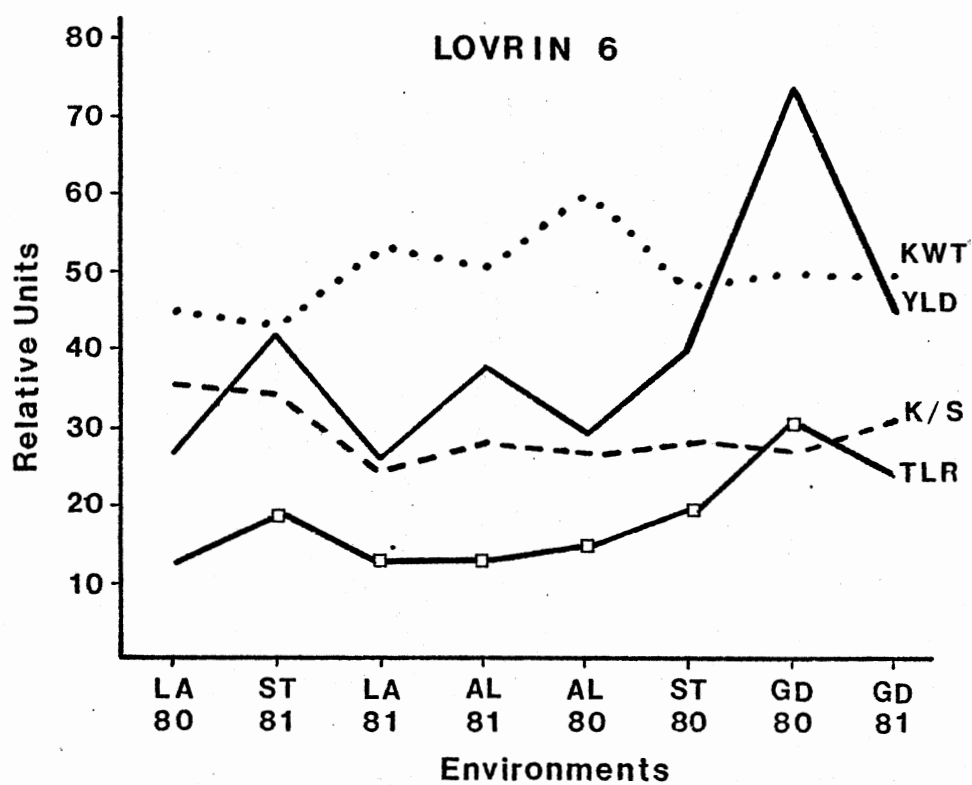   for F23-71.

Fig. 6. Yield and yield components plotted against environments for Lovrin 6.

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