THESIS

Thesis for the Degree of Ph.D.

MICHIGAN STATE UNIVERSITY

JOHN BARNARD

1978

This is to certify that the

thesis entitled

GENOTYPE-ENVIRONMENT EFFECTS IN OATS

presented by

John Barnard

has been accepted towards fulfillment
of the requirements for

PhD degree in Crops Breeding

Major professor

Date 2/21/78

ABSTRACT

GENOTYPE-ENVIRONMENT EFFECTS IN OATS

By

John Barnard

The genotype-environment effects in the yield components of oats were investigated. The yield components of oats; panicle number, seeds per panicle, and seed weight, develop sequentially. Consideration of the developmental sequence led to the analysis of each component after adjustment for the effects of preceding components in the sequence. Analysis demonstrated the importance of prior yield components in determining the variability of a given component. In the case of the component seeds per panicle, adjustment for panicle number resulted in no residual environmental effect. In the case of seed weight, adjustment for prior components enhanced both genotypic and environmental effects when these were compared with unadjusted values. In no case was genotype by environment interaction modified by the adjusted analysis.

GENOTYPE-ENVIRONMENT EFFECTS IN OATS

By

John Barnard

A THESIS

Submitted to

Michigan State University

in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Science

1978

ACKNOWLEDGMENTS

The author expresses his deepest appreciation to Dr. Grafius, his advisor for the duration of his graduate study. Thanks are also due Professors Adams, Cress, Magee, Harrison and D. Smith who formed the author's examining committee.

TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Genotype by environment analyses are of considerable importance in determining ranges of adaptation and in detecting the success of selection over a range of environments.

Much interest is centered on the genotype-environment interaction which is defined as the failure of a set of genotypes to maintain the same relative performance when grown in different environments. A consideration of the genotype-environment interaction in plant breeding leads to a choice of producing (i) widely adapted varieties giving acceptable performance in several environments, or (ii) varieties which are more particularly adapted to specific environments (Frankel, 1958). The two approaches are not mutually exclusive and their relative merits will depend on the specifics of the crop in question.

The influence of environment on the yield component sequence appears to be complex. Yield components are not independent of each other but comprise a multivariate system. Observations on one component contain information that is often, if not always, to an extent confounded with that of previous events in the sequence.

It is of interest to examine the character of a component in a sequential system in isolation from prior events in the said system. Analyses that separate 'prior' and 'present' sources of variability not only provide new information on the character of the component in question but also permit an explicit assessment of the degree of influence of prior components.

The present work examines the genotype-environment relationships in the yield component sequence of oats. A comparison is drawn between analyses performed when prior components in the sequence are ignored and when they are (linearly) eliminated.

LITERATURE REVIEW

Analysis of Genotype-Environment Experiments

Statistical treatments of the genotype-environment, henceforth abbreviated as GE, interaction are based on the widely used concept of the linear model. Acceptance of the linear model allows observations on random variables to be additively partitioned into components of variation, the components being generally ascribable to known (or presumed) sources of variation.

Under the circumstances of a suitably designed experiment the linear model permits an evaluation of the relative contributions of these components to total variation by means of the analysis of variance and related techniques.

Let an experiment be constructed with t genotypes grown in s environments with ith genotype repeated r times within the jth environment; then under the assumption of a linear model the performance, with respect to some characteristic, of the kth replicates of the ith genotype in the jth environment may be represented by Y_{ijk} such that

$$Y_{ijk} = \mu + d_i + e_j + g_{ij} + u_{ijk} \qquad [1]$$

where μ is the general mean, estimated by Y.../rst,

d_i is the genetic effect due to the ith genotype,

e_j is the environmental effect due to the jth environment,

g_{ij} is the GE effect due to the ith genotype being grown in the jth environment,

u_{ijk} is the error associated with the kth replicate of the ith genotype grown in the jth environment. For the usual tests of significance the assumption is made that the u_{ijk} $N(o,\sigma^2)$.

Analysis of variance of this simple form of GE model may follow a partition of degrees of freedom as in Table 1.[1]

In the GE models to be considered various subdivisions of within genotype variation are made.

Rowe and Andrew (1964) and Eberhart and Russell (1966) partition within genotype variation into degrees of freedom due to regression on an estimate of the environmental component and deviations from this regression. This approach, first described by Yates and Cochran (1938) assumes a linear relationship of the form:

$$\bar{y}_{ij} = \bar{y}_i + \beta_{iej} + \delta_{ij} \qquad [2]$$

where $\bar{y}_{ij}$ is the mean of the ith genotype grown in the jth environment,

---

[1]Throughout this discussion it will be assumed, for simplicity, that variation due to replication within environments and variation due to genotype-replicate interaction within environments can be pooled to give a valid estimate of experimental error.

Table 1. GE analysis of variance following model [1]

Source	d.f.	Sum of squares
Genotypes	t-1	$\Sigma Y^2_{i..}/rs - Y^2.../rst$
Within genotypes	t(s-1)	
Environments	s-1	$\Sigma Y^2_{.j.}/rt - Y^2.../rst$
GE	(t-1)(s-1)	$\Sigma\Sigma Y^2_{ij.}/r - \Sigma Y^2_{i..}/rs - \Sigma Y^2_{.j.}/rt + Y^2.../rst$
Error	st(r-1)	$\Sigma\Sigma\Sigma Y^2_{ijk} - \Sigma\Sigma Y^2_{ij.}/r$

$\bar{y}_i$ is the mean of the ith genotype over all environments,

β_i is the coefficient of regression of $\bar{y}_{ij}$ on the estimated environmental component, e_j,

δ_{ij} is the deviation from regression in the (ij)th cell.

Recognizing that $\bar{y}_i = \mu + d_i$, total degrees of freedom are partition as in Table 2.

In Eberhart and Russell's treatment the regression coefficients and the deviation sum of squares for each genotype provide 'stability' parameters. A stable genotype is defined as one with unit regression coefficient and zero deviation sum of squares. An estimate of the environmental component is taken to be the environmental mean, Y.j./rt, however, it is recognized that the non-independent nature of these quantities vitiates strict F-tests.

Finlay and Wilkinson (1963) also utilize the technique of regressing individual yields on environmental means to generate stability statistics.[1] Genotypes with regression coefficients approaching unity demonstrate an average stability over all environments (i.e. a low order of interaction). Genotypes with coefficients less than or exceeding

---

[1]The interaction sum of squares with (t-1) degrees of freedom appearing in Finlay and Wilkinson's table 2 is somewhat confusingly called regression sum of squares. It presumably is a sum of squares due to differences, or heterogeneity, of regression coefficients.

Table 2. GE analysis of variance partitioning total within genotype variation by regression on environment (after Eberhart and Russell, 1966)

Source	d.f.	Sum of squares
Genotypes	t-1	
Within genotypes	t(s-1)	
Environments (linear)	1	$\frac{1}{rt}(Y_{.j}.e_j)^2/\Sigma e_j^2$
GE (linear)	t-1	$\Sigma_i[\frac{1}{r}(\Sigma_j Y_{.j}.e_j)^2/\Sigma e_j^2]$-env(linear)
Deviations	t(s-2)	
Genotype 1	s-2	
.	.	
.	.	
Genotype t	s-2	
Error	st(r-1)	

unity demonstrate a greater or lesser than average stability respectively. Practical assessment of a particular genotype must be made, it is suggested, with reference to both the respective genotypic mean performance as well as regression coefficient.

Other treatments of the GE analysis concern themselves with a partition of GE variation *per se*.

Perkins and Jinks (1968) express the GE component, g_{ij}, as a linear function of the environmental component

$$g_{ij} = \beta_{di} e_j + \delta_{ij}$$

which when substituted into [1] gives a model of the form

$$Y_{ijk} = \mu + d_i + e_j + \beta_{di} e_j + \delta_{ij} + u_{ijk} \qquad [4]$$

β_{di} being the regression coefficient for the ith genotype,
δ_{ij} being the deviation from regression in the jth environment.

Proceeding from [4] Perkins and Jinks subdivide degrees of freedom as in Table 3.

Significance of either heterogeneity or deviation mean squares indicates the presence of GE interaction. The relative magnitudes of the two mean squares indicates the reliability of the predictions made on the basis of regression.

Fripp and Caten (1971) point out that the parameters of [2] and the parameters of [4] are simply related. β_i is equal to $1 + \beta_{di}$.

Table 3. GE analysis of variance partitioning GE interaction (after Perkins and Jinks, 1968)

Source	d.f.
Genotypes	t-1
Environments	s-1
GE	(t-1)(s-1)
Heterogeneity of regressions	t-1
Deviations	(t-1)(s-2)

Freeman and Perkins (1971) detail statistical objections to the use of non-independent estimates of the environmental component. They note that when non-independent estimates are in fact used the sum of squares for environment-linear in Table 2 is equal to the environment sum of squares in Table 3 with a consequent ambiguity in degrees of freedom. Freeman and Perkins propose to use independent estimates, say z_j, such as control genotypes or additional replications, and suggest a model of the form:

$$\bar{y}_{ij} = \mu + d_i + \bar{\beta} z_j + \bar{\delta}_j + \beta_{di} z_j + \delta_{dij}$$

in which $\bar{\beta}_{zj} + \bar{\delta}_j$ is an expansion of the environmental component of [1] in terms of $\bar{\beta}$, the coefficient of the combined regression of y_{ij} on z_j, and $\bar{\delta}_j$, the associated residuals. $\beta_{di} + \delta_{dij}$ is an expansion of the GE component of [1] in terms of $\beta_{di} = \beta_i - \bar{\beta}$ and $\delta_{dij} = \delta_{ij} - \bar{\delta}$. Although average

stability will not necessarily be associated with a unit regression coefficient, as when environmental means replace the z_j, less stable genotypes will be associated with larger coefficients and more stable genotypes will be associated with smaller coefficients. Under the circumstance that the $\bar{\delta}_j$ are (statistically) homogenous and $\bar{\beta}$ does not differ from unity than [6] reduces to [4].[1] The analysis of variance procedes as in Table 4.

Environment and Yield Components

Grain yield in cereal crops is the product of a number of yield components (e.g. Grafius, 1965). Thus in oats the components are taken to be the morphological traits tiller number, seed number per panicle and seed weight. The complex trait grain yield is the numerical product of these components, is therefore completely determined by these components, and no change in yield can occur unless there are changes in one or more of these components.

Yield components are not, in general, independent of each other in their expression but comprise a complex interacting system. The components are not formed simultaneously but differentially in accordance with an ontogenetic sequence. Thus in the small grains tiller number is established before seed number per panicle, and the

[1] If environment mean is used to estimate e_j then these two conditions will be fulfilled and [4] will be appropriate.

Table 4. GE analysis of variance assuming an independent estimate of environment (after Freeman and Perkins, 1971)

Source	d.f.	Sum of squares
Genotypes	t-1	
Environments	s-1	
Combined regression	1	$[(\Sigma Y_{.j.} Z_j)^2/rt]/\Sigma Z^2_j$
Residual	s-2	
GE	(t-1)(s-1)	
Heterogeneity of regressions	t-1	$[\Sigma_i (\Sigma_j Y_{ij.} Z_j)^2/r - (\Sigma Y_{.j.} Z_j)^2/rt]/\Sigma Z^2_j$
Residual	(t-1)(s-2)	
Error	st(r-1)	

establishment of seed number per panicle precedes the determination of seed size.

It may be postulated that in a finite environment, using environment, in the most general sense, there is competition for common resources between components within the plant with the result that negative associations would tend to be observed. Such is the case (Adams, 1967 and references).

The notion of compensatory reaction in sequential components was first suggested by Adams (loc. cit.). Under conditions of constant but limiting environmental input it was proposed that a primary trait, say X, would utilize more or less input and a second trait, Y, would tend to use up any residual in a compensatory fashion. In a series of observations over a number of genotypes, each demonstrating a different degree of expression for X, X would then tend to be negatively correlated with Y.

Under a second model of fluctuating environmental input, Adams explains compensation in terms of a phasing of input with the ontogeny of the plant.

The interpretation of negative inter-component correlations as the result of environmental stresses during the growing season was made by Grafius (1969). Correlation coefficients computed on the basis of environment mean component values were used as an indication of between environment stress and as such measured the differential

distribution of environmental resources between environments. Correlation coefficients computed on the basis of genotype means within environments were used as a measure of within location stress. Low correlations were interpreted as a 'less forced' developmental situation with less competition between components.

Thomas et al. (1971 a,b,c) applied Gram-Schmidt orthogonalization to yield component sequences in barley and rice. Once again inter-component correlations were taken as an indication of stress existent in the genotype set within the environment where it was grown. Orthogonalization of the component data was used to adjust out the influence of correlation. A GE analysis (Thomas et al., 1971c) involving unadjusted and adjusted data demonstrated an enhanced role of GE interaction in determining variability in the adjusted data.

A similar study undertaken by Voysest (1970) demonstrated changes in the importance of sources of variance. When the effects of prior traits were adjusted out of the yield component sequence an increase in the contribution of the GE interaction was observed.

Grafius and Thomas (1971) examined the yield component sequence in oats by means of a second order recurrence equation. Convergently, divergently and continuously oscillating component sequences were considered. The

implication of weak 'direct' genetic control of later components in the sequence under conditions of significant oscillation was recognized. In particular it was observed that seed size was to a great extent determined by tiller number and seed number per panicle.

MATERIALS AND METHODS

Thirty six lines of oats were grown in three Michigan locations. At two locations measurements on tiller number per unit area (X), seed weight (Z) and grain yield per unit area (W) were taken. At the third location observations on seed weight (Z) and grain yield (W) were taken. Seed number per panicle (Y) and seed number per unit area (XY) were computed from the relationships

$$Y = W / (X\ Z)$$

$$XY = W / Z$$

Simple lattice designs with four replications were used at each location. The incomplete block structure was ignored for the present study. Logarithmic transformation of all data was effected prior to statistical analysis.

GE relationships in the yield component sequence were examined by a comparison of source variation when the effects of the sequence were ignored and when the effects of the sequence were eliminated. Analysis ignoring sequence followed the partition in Table 1. To eliminate linear prior sequence effects model [7] was constructed.

$$Y^n_{ijk} = m^n + d^n_i + e^n_j + g^n_{ij} + \sum_{i}^{m<n} b^m_j Y^m_{ijk} + u^n_{ijk} \qquad [7]$$

In [7]

Y^n_{ijk} is the observation on the nth yield component of the ith genotype in the kth replicate of the jth environment,

m^n is the general mean of the nth yield component,

d^n_i is the genetic component due to the ith genotype for the nth yield component,

e^n_j is the environmental component due to the jth environment for the nth yield component,

g^n_{ij} is the GE component due to the ith genotype being grown in the jth environment,

$\sum_{i}^{m<n} b^m_j Y^m_{ijk}$ is a cumulative least squares adjustment taking account of linear effects due to the n-1 yield components prior to the nth in the component sequence. Coefficients, b^m_j are prescribed for each environment (hence the suffix j),

u^n_{ijk} is the stochastic error associated with the $(^n_{ijk})$th observation.

Equivalence With the Approach Used by Thomas et al. (1971a)

Given an n x p matrix, $\underline{X}$, comprising n observations on each of p variables, a matrix, $\underline{Y}$, may be formed by the Gram-Schmidt factorization

$$\underline{X} = \underline{Y}\ \underline{G} \qquad [8]$$

such that for any two column vectors in $\underline{Y}$, say $\underline{y}_i$ and $\underline{y}_j$, their scalar product, $\underline{y}_i'\underline{y}_j$, is zero, i.e. $\underline{y}_i$ and $\underline{y}_j$ are orthogonal.

The jth column of $\underline{Y}$ is determined by the function

$$\underline{y}_j = x_j - \sum_{i=1}^{j-1} \frac{\underline{y}_i'\underline{x}_j}{\underline{y}_i'\underline{y}_i}\ \underline{y}_i \qquad [9]$$

If the variables comprising the columns of $\underline{X}$ are random variables then the various scalar products entering into [9] are the appropriate product moments involving the $\underline{y}_i$ and the $\underline{x}_j$ and the operations following the summation sign in [9] can be identified with Rao's (1952) pivotal condensation procedure for computing $\underline{G}^{-1}$.

$\underline{y}_j$ is in fact the residual vector associated with the least squares estimation of $\underline{x}_j$ on the $\underline{y}_i$ for all i<j. In other words, the jth column of $\underline{Y}$ is determined by the linear regression of the corresponding column of $\underline{x}$ on the preceding columns of $\underline{Y}$.

$$\hat{\underline{x}}_j = \underline{Y}_{<j}\ \underline{a} \qquad [10]$$

where $\underline{Y}_{<j}$ is taken to mean the first j-1 columns of $\underline{Y}$.

To demonstrate the equivalence of the adjustments used by Thomas *et al.* (*loc. cit.*) and the adjustments in [7] it is sufficient to show that the residuals associated with

[10] are identical with the residuals associated with a more familiar form of least squares equation

$$\hat{\underline{x}}_j = \underline{X}_{<j}\ \underline{b}$$

the residuals in each case being defined by

$$\underline{y}_j = \underline{x}_j - \underline{Y}_{<j}\ \underline{a}$$

and

$$\underline{y}_j = \underline{x}_j - \underline{X}_{<j}\ \underline{b}$$

respectively.

The following equality must be demonstrated.

$$\underline{Y}_{<j}\ \underline{a} = \underline{X}_{<j}\ \underline{b}$$

From [8] one obtains

$$\underline{X}_{<j}\ \underline{G}^{-1}_{<j}\ \underline{a} = \underline{X}_{<j}\ \underline{b}$$

Premultiplying by $\underline{X}^{-1}_{<j}$ one has

$$\underline{G}^{-1}_{<j}\ \underline{a} = \underline{X}_{<j}\ \underline{b} \qquad [11]$$

At this point, [11] is recognizable as the back substitution following triangular decomposition of the moment matrix $\underline{X}'_{<j}\ \underline{X}_{<j}$ (for example following the forward solution of the abbreviated Doolittle algorithm).

To complete the demonstration of identity it is only necessary to factor $\underline{a}$ and $\underline{b}$ in [11] by their respective projection matrices to give

$$\underline{G}_{<j}^{-1} (\underline{Y}'_{<j}\underline{Y}_{<j})^{-1} \underline{Y}'_{<j}\underline{X}_j = (\underline{X}'_{<j}\underline{X}_{<j})^{-1}\underline{X}'_{<j}\underline{X}_j$$

Substituting for $\underline{X}_{<j}$ gives

$$\underline{G}_{<j}^{-1} (\underline{Y}'_{<j}\underline{Y}_{<j})^{-1} \underline{Y}'_{<j}\underline{X}_j = (\underline{G}'_{<j}\underline{Y}'_{<j}\underline{Y}_{<j}\underline{G}_{<j})^{-1} \underline{G}'_{<j}\underline{Y}'_{<j}\underline{X}_j$$

Simplification yields the basic matrix identity

$$\underline{G}_{<j}^{-1} (\underline{Y}'_{<j}\underline{Y}_{<j})^{-1} \underline{G}'^{-1}_{<j} = (\underline{G}'_{<j}\underline{Y}'_{<j}\underline{Y}_{<j}\underline{G}_{<j})^{-1}$$

Hence the identity of the two approaches is assured.

A minor inconsistency to emerge from a comparison of the present approach and that of Thomas *et al.* (1971c) involves an error in assignment of degrees of freedom on the part of the latter authors. Error degrees of freedom should have been reduced to take account of adjustment by the concomitant yield components.

RESULTS

Results of the two location analysis, with a 'complete' yield component sequence will be examined first.

The analysis of variance for yield (Table 5) demonstrates significance of genotypic and environmental main effects and the GE interaction. A comparison of the variance ratios indicates that environmental variation was of major importance in determining variability in yield.[1]

An examination of the analyses of variance for the X-Y-Z yield component sequence shows a differential degree of determination by the sources of variance.

In the case of tiller number (X) environment was the prime source of variation although a very highly significant genotype effect was also apparent (Table 6). No significant GE interaction was detected.

The second component of the sequence, seed number per panicle (Y), demonstrated significance of main effects and GE interaction (Table 7). Determination of the variability of Y closely resembled that of yield itself.

---

[1] It is fully recognized that an F-test of environmental against error variance is not really appropriate owing to the 'restriction error', to use Anderson's (1970) terminology, appearing in the expectations of the mean squares for environments. However an informal comparison will suit present purposes.

No significant environmental effect was discernable for seed weight (Z, Table 8). Although a very highly significant GE interaction was indicated, a much larger variance ratio was demonstrated for the genotypic effect.

Tables 9 and 10 summarize the variance analyses when the linear effects of prior components in the yield component train were statistically eliminated. Inasmuch as tiller number is the first component in the sequence, as presently defined, no changes in the analysis are indicated. Table 6 therefore remains unaltered.

When seed number per panicle is re-analyzed eliminating the effect of tiller number within each environment then the remaining environmental effects do not contribute significantly to variation (Table 9). Genotype and GE interaction both yield very highly significant variance ratios but tiller number is by far the most important source of variance.

In the case of seed weight (Table 10), an elimination of the effects of tiller number and seed number per panicle reduces the influence of genotype. In this case main effects and interaction are significant and once again the effects of prior traits in the yield component sequence are important determinants of variability in the current component.

The three-location analyses cover a wider range of variability.

The importance of the environment effect in yield and throughout the yield component sequence is shown by Tables 11 through 13. As there are only two yield components resolved in this case an adjusted analysis can only be constructed for seed weight (Z, Table 14).

Eliminating the effect of XY reduces the environmental on Z to non-significance and reduces determination by genotypes although the latter still remain very highly significant. The effect of XY in determining variability in Z is very highly significant.

Table 5. Analysis of variance for seed yield, W(log gms m^{-2})

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00573	2.63	***
Environments	1	.42980	197.15	***
GE	35	.00915	4.19	***
Error	216	.00218		

*** indicates significance at $P < .001$.

Table 6. Analysis of variance for tiller number, X(log)

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00503	2.63	***
Environments	1	.05947	31.49	***
GE	35	.00225	1.19	
Error	216	.00189		

*** indicates significance at $P < .001$.

Table 7. Analysis of variance for seeds per panicle, Y(log)

Source	d.f.	Mean square	Variance ratio	
Genotype	35	.01158	2.98	***
Environment	1	.80924	208.28	***
GE	35	.01275	3.28	***
Error	216	.00389		

*** indicates significance at P < .001.

Table 8. Analysis of variance for seed weight, Z(log mg)

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00525	12.92	***
Environment	1	.00000	.00	
GE	35	.00149	3.68	***
Error	216	.00041		

*** indicates significance at P < .001.

Table 9. Adjusted analysis of variance for seeds per panicle, Y, eliminating the linear effect of X within environments

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.01209	5.22	***
Environments	1	.00293	1.27	
GE	35	.00859	3.72	***
X (environments)	2	.17199	74.32	***
Error	214	.00231		

*** indicates significance at P < .001.

Table 10. Adjusted analysis of variance for seed weight, Z, eliminating the linear effects of X and Y within environments

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00248	6.78	***
Environments	1	.00316	8.65	**
GE	35	.00145	3.98	***
X,Y (environments)	4	.00257	7.02	***
Error	212	.00037		

** indicates significance at P < .005.

*** indicates significance at P < .001.

Table 11. Analysis of variance for seed yield, W(log gms m^{-2})

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00966	4.12	***
Environments	2	.21503	91.67	***
GE	70	.00738	3.14	
Error	324	.00235		

*** indicates significance at P < .001.

Table 12. Analysis of variance for seed number, XY(log m^{-2})

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.02489	10.05	***
Environments	2	.30573	124.05	***
GE	70	.00759	3.08	***
Error	324	.00246		

*** indicates significance at P < .001.

Table 13. Analysis of variance for seed weight, Z(log mg)

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00776	14.45	***
Environments	2	.09761	181.89	***
GE	70	.00136	2.53	***
Error	324	.00054		

*** indicates significance at P < .001.

Table 14. Adjusted analysis of variance for seed weight, Z, eliminating the linear effect of XY within environments

Source	d.f.	Mean square	Variance ratio	
Genotypes	35	.00359	7.34	***
Environments	2	.00133	2.72	
GE	70	.00122	2.48	***
XY (environments)	3	.00562	11.48	***
Error	321	.00049		

*** indicates significance at P < .001.

DISCUSSION

The examination of variates in isolation from concomitant measurements is a well established technique in biometry. The procedures herein differ from more common covariance approaches in a matter that is computationally trivial but philosophically of some note.

A major assumption in the more usual applications of covariance techniques to data analysis is that there is a homogeneity of regressions for all data cells. Such an assumption is often reasonable and the dangers of its violation easily recognized. If the assumption is unwittingly violated then the treatment effects will be adjusted in a manner that will not make them amenable to easy interpretation.

In the present analysis, and those of Thomas *et al.* (1971 a,b,c), the assumption of regression homogeneity is not made in general but is restrticted to specific subsets of the data, *viz.* environments, in accordance with an *a priori* biological rationalization.

More specifically then, a characterization of the growing season is made by means of the recurrence relationships observed to hold between the components of yield. Such a recurrence relationship is considered to reflect the

temporal and physical distribution of environmental resources and hence parametizes, to an extent, the total environment in which the genotype grows. An analysis of an event in the yield component sequence should therefore take account of prior events as well as current environment for both will determine variability in the current event.

The recurrence functions for two of the environments presently analysed were previously determined by Grafius (1971). Biologically, the difference in recurrence between locations can reasonably be explained. One location (Kalamazoo) is characterized by an early warming followed by a degree of summer drought. Such conditions tend to promote profuse tillering followed by restriction (by both the prior component, tiller number, and current water stress) on seed number per panicle. The second location is characterized by a more uniform degree of environmental input.

Given different recurrence functions for each environment the analysis presumes to adjust observations to uniform prior component means. This procedure might be more popularly phrased as an analysis 'holding prior components constant'.

When this is done the effects of prior yield components in determining variability of the current component appears to be of major importance.

In the case of seed number per panicle in the two location analysis and seed weight in the three location analysis a reduction in the 'direct' environmental contribution was apparent. In general this is to be expected since we are attempting to fit parameters that characterize prior environmental events. These results contrast to an extent with the results of Thomas et al. (1971c) who observed the contribution of the genotypic main effect to be most reduced. In the case of seed weight in the two location analysis much of the adjustment was at the expense of the genotypic main effect and the environment mean square became significant.

The assumption of uniformity of the within environment regression coefficients is made for the present analysis. It is fully recognized that some variation between genotypes may occur with respect to these coefficients. Unfortunately the four replicates within each location proscribes any closer examination of this point. It would indeed be of interest to extract any within genotype recursion and any GE interaction of these functions.

LITERATURE CITED

Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, Phaseolus vulgaris. Crop Science, 7, 505-510.

Anderson, V. L. 1970. Restriction errors for linear models (an aid to develop models for designed experiments). Biometrics, 26, 255-267.

Eberhart, S. A. and W. A. Russell. 1966. Stability parameters for comparing varieties. Crop Science, 6, 36-40.

Finaly, K. W. and G. N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res., 14, 742-754.

Frankel, O. H. 1958. The dynamics of plant breeding. J. Aust. Inst. Agric. Sci., 24, 112-123.

Freeman, G. H. and J. M. Perkins. 1971. Environemtnal and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. Heredity, 27, 15-23.

Fripp, Y. J. and C. E. Caten. 1971. Genotype-environment interactions in Schizophyllum commune. I. Analysis and character. Heredity, 27, 393-407.

Grafius, J. E. 1965. A geometry of plant breeding. Mich. State Univ. Agric. Expt. Sta. Res. Report #7.

Grafius, J. E. 1969. Stress: a necessary ingredient of genotype by environment interaction. 2d. International Barley Genetics Conference. Pullman, Washington.

Grafius, J. E. and R. L. Thomas. The case for indirect genetic control of sequential traits and the strategy of deployment of environmental resources by the plant. Heredity, 26, 433-442.

Perkins, J. M. and J. L. Jinks. 1968. Environmental and genotype-environment components of variability. III. Multiple lines and crosses. Heredity, 23, 339-356.

Rowe, P. R. and R. H. Andrew. 1964. Phenotypic stability for a systematic series of corn genotypes. Crop Science, 4, 563-567.

Thomas, R. L., J. E. Grafius and S. K. Hahn. 1971. (a). Transformation of sequential quantitative characters. Heredity, 26, 189-193.

Thomas, R. L., J. E. Grafius and S. K. Hahn. 1971. (b). Genetic analysis of correlated sequential characteris. Heredity, 26, 177-188.

Thomas, R. L., J. E. Grafius and S. K. Hahn. 1971. (c). Stress: an analysis of its source and influence. Heredity, 26, 423-432.

Voysest, O. V. 1970. An attempt to overcome the yield-dampening effect of negative correlations among yield components in beans (Phaseolus vulgaris L.). Ph.D. Thesis, Mich. State Univ.

Yates, F. and W. G. Cochran. 1938. The analysis of groups of experiments. J. Agric. Sci., 28, 556-580.