

## Pattern Analysis of Genotype Adaptation and Genotype x Environment Interactions in the Uniform Peanut Performance Tests<sup>1</sup>

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### ABSTRACT

Genotype x environment (g x e) interactions can confound comparisons among peanut (*Arachis hypogaea* L.) genotypes in multi-environment genotype trials. Herein g x e interactions in two data sets constructed from the Uniform Peanut Performance Tests (UPPT) over the period 1973-1978 were examined. Numerical classification and ordination techniques were used to examine genotype adaptation and environmental groupings.

Because of the harvest strategy adopted in specific trials, maturity differences among genotypes may have influenced genotype yields and rankings in these trials. For example in trials harvested 151-176 days after planting, Early Bunch yielded 951 kg ha<sup>-1</sup> less than the average of Florunner, Tifrun and UF 714021. Conversely in trials harvested 129-141 days after planting, Early Bunch was 700 kg ha<sup>-1</sup> higher yielding than the average of Florunner, Tifrun and UF 714021. Our results suggest that entries in UPPT trials be harvested in order of their maturities where such maturity differences are known. In any year, performance of new lines should be compared jointly with that of a number of standard genotypes as performance of any one standard may not be indicative of its long term average.

There was a degree of regional adaptation of certain genotypes in that, relative to other genotypes, Florigiant performed poorly and Florunner well in southeastern United States environments. However an environmental classification based on g x e interaction effects indicated that, over all genotypes, there were no temporal or closely related regional groups of environments with similar g x e interactions. No evidence was found that genotypes from different breeding programs had substantially different environmental adaptation responses.

Key Words: *Arachis hypogaea* L., groundnut, cluster analysis, cultivar evaluation.

Promising peanut (*Arachis hypogaea* L.) breeding lines need to be assessed over a wide range of environments in the United States because of significant genotype x environment (g x e) interactions (26, 28). Such a set of trials is the Uniform Peanut Performance Test (UPPT) where new lines and existing cultivars are compared annually in the seven major peanut production states. Entries change over time as new material emanates from the various breeding programs (11).

Annually published results allow comparison among entries within each environment but do not readily facilitate meaningful comparisons among entries across locations. Indeed, Hammons and Branch (11) cautioned against the latter because of the diversity of conditions

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which exist among locations. They were implicitly stating that efficient comparison and interpretation of genotype response is made difficult by the existence of  $g \times e$  interaction. Analysis of patterns of performance in multi-environment trials can provide valuable information regarding the form of differences in genotype performance and the influence of particular environments on performance.

Analysis of variance and related procedures give only a general characterization of responses. Linear regression of response of genotypes across environments is only informative where  $g \times e$  interactions have a high linear association with an environmental index. Where this is not the case, deviations from regression include much of the dynamic nature of the response. Non-linearity of  $g \times e$  interactions is thought to be a common situation in field crops (22). This limitation has led to the application of multivariate techniques to analyse  $g \times e$  interactions and genotype adaptation.

Pattern analysis (27) includes various multivariate data analysis techniques which aim to extract underlying patterns of variation in the data, thus simplifying description of the observed responses. Numerical classification (1,2,3,4,5,6,18,23,24,25) and ordination (8, 18) are two major fields of pattern analysis which substantially yet efficiently reduce the complexity of large data sets with retention of the dynamic nature of genotypic responses. In the context of multi-environment testing of genotypes, a primary objective of genotypic classification is to reorganize the data in a way which permits generation of useful hypotheses about genotypic adaptation. In addition environments may be classified retrospectively to facilitate choice of future test environments where genotypic adaptation differences may be detected (1,2,3).

The purpose of this study was to examine genotypic adaptation,  $g \times e$  interaction, and environment grouping in the UPPT over the years 1973-78.

## Materials and Methods

Data from UPPT trials conducted over the period 1973-1978 (10,11,13,14,15,16) were analysed. Two data sets were constructed to represent a wide sampling of UPPT environments with a small number of common cultivars and a restricted sampling of UPPT environments in one year with a larger number of cultivars. Set one consisted of six virginia type cultivars and breeding lines (Floriant, VA 72R, Early Bunch, Florunner, UF 714021, and Tifrun) evaluated in 47 environments from 1973 to 1977 (Table 1). Set two consisted of 11 virginia type cultivars and breeding lines evaluated in 14 environments in 1978 (Table 2) and is typical of UPPT data collected annually. The origin and description of genotypes, aspects of the test environments, and experimental details have been described (10,11,13,14,15,16). This study involved analysis of pod yield ( $\text{kg ha}^{-1}$ ) only, using genotype means for each trial as original data.

Neither an error variance nor a coefficient of variation was presented in the UPPT reports so significance testing for  $g \times e$  interactions in combined analyses of variance across genotypes and environments was not possible. Linearity of  $g \times e$  interaction effects plotted against an environmental index (7) was only 12.7% and 10.6% in data sets one and two respectively so that joint linear regression analysis (7,20) was uninformative in describing productivity responses of genotypes over environments.

Pattern analysis procedures were used to examine genotypic responses and group environments. An agglomerative hierarchical clustering technique was employed with unstandardized squared Euclidean distance (SED) between individuals as the measure of dissimilarity and incremental sum of squares (ISS) as the fusion strategy (17).

Table 1. Uniform Peanut Performance Test environments from 1973 to 1977 in data set one, groups from their classification based on genotype  $\times$  environment interaction effects, and genotype mean yields.

Group	Code	Year	Location	Pod yield	Group	Code	Year	Location	Pod yield
				$\text{kg ha}^{-1}$					$\text{kg ha}^{-1}$
I	12	1976	Lewiston, NC (E)	4098	V	15	1976	Plains, GA (I)	5028
	13	1976	Lewiston, NC (L)	4062		25	1975	Plains, GA (I)	5029
	40	1974	Jay, FL	4330					
	42	1974	Stephenville, TX	3619	VI	6	1977	Gainesville, FL	5202
II	7	1977	Marianna, FL	4217		17	1976	Tifton, GA (NI)	5302
	32	1975	Jay, FL	3330		28	1975	Headland, AL (I)	6025
	34	1975	Stephenville, TX	4648		29	1975	Headland, AL (NI)	6215
	44	1975	Tifton, GA	4112		31	1975	Marianna, FL	5262
	47	1973	Marianna, FL	3966		37	1974	Tifton, GA	5993
III	8	1977	Jay, FL	3774		46	1973	Gainesville, FL	4962
	21	1976	Stephenville, TX	3383	VII	2	1977	Lewiston, NC	4845
	22	1975	Suffolk, VA	5721		4	1977	Tifton, GA (NI)	4889
	43	1974	Pearson, TX	4767		9	1977	College Station, TX	4436
	45	1973	Headland, AL	3022		24	1975	Tifton, GA (I)	5113
IV	5	1977	Headland, AL	3914		30	1975	Gainesville, FL	5789
	18	1976	Marianna, FL	5309	VIII	1	1977	Suffolk, VA	3675
	19	1976	Jay, FL	4687		3	1977	Tifton, GA (I)	5980
	23	1975	Lewiston, NC	3242		10	1977	Stephenville, TX	4500
	35	1975	College Station, TX	4321		11	1976	Suffolk, VA	4687
	35	1974	Suffolk, VA	4298		14	1976	Tifton, GA	5966
	38	1974	Headland, AL	4411		16	1976	Plains, GA (NI)	4333
	39	1974	Marianna, FL	5496		20	1976	College Station, TX	3766
	41	1974	College Station, TX	4712		26	1975	Plains, GA (NI)	4508
						27	1975	Tifton, GA (NI)	4827
						36	1974	Lewiston, NC	3979
				Standard error (for environment means)					198
				Genotype				Genotype	
				Floriant				Florunner	4711
				VA 72R	4538			Tifrun	4771
				Early Bunch	4402			UF 714021	4737
				Early Bunch	4638				
				Standard error (for genotype means)					71

E = Early harvest, L = Late harvest, I = Irrigated, NI = Non-irrigated.

Table 2. Genotypes and environments from Uniform Peanut Performance Tests in 1978 used in data set two.

Genotype	Pod yield	Code	Environment	Pod yield
	$\text{kg ha}^{-1}$			$\text{kg ha}^{-1}$
Tifrun	4731	1	Suffolk, VA	4210
Florunner	4750	2	Lewiston, NC	4271
UF 75102	4806	3	Tifton, GA	6177
UF 77318	4417		(Irrigated)	
Early Bunch	4675	4	Plains, GA	4184
NC 7 (NC 17209)	4520		(Irrigated)	
Floriant	4478	5	Plains, GA	3995
VA 72R	4209		(Non-irrigated)	
NC 17922	4329	6	Tifton, GA	6108
VA 760513	4390		(Non-irrigated)	
NC 17921	4357	7	Tifton, GA	5097
			(No-Insecticide)	
		8	Headland, AL	5200
		9	Gainesville, FL	5442
		10	Marianna, FL	4363
		11	Jay, FL	4104
		12	College Station, TX	3427
		13	Stephenville, TX	4040
		14	Ft Cobb, OK	2589
Standard error	111			125

The ISS strategy requires that the fusion made at each level in the classificatory process is the one which results in least increase in the within-group sum of squares. For all classifications, the computer program SAHN in the Commonwealth Scientific and Industrial Research Organization (CSIRO) TAXON library was used (21).

To summarize genotypic responses, a genotype was considered as an individual specified by attributes, each of which was the mean yield of the genotype in each environment. In both data sets, genotypes were classified into groups with the SED dissimilarity measure calculated from the array of  $g \times e$  mean yields. Genotypic yield was also plotted against an environmental index based on environment mean yield (7). To simplify these performance plots, the number of x-axis points was reduced by grouping environments in a manner similar to that used for genotypes. That is, an environment was considered as an individual specified by attributes, each of which was the mean yield of a genotype in that environment. Experience with a range of data sets indicates that environment mean yield is the major factor influencing this type of environment grouping, i.e. environments with similar productivity levels tend to cluster together.

The importance of specific environments or groups of environments in differentiating genotype responses or in formation of the overall genotype classification was assessed by contributions analysis (23, 24). Here, the squared difference between the mean yields of two genotype groups in an environment was taken as a measure of the contribution of that environment to the separation of the genotype groups.

For extraction of environmental patterns in set one we carried out a classification of the 47 environments based on  $g \times e$  interaction effects to investigate whether there existed regional or temporal environment groups within which relative genotypic performances were similar. Note that with environment mean yields removed prior to classification, we are attempting here to group together environments that elicit a similar pattern of responses in the six genotypes. We are not attempting to group environments with similar productivity levels. An environment was considered as an individual specified by attributes, each of which was the  $g \times e$  interaction effect attributable to a genotype in that environment. The SED dissimilarity measure between environments was calculated from the array of  $g \times e$  interaction effects. The importance of specific genotypes in forming this environment classification was assessed by contributions analysis (23, 24). Here the squared difference between the  $g \times e$  interaction effects of two environment groups for a genotype was taken as a measure of the contribution of that genotype to the separation of the environment groups.

Distribution of the 47 environments in the six dimensional space determined by the  $g \times e$  interaction effects of the six genotypes was examined using an ordination procedure (9). This was a principal coordinate analysis using the CSIRO program GOWER (21). For dissimilarity measured by SED, this is identical to a standard principal component analysis.

## Results and Discussion

### Data Set One

**Mean Performance.** Mean pod yield over all genotypes and environments was  $4633 \text{ kg ha}^{-1}$ . Highly significant ( $P < 0.01$ ) differences existed among environments and genotypes when these main effects were tested against the  $g \times e$  interaction source of variation. Mean pod yields for the highest yielding environments were approximately twice those for the lowest yielding environments (range  $3022\text{--}6213 \text{ kg ha}^{-1}$ ). The range in genotype mean yields averaged over 47 environments ( $4402\text{--}4771 \text{ kg ha}^{-1}$ ) was much smaller than that for environment means (Table 1).

**Genotype Classification and Response.** The dendrogram corresponding to the classification of the six genotypes is shown in Fig. 1. Productivity responses of the genotypes are shown in Fig. 2. The environment classification based on mean yield, conducted to reduce the number of x-axis points in the response plots, was truncated at the eight group level. Here 85% of the total sum of squares in the original array of  $g \times e$  mean yields was retained in the reduced array of six genotypes and eight environment groups.

Florigiant and VA 72R did not exploit the productivity potential of high yield environments as well as the other genotypes (Fig. 2). At these higher productivity levels, however, Florigiant tended to be higher yielding than VA 72R. In the lower yielding environment group 83 where trials were harvested 151-176 days after planting, Florigiant and VA 72R had substantially higher yields than the other four genotypes. This suggests they were late maturing and hence less affected by delayed harvesting than genotypes under node B (Fig. 1).

The separation of Early Bunch from Florunner, Tifrun, and UF 714021 (node B) was due largely to differ-

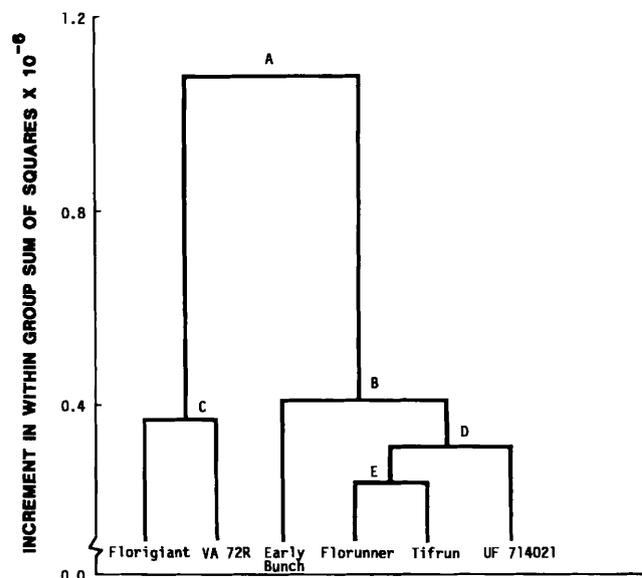


Fig. 1. Pod yield dendrogram for classification of six peanut genotypes in data set one.

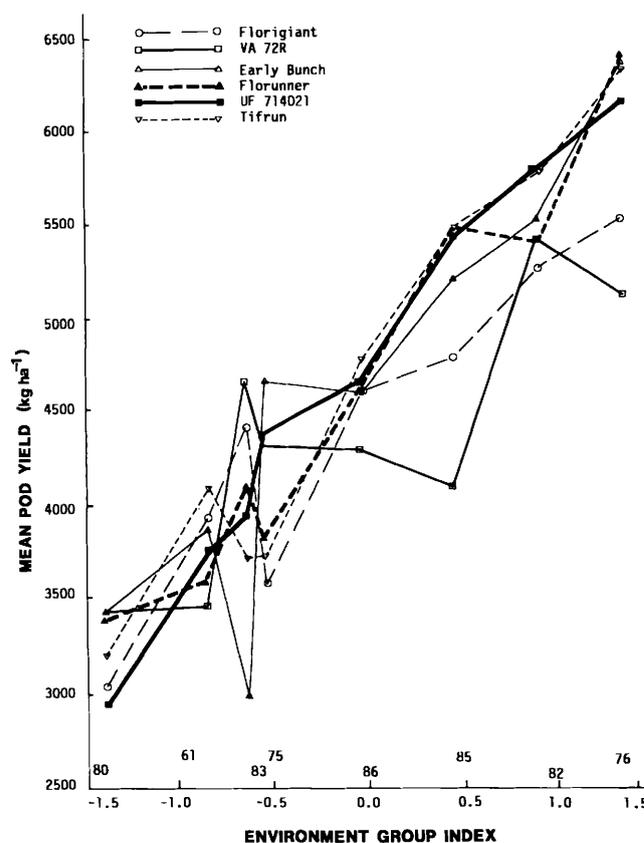


Fig. 2. Pod yield responses of six genotypes across environments in data set one. Eight environment groups, determined from the array of  $g \times e$  mean yields, are numbered 61-86 along the x-axis.

ences in relative performance in environment groups 83 and 75 (Fig. 2). Early Bunch is a shorter season genotype (19) so its low yield in environment group 83 ( $951 \text{ kg ha}^{-1}$  less than the average of the other three) may have resulted from the late harvests in these trials (151-176 days after planting). Conversely in environment group 75 where harvesting occurred earlier (129-

141 days after planting), Early Bunch was 700 kg ha<sup>-1</sup> higher yielding than the average of the other three genotypes. In the low yielding environment groups 80 and 61, Early Bunch was among the highest yielding genotypes in the set. This might have resulted from some form of stress avoidance or tolerance associated with its earlier maturity and/or inherent heterogeneity (19).

Florunner, Tifrun, and UF 714021 were the highest yielding genotypes over all environments, and all were high yielding in medium to high productivity environments (Table 1 and Fig. 2). In earlier harvested trials (environment group 75), UF 714021 was 605 kg ha<sup>-1</sup> higher yielding than the average of Florunner and Tifrun. This suggests it was somewhat earlier maturing than Florunner and Tifrun.

**Environment Classification.** The dendrogram corresponding to the classification of the 47 environments on the basis of  $g \times e$  interaction effects is shown in Fig. 3 and composition of environment groups is given in Table 1. The classification was truncated at the eight group level where 68% of  $g \times e$  interaction sum of

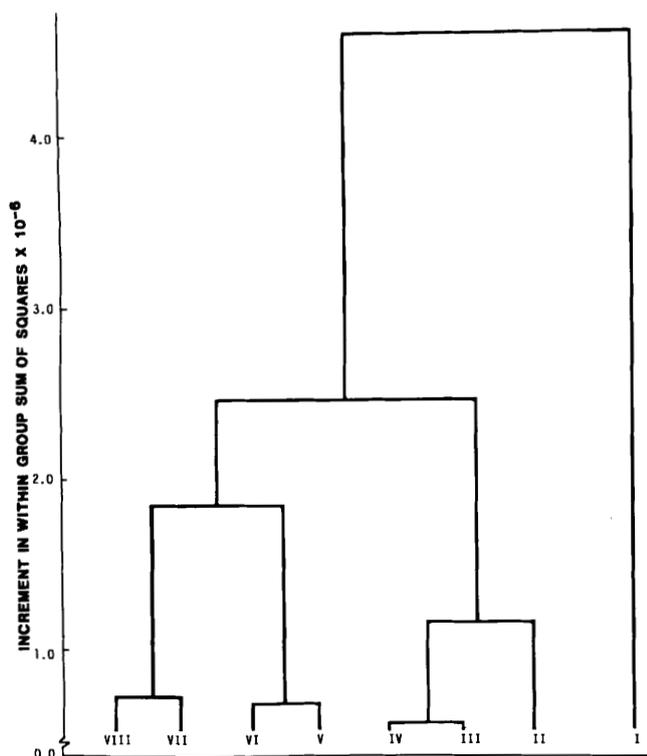


Fig. 3. Dendrogram for classification of 47 environments in data set one based on genotype  $\times$  environment interaction effects. Group composition given in Table 1.

squares was retained among groups. Note that these eight environment groups were determined from the array of  $g \times e$  interaction effects and so are unrelated to the eight environment groups used in plotting the genotype responses of Fig. 2. The first three principal axes of the environment ordination accounted for 44, 23, and 14% of information in the original six dimensions. Co-ordinates for the 47 environments on the first two axes are plotted in Fig. 4. Equal scaling on x and

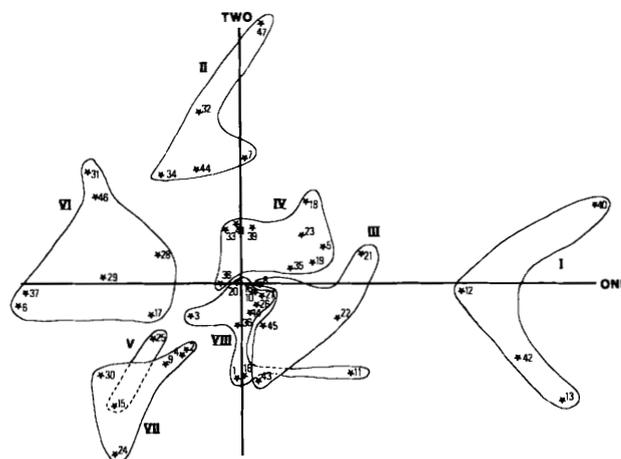


Fig. 4. Spatial arrangement of 47 environments for pod yield in two dimensions obtained by ordination procedures. Group composition given in Table 1.

y axes was used so the distribution of environments on an axis reflects variation accounted for by that axis. Boundaries were drawn around groups identified by classification and some groups overlie others in the dimension of the third axis. Clearly, environment groups distantly related in classification occupied different positions in space; that is, classification has identified groups of environments with dissimilar patterns of  $g \times e$  interactions.

Most groups contained environments from several years so there was little, if any, temporal grouping of environments with similar  $g \times e$  interactions. Groups I, II, III, and IV in particular contained environments from northern, south eastern, and western peanut production areas so there was no clear regional grouping of environments with similar  $g \times e$  interactions over all genotypes. This agrees with results of Tai and Hammons (26) and Wynne and Islieb (28) who found genotype  $\times$  year  $\times$  location interactions generally were more important than genotype  $\times$  year or genotype  $\times$  location interactions.

Environment groups V and VI separated from VII and VIII largely because of performances of Florigiant and Florunner. Groups V and VI consisted of southeastern environments (Florida, Georgia, and Alabama) whereas groups VII and VIII contained northeastern, Georgia, and Texas environments, but none from Alabama and only one from Florida. In the southeastern groups (V and VI), Florigiant had large negative and Florunner large positive  $g \times e$  interaction effects. In groups VII and VIII Florigiant had large positive and Florunner zero  $g \times e$  interaction effects. That is, relative to other genotypes, Florigiant performed poorly and Florunner well in southeastern environments and the reverse tended to occur in northeastern and western environments. Thus although there was no overall regional environment grouping for  $g \times e$  interactions, our results suggest there is a degree of regional adaptation of certain genotypes. Group II separated from groups III and IV mainly because of large positive  $g \times e$  interaction effects for Early Bunch and large negative  $g \times e$  interaction effects for Florigiant in group II. This group contained mainly southeastern environments where again Florigiant seemed to perform poorly relative to

other genotypes.

Group I environments were the last to fuse with others during classification (Fig. 3) and were clearly separated from other groups by ordination (Fig. 4). Genotype contributions to this classification indicated Early Bunch and VA 72R were most important in differentiating group I environments from the remainder. Early Bunch had large negative and VA 72R large positive  $g \times e$  interaction effects in group I. Harvesting in group I generally occurred late (151-176 days after planting) and this may have disadvantaged the earlier maturing Early Bunch and favored VA 72R. These results emphasize the entry specific nature of assessments of  $g \times e$  interactions, in that results obtained depend on the particular populations of genotypes and environments used or sampled.

#### Data Set Two

**Mean Performance.** Highly significant ( $P < 0.01$ ) differences existed among environments and genotypes when these main effects were tested against the  $g \times e$  interaction source of variation. Mean pod yield was 4515 kg ha<sup>-1</sup> with a range over environments of 2589-6177 kg ha<sup>-1</sup> and over genotypes of 4209-4806 kg ha<sup>-1</sup> (Table 2).

**Genotype Classification and Response.** The dendrogram corresponding to the classification of the 11 genotypes is shown in Fig. 5. Productivity responses of the genotypes are shown in Fig. 6. Here the environment classification based on mean yield, conducted to simplify the response plots, was truncated at the seven group level where 95% of the total sum of squares in the original  $g \times e$  array was retained in the reduced 11

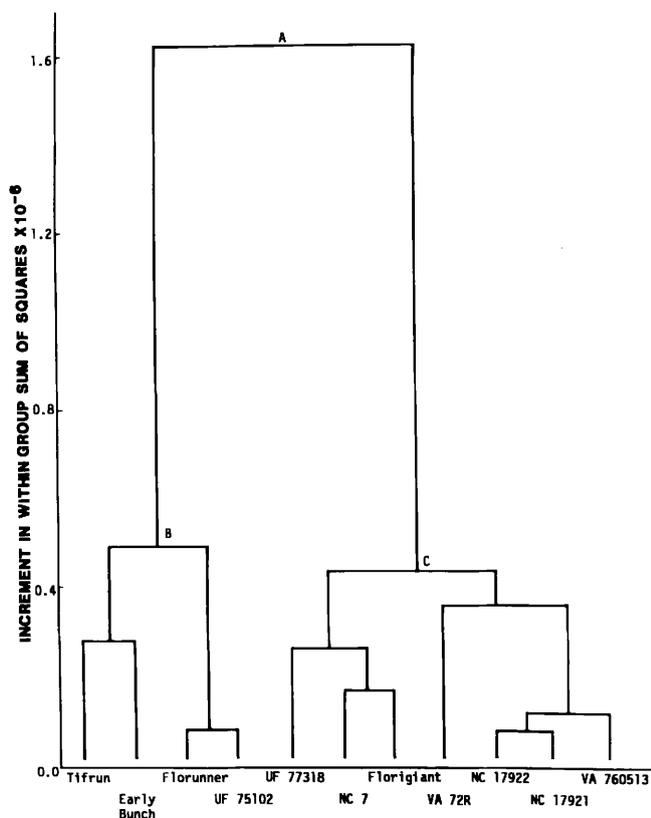


Fig. 5. Pod yield dendrogram for classification of 11 peanut genotypes in data set two.

genotype  $\times$  7 environment group array. Composition of non-singular environment groups on the x-axis was as follows: group 19 - environments 1,2,4,5,10, and 11; group 20 - environments 3 and 6; group 21 - environments 7 and 9 (Table 2).

Tifrun, Early Bunch, Florunner, and UF 75102 (node B) had higher mean yields than genotypes under node C. This resulted mainly from their considerably higher yield (average 5018 kg ha<sup>-1</sup>) at Stephenville compared to that of other genotypes (average 3481 kg ha<sup>-1</sup>). The Stephenville environment was characterized by hot dry conditions during flowering which appeared to delay fruit set for most genotypes (11). Possibly these node B genotypes were able to withstand, or their peak flowering periods did not coincide with, the hot dry conditions at flowering. Alternatively they may have had higher pod growth rates and so achieved higher yields than other genotypes in spite of delayed flowering.

Although the four genotypes under node B had similar mean yields, Florunner and UF 75102 had higher yields (3411 kg ha<sup>-1</sup> average) in the low productivity environment 14 (Ft Cobb) than Tifrun and Early Bunch (2274 kg ha<sup>-1</sup> average). The Ft Cobb trial was harvested 159 days after planting and this may have disadvantaged the earlier maturing Early Bunch. Of genotypes under node C NC 7, Florigiant, and UF 77318 tended to be higher yielding in the lowest (Ft Cobb) and highest (Tifton) productivity environments than VA 72R, NC 17922, NC 17921, and VA 760513. Reasons for these productivity response differences are not known.

## General Discussion

In some UPPT trials all entries were harvested simultaneously whereas in others entries were harvested at different times to accommodate their differential maturity. This non-uniformity of harvest date relative to cultivar maturity, both within and among locations and years, is a standard production procedure in valid peanut cultivar evaluation. The approach is sanctioned by all U. S. peanut breeders. Productivity response plots in our study indicated that maturity differences among genotypes influenced observed genotypic yields and rankings in specific trials. Pattern analysis procedures used in our study facilitated identification of those cases where  $g \times e$  interactions may have been confounded by genotypic maturity differences resulting from the harvest strategy adopted. Our results suggest that the differential harvesting procedure should be adopted in the UPPT where maturity differences among entries are known. If relative maturities of entries are unknown, then the strategy of multiple harvests for all entries should be considered.

As there was little temporal or regional grouping of environments with similar  $g \times e$  interactions, it would be unnecessary to deliberately stratify UPPT test environments by years or regions if assessment of relative genotypic performance was the only objective. The only requirement would be to choose environments which covered the range of year  $\times$  location variation. The number of such environments would be determined by the desired type one error probability for assessing a new genotype's superiority. Obviously estimation of

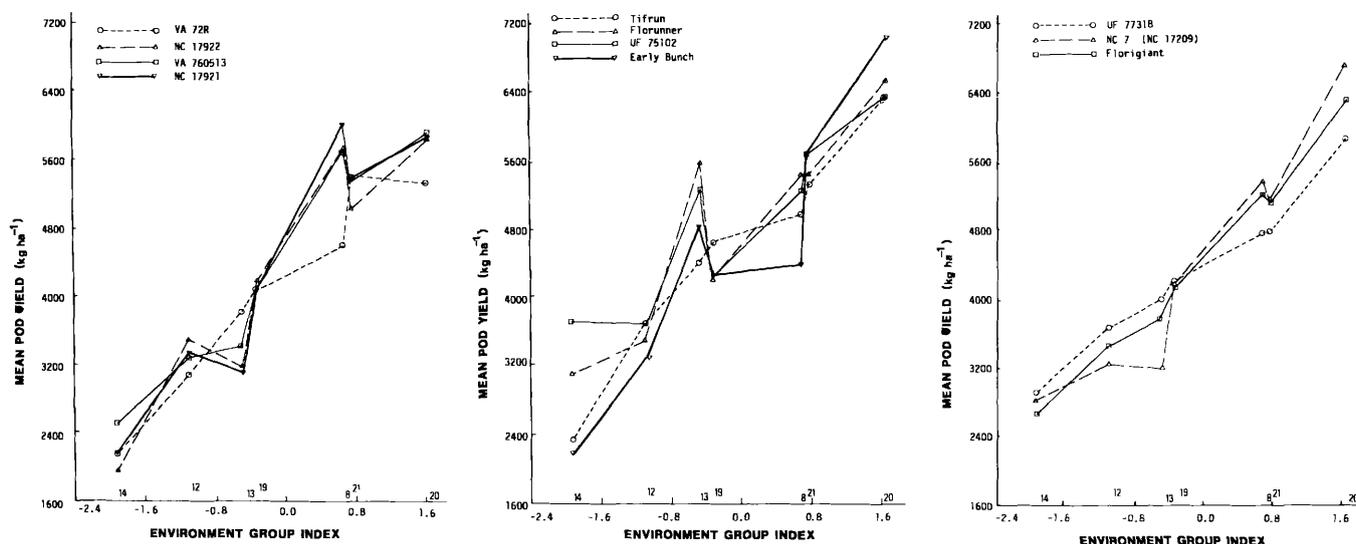


Fig. 6. Pod yield responses of 11 genotypes across environments in data set two. Seven environment groups, determined from the array of  $g \times e$  mean yields, are numbered 8-21 along the x-axis.

achievable yield potential for each genotype in an environment is also an objective of such trials. Although the highest productivity environments in data set one (groups 76, 82, and 85 of Fig. 2) occurred in Georgia, Florida, and Alabama, lower productivity environments occurred in all seven states. The current strategy of locating the majority of UPPT trials in the southeast each year thus seems reasonable.

Plant breeders have greater confidence in assessing a genotype's yield potential and adaptation when a wide range of environments have been sampled, especially in the presence of substantial  $g \times e$  interaction. In our study, set one represented a wide environment sampling and set two a more restricted sampling of environments in one year. Some genotypes exhibited similar, and others dissimilar adaptation responses across the two sets. For example in set two, yields of Florigiant and Florunner increased steadily and at approximately the same rate as the environment mean yield increased. However in the more extensive set one, yield of Florigiant was lower and increased at a slower rate than that of Florunner as environment mean yield increased. These results suggest productivity responses of standard genotypes should be determined over a wide sampling of environments. In UPPT reports, new breeding lines are compared with these standard genotypes each year. In any year the performance of these new lines should be compared jointly with that of a number of standard genotypes as performance of any one standard may not be indicative of its long term average.

Shorter and Norman (25) found that in Australia genotypes of dissimilar genetic origin had dissimilar productivity responses across environments. Genotypes included in our study emanated from a number of U. S. breeding programs. We found no evidence that genotypes from different programs had substantially different environmental adaptation responses. This may be indicative of a somewhat similar and narrow genetic base used in these programs for yield improvement (12). Alternatively it may indicate that selection objectives and selection environments encountered during geno-

type development are similar across the various programs.

Pattern analysis of genotypes (classification and productivity responses over environments) could be conducted annually for the UPPT. New genotypes with productivity responses similar to those of standard genotypes, or differing from the standards in desired directions, could be detected. Such analyses could be published at the same time as the original data and would expand the value of the data, particularly if adequate information on aspects of the test environments was documented. Interpretation of the analyses would, correctly, be the responsibility of the breeder and any collaborators in the testing program.

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