Environmental Response Patterns in Commercial Classes of Common Bean (*Phaseolus vulgaris* L.) *

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Summary. The yield data of 39 cultivars of diverse commercial classes of beans (*Phaseolus vulgaris* L.) planted in seven locations in Michigan were subjected to cluster and canonical variate analyses. The essential findings and conclusions can be summarized as follows: (1) Cluster analysis classified the cultivars into sub-sets or clusters almost identically coinciding with their commercial class designation. Canonical variate analysis completely confirmed the sub-groupings. Within class similarities were attributed to a narrow genetic base resulting from a common genetic relationship, or at least sharing of a common gene pool. (2) It was found that two clusters could possess almost identical mean (cluster mean) yields, and deviate in opposite directions over the same range of environments. (3) When total genotype × environmental interaction variance was partitioned into between and within clusters, the cluster × environment portion constituted 80% of the total. (4) These results imply that if the behavior of a given cultivar across a series of environments is known, the behavior of all other members of the class across a similar range of environments would be predictable.

Key words: Cluster analysis – Canonical variate analysis – Genotype × environment interaction

Introduction

Repeated testing of breeding lines and populations over time and space and selection for a minimal degree of genotype × environment (GE) interaction, i.e., relative consistency of performance, is a common feature of all plant breeding programs. Three approaches, each with some modifications and variations, have been

devised to assess the magnitude of GE interaction and its implication in applied plant breeding.

Conventional analysis of variance produces an overall estimate of GE interaction, but fails to provide estimates of GE interaction associated with individuals or sub-groups of genotypes. In addition, the underlying assumptions of analysis of variance such as additivity of effects and homogeneity of variances are likely to be violated in larger experiments.

The regression approach, first suggested by Yates and Cochran (1938), employs regression of genotypic means upon an environmental index obtained by averaging the performance of all genotypes in each environment. Mandel (1961) partitioned the interaction term of an m × n 2-way able into slopes, associated with the homogeneity of m regression lines and residuals. The analysis proposed by Mandel allows for a systematic method of evaluating GE interactions. Finlay and Wilkinson (1963), and Eberhart and Russell (1966) suggested statistical parameters for the assessment of cultivar stability in plant breeding programs. The regression approach, based on an a priori assumption of linearity of genotypic response to environmental variations, has been widely accepted as a powerful tool for the study of cultivar adaptability in many crop species. However, the assumption of linearity is far from being a universal phenomenon (Freeman 1973); thus the regression method ignores the nature of deviations from regression that, if of appreciable magnitude, could have biological significance (Verma and Chahal 1978). Due to the above reason and for the purpose of classifying genotypes and/or environments, with a minimum of within group GE interaction, recourse has been had into the area of multivariate statistics.

Mandel (1972) and Gollob (1968), using techniques of principal component and factor analyses, partitioned the interaction sum of squares into principal components and factors, respectively. Their methods, though especially useful where experiments lack replication, produce mathematical artifacts that are not easily interpretable in a biological context.

Abou-El-Fittouh et al. (1969) used cluster analysis to classify cotton (*Gossypium hirsutum* L.) testing regions of the Cotton Belt with regard to GE interaction. Muntgomery et al. (1974), Lin and Thompson (1975), Byth et al. (1976), Shorter et al. (1977), and Ghaderi et al. (1980) used procedures combining the regression method with cluster analysis technique.

In the present study we used procedures of cluster and canonical variate analyses to investigate the performance of 39 diverse commercial bean cultivars under seven environments. Cluster analysis was carried out independent of commercial grouping of cultivars because the objective was rather exploratory to see if cultivars in the same commercial class would respond similarly to the changing environments. Geometrically, the genotypes could be visualized as a cloud of points in a seven dimensional hyperspace whose coordinates correspond to the performance of genotypes in the seven environments. Genotypes were classified according to their contiguity in this hyperspace. While cluster analysis classifies entries according to their phenetic similarities, canonical variate analysis begins with an already defined set of groups and proceeds to investigate inter-relationships among those groups. Again in a geometric space, the groups were represented by swarms of points and our objective was to investigate, employing canonical variate analysis, the position and orientation of the swarms relative to each other. Such a study could have important bearings in bean breeding programs, such as the one at Michigan State University, where cultivars of diverse commercial types are being developed.

Materials and Methods

Experimental Procedure

Ninety eight cultivars and breeding lines of different bean types were planted in eight locations in 1980. The entries were grown in two-row plots, each 5.4 m long. Distance between the rows was 50 cm, and plants were spaced 6 and 7.5 cm apart in the row for small and large seeded cultivars respectively. Four replications were used. Standard cultural practices were employed throughout the experiment. At harvest, plants from 4.5 m of the center of each plot were sampled. Yield data for 39 entries common to seven of the locations were selected for the present study (Tables 1 and 2). The locations were in Saginaw, Huron, Sanilac, Gratiot, Bay, Montcalm, and Tuscola counties of East-Central Lower Michigan.

Statistical Procedure

a) Cluster Analysis

In this analysis each genotype was presented as a vector whose elements corresponded to the performance of that genotype in each environment. Measurements of similarity were based on the simple correlation (r) of genotypes over environments. A procedure, based on a complete linkage method, was used to perform a hierarchical, agglomerative, and polythetic clustering analysis (Wishart 1978). The analysis starts by forming one cluster containing the two closest genotypes, with regard to their similarity of performance across the environments, and continues to group the remaining genotypes successively until they all form a single cluster. The level of truncation of the process was chosen as 9 clusters to correspond to the number of commercial classes. Cluster means were calculated for each

Table 1. Mean vectors (tons/ha) of six commercial classes of beans planted in seven locations

Location (County)	Commercial class					
	Navy	Black	D. R. Kidney	L. R. Kidney	Pinto	Small Red
Gratiot	1.77	1.72	1.96	2.31	1.97	1.78
Bay	1.92	2.02	2.01	1.65	1.88	1.81
Saginaw	1.07	1.05	1.25	1.33	1.48	1.25
Sanilac	1.93	2.10	1.40	1.25	2.04	2.31
Tuscola	2.01	2.59	2.39	2.25	2.25	2.08
Huron	1.73	1.63	1.97	2.18	0.96	1.07
Montcalm	1.59	1.89	2.36	2.52	2.15	1.89

location and an environmental index was obtained by averaging over the cluster means at each location. Such a procedure of calculating an environmental index would give equal weight to different clusters of cultivars each characterized by a distinct mode of response to environment.

b) Canonical Variate Analysis

Six commercial classes, each with a minimum of three cultivars, were subjected to the analysis (Table 1). Before proceeding with the analysis, the homogeneity of the variance-covariance matrices of the groups were tested by using the Box's procedure (Klecka 1975) and were found to be homogeneous—a pre-requisite to the analysis. Canonical variate analysis produces a number of functions that if applied to the original data, maximizes the between group differences. In the hyperspace analogy, a set of axes, usually perpendicular to one another, are inclined in such a manner that maximum separation among groups is obtained. The Genstat (Avley et al. 1977) package was used to carry out the analysis. The between (B) and within (W) matrices of sums of squares-sums of products were calculated and the canonical variates corresponding to the eigenvectors (t) and eigenvalues (z) were found from the following relationships:

$$(B - zW) t = 0$$
$$| B - zW | = 0.$$

The latter relationship is the determinantal form of the first equation. The notations used are those of Blackith and Reyment (1971). Once the data are transformed to the canonical axes, the distance between canonical means of the groups correspond to Mahalanobis' generalized distance (Avley et al. 1977).
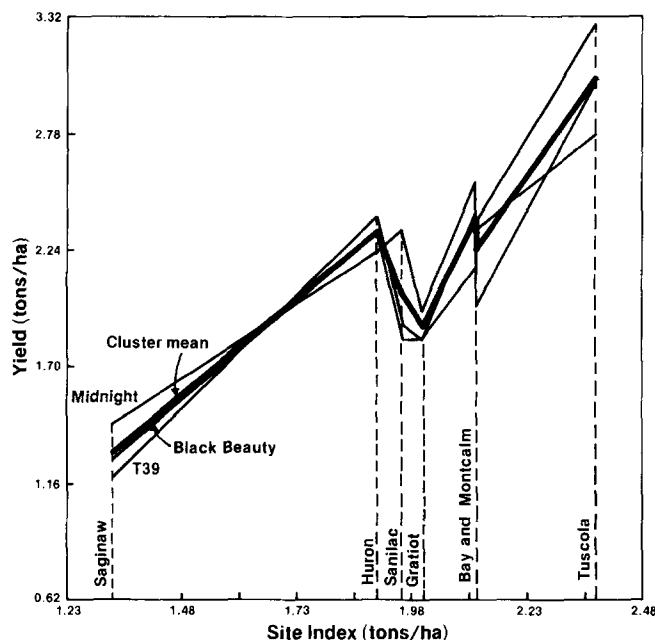
Results and Discussion

The results of the cluster analysis are summarized in the form of a dendogram in Table 2. Clusters I and II are composed of navy bean, with one exception, and black bean entries respectively. Most members of clusters I and II are standard Michigan cultivars. 'Seafarer', 'Tuscola', and 'Sanilac' are closely related and all three share some relationship to 'Fleetwood' and 'Kentwood'. 'Black Turtle Soup', abbreviated as B.T.S., is an old Venezuelan land race from which 'T39': has been
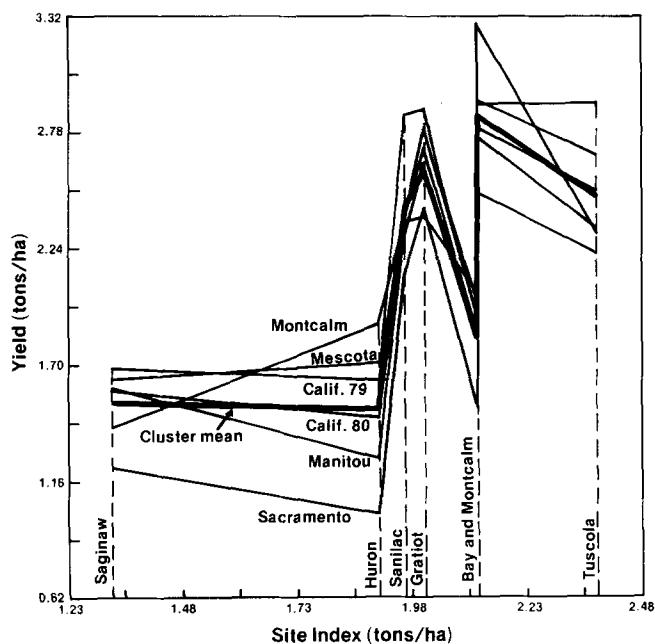
Table 2. Cluster dendogram, origin, commercial class, and mean yield of 39 cultivars of dry beans

Cluster Dendogram	Entry	Origin	Commercial Class	Mean Yield
I	Seafarer	Michigan	Navy	1.704
	Kentwood	Canada	Navy	1.831
	Aurora	New York	Navy	1.832
	Sanilac	Michigan	Navy	1.814
	Fleetwood	Canada	Navy	2.318
	Tuscola	Michigan	Navy	1.700
	B.T.S.	Venezuela	Black	1.890
	N.W.395	Washington	Navy	1.632
II	T39	Venezuela	Black	2.086
	Black Beauty	Idaho	Black	2.057
	Midnight	Colombia	Black	2.296
III	Bunsi	Colombia	Navy	2.357
	Swedish Brown	Sweden	Large Brown	2.336
IV	Montcalm	Michigan	D.R. Kidney	2.159
	Mescota	Michigan	L.R. Kidney	2.361
	Manitou	Michigan	L.R. Kidney	2.121
	Sacramento	California	L.R. Kidney	1.845
	California 80	California	L.R. Kidney	2.214
	California 79	California	L.R. Kidney	2.314
V	Charlevoix	Michigan	D.R. Kidney	2.215
	Red Kloud	New York	L.R. Kidney	2.111
	Royal Red	Washington	D.R. Kidney	2.119
	California 69	California	D.R. Kidney	2.051
VI	Mich. Imp. Cran.	Michigan	Cranberry	1.879
	Swan Valley	Michigan	Navy	2.165
	U.I.50	Idaho	Cranberry	1.770
	Steuben	New Engl.	Yellow Eye	1.564
VII	Maine	New Engl.	Yellow Eye	1.223
VIII	U.I.114	Idaho	Pinto	2.070
	N.W.410	Washington	Pinto	2.026
	N.W.590	Washington	Pinto	2.163
	U.I.111	Idaho	Pinto	1.985
	N.W.59	Washington	Small Red	1.808
	N.W.63	Washington	Small Red	1.858
IX	Wyo.166	Wyoming	Pinto	1.986
	Columbia	Washington	Pinto	1.916
	Olathe	Colorado	Pinto	2.250
	Rufus	Washington	Small Red	2.187
	Ouray	Colorado	Pinto	1.912

Fig. 1. Mean response of cluster II and its members to site index

Fig. 2. Mean response of cluster IV and its members to site index

selected. 'Midnight' is a recent black cultivar selected from experimental lines originating in the same general area – Central America and Northern South America. Cluster III is comprised of 'Bunsi' and 'Swedish Brown'. While 'Bunsi', a high yielding navy bean cultivar from Colombia, is a close neighbor of navy and black clusters, its differences in environmental response has placed it with 'Swedish Brown' in a separate cluster. Light and dark red kidney beans constitute clusters IV and V. Proximity of the two clusters is an indication that they share a similar but not identical response pattern. 'Montcalm', 'Mecosta', 'Manitou', and 'Charlevoix', all sharing in the gene pool of the eastern US kidney beans, were developed for specific production areas of Michigan. The western kidney cultivars, though genetically more distant from the eastern kidney beans (Adams 1977) performed similarly to the latter. Cranberry bean cultivars, 'Michigan Improved Cranberry' and 'U.I. 50', fell into cluster VI. In addition, this cluster

contains two other members, 'Swan Valley' and 'Steuben' which are navy and yellow eye beans respectively. 'Swan Valley' is a new release from Michigan with a pedigree different from the existing navy beans. Cluster VII, a uni-member cluster, contains only 'Maine', a yellow eye cultivar which showed a high degree of similarity to 'Steuben'. The composition of clusters VIII

and IX are similar, each containing pinto beans, in a larger proportion, and small red entries. All pinto and small red entries were developed in the western states where they are grown under irrigated semi-arid conditions. The pintos and small reds are related by pedigree and by the principal components distance analysis of Adams (1977).

Cluster analysis classified the cultivars into clusters almost identical to that of their commercial designations. Similarity of response pattern among members of the same cluster is evident from figures in which the performances of clusters II and V (Figs. 1, 2, respectively) have been plotted against a site index obtained by averaging the mean of all clusters in each location. The figures also indicate that, while it is possible for the two clusters to possess almost identical means, 2.14 and 2.16 ton/ha respectively, the members of the two clusters may perform in opposing directions in the same environments. When the total G×E interaction was partitioned into between and within clusters, the between cluster×environment interaction constituted a major portion of the total interaction (Table 3). In addition, members of the same cluster should possess the same regression slopes (Ghaderi et al. 1980; Muntgomery et al. 1974).

Position of the entries in the canonical plane obtained by plotting the first against the second canonical variate, together accounting for 88.81% of the total variation, revealed the same type of relationship as obtained by cluster analysis. This is indicated by successful classification of all genotypes, with one exception, into their own commercial class by using individual performances on the canonical variables (Table 4). Each commercial class occupied a more or less distinct region of the canonical plane, however, some overlapping of small red and pinto beans was evident (Fig. 3). From Fig. 3, and the matrix of
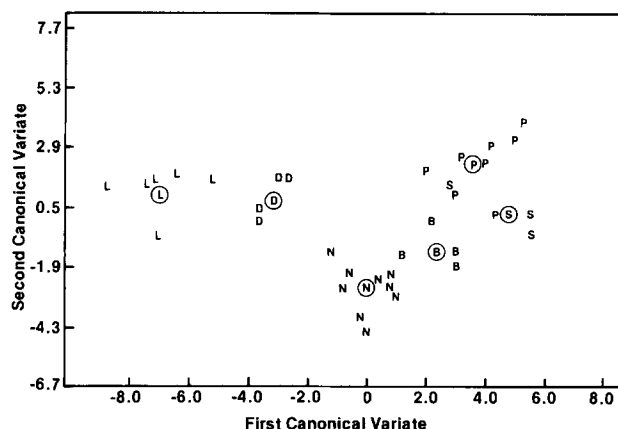

Fig. 3. Position of the cultivars in the canonical plane obtained by plotting the first against the second canonical variates

Table 3. Analysis of variance for yield (tons/ha) for 39 cultivars of dry beans planted in seven locations and classified into nine clusters

Source of variation	D. F.	S. S.	M. S.
Genotypes (G)	38	66.09	1.74**
Locations (L)	6	107.95	17.99**
G×L	228	143.33	0.63**
Clusters (C)×L	48	115.03	2.40**
G/C×L	180	28.30	0.16**
G/C1×L	42	6.13	0.15**
G/C2×L	12	1.13	0.09
G/C3×L	6	0.40	0.07
G/C4×L	30	3.41	0.11
G/C5×L	18	3.02	0.17**
G/C6×L	18	2.80	0.15**
G/C8×L	30	7.44	0.25**
G/C9×L	24	3.97	0.16**
G×Rep/L	798	53.08	0.07

** F-value significant at the 1% level of probability

Table 4. Summary of the classification of cultivars using their performances on the canonical variables

	Navy	Black	D. R. Kidney	L. R. Kidney	Pinto	Small Red
Navy	9	0	0	0	0	0
Black	0	4	0	0	0	0
D. R. Kidney	0	0	4	0	0	0
L. R. Kidney	0	0	0	6	0	0
Pinto	0	0	0	0	7	1
Small Red	0	0	0	0	0	3

Table 5. Mahalanobis' generalized distances among six commercial classes of beans based on their phenotypic performance (yield) over seven locations

Commercial Class	Navy	Black	D. R. Kidney	L. R. Kidney	Pinto	Small Red
Navy	0.00					
Black	5.34	0.00				
D. R. Kidney	5.67	6.58	0.00			
L. R. Kidney	8.20	10.36	4.66	0.00		
Pinto	6.45	5.63	7.61	10.95	0.00	
Small Red	5.73	4.95	8.44	11.73	2.52	0.00

Mahalanobis' generalized distances (Table 5) three groups, each containing two classes could be recognized: navy and black; light and dark red kidney; and pinto and small red. The distances between classes of the same group were usually smaller than the distances between classes of different groups. The intragroup distances were: navy vs. black, 5.34; light red kidney vs.

dark red kidney, 4.66; and pinto vs. small red, 2.52. On the other hand, light red kidney had distances of 10.95 and 8.20 with pinto and navy classes respectively, etc.

The size, shape, and the color (solid or patterned) of the seed are the characteristics that distinguishes one class of bean from another. The results of the present analyses may lead one to suggest that differences in seed characteristics could account for the differential response pattern among classes. It is generally acknowledged among bean workers that colored-seeded types display greater robustness than noncolored types, particularly in seedling emergence and stand establishment under adverse soil or moisture conditions. Thus, if location yield differences could be attributed to unfavorabe soil conditions, this interpretation might conceivably explain the behavior of the white-seeded class as compared to the colored classes. It would not, however, explain the discrimination among the colored classes themselves, that is, blacks versus light reds versus dark reds, versus pintos, etc, unless the pigments or associated pre-cursors or degraded products of pigments are specifically active in conditioning the response of varieties in each cluster to the soil conditions at each location.

A narrow genetic base could account for a major portion of within class similarities (Adams 1977). Hybridization among cultivars of different classes produces great amounts of variability with respect to seed characteristics, most of which are of little value to a highly specialized market. Contrariwise, plant breeders have inter-crossed cultivars of the same class extensively, out of which reduced levels of genetic variability are generated. Cultivars of the same class, despite their physical isolations, share more or less the same restricted gene pool.

The nature of stress, a pre-requisite to G × E interaction, is not the same for all commercial classes. Taking response to disease for example, while kidney beans may suffer from bacterial halo blight, pinto or navy beans are not damaged by this disease. On the other hand, rust could inflict serious damages to pinto and navy beans, whereas kidney beans are fairly tolerant of rust (in Michigan). Therefore, patterns of differential disease resistance among commercial classes, with the various locations being characterized by different specific diseases could in principle lead to the yield clusters being highly identified with commercial classes. Although this interpretation is plausible, it is thought not applicable in the present case because diseases were not observed in sufficient degree to serve as a discriminating force.

Agro-physiologic response factors, unknown at this time but closely associated with those seeds and allometrically-correlated plant characteristics which determine commercial classes, could account for differential yield response patterns of the clusters or classes to a range of physical environments. Two requirements have to be satisfied to make this interpretation acceptable: (1) Members of a given cluster should be genetically related, not necessarily through common ancestry, but by sharing genes in common. There is evidence in support of this assertion. (2) A particular cluster must respond in its own unique way to each location. This appears fulfilled in the present data.

The seven environments, with high accuracy, sorted out the 39 cultivars into sub-sets (clusters) of similarly responding cultivars The outcome is analogous to host-parasite relations, where the differential hosts (environments) selectively sort out the various isolates of the pathogen (cultivars) into similarly responding races (varietal clusters).

It is not known at this time whether the environmental forces involved are "one-time" occurrences or whether they are recurrent at each location, nor is it known whether soil or crop management changes would or could lead to greater similarity among locations.

The results obviously bear upon the question of breeding for broad "general" adaptability or narrow "specific" adaptability. If the current trend of breeding continues, development of specific classes of beans for specific regions of production would utilize advantageously most of the interaction. On the other hand, with a broader genetic base, that could be accomplished through introduction of exotic germplasm as a component of a long term breeding strategy, development of cultivars adapted to a wider range of environments may be more practical.

Yield is a complex trait, therefore, within group similarities for response pattern could reflect similarity of gene complexes. Such a genetic homogeneity poses certain production problems. The implications of genetic homogeneity with regard to vulnerability to pathogenic organisms have been documented in several crop plants. Differential response of classes to pathogenic organisms is an indication that stratification of gene complexes has occurred. Other types of stress could also result in significant damages in genetically homogeneous populations, once the stress levels reach serious proportions. This is clearly indicated in Figure 1 where all members of cluster II suffered from some kind of stress in Saginaw County, that resulted in the lowest yield.

The analyses used provided effective method to systematically investigate the response patterns of a set of cultivars. However, one should not overlook the fallacies of cluster analysis. Different measures of similarity and distance, for which no objective selection criteria is available, could lead to different types of classification. Furthermore, there is no objective method

of selecting the truncation level or the number of clusters.

Clearly, these findings raise more questions than answers, questions which must be addressed in future specially designed trials.

Acknowledgement

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