

Genetic Variability And Heritability For An Intercultivar Cross Of Peanuts¹

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ABSTRACT

Genetic variances for yield and several fruit traits for the F₅ and F₆ generations of an intercultivar peanut (*Arachis hypogaea* L.) cross were estimated by maximum likelihood procedures from a nested mating design. Estimates of additive and additive by environmental variances were significant for yield and the fruit traits for the cross between the two Virginia (ssp. *hypogaea* var. *hypogaea*) cultivars. Estimates of additive by additive variance were essentially zero for all traits; however, estimates of additive by additive by environmental variances were larger than their associated standard deviations for all traits except yield.

Narrow sense estimates of heritability over reciprocal crosses and environments ranged from 0.54 for yield to 0.89 for fruit length. Progress from selection in late generations should be expected for this peanut cross.

Keywords: *Arachis hypogaea* L., additive genetic variance, maximum likelihood estimators.

Introduction

Estimates of genetic variance provide information on the inheritance of quantitative characters and are useful in developing breeding procedures. Numerous studies of genetic variability in self-pollinated species have been conducted (1, 2, 4, 5, 6, 7, 8). The general conclusion from these studies is that most of the genetic variance for important agronomic traits is additive (1, 7, 8), although occasionally nonadditive genetic variance is significant (1, 4, 7, 8).

Few estimates of genetic variance for the self-pollinated peanut (*Arachis hypogaea* L.) have been made for important agronomic traits. Lin (6) found genetic variance to be principally due to dominance for number and weight of pods when F₂-F₃ progenies of a Spanish (ssp. *fastigiata* var. *vulgaris*) by Virginia (ssp. *hypogaea* var. *hypogaea*) cross were analyzed. Combining ability studies from diallels involving Spanish, Virginia, and Valencia (ssp. *fastigiata* var. *fastigiata*) lines have shown significant estimates for both general and specific combining ability for yield and several other economically important traits (11, 12). The significant specific combining ability estimates are indicative that either dominance or epistasis or both may be important for these peanut crosses. No

reports of epistatic variance for quantitative traits in peanuts were found, although Hammons (3) suggests that many of the important traits are probably based upon epistatic gene interactions.

Since the possibility of using hybrids in peanuts seems remote at present, this study was designed to estimate for a cross of two Virginia cultivars, the additive and additive x additive genetic variance, both of which are useful in breeding procedures utilizing homozygous lines.

Materials and Methods

Field Procedures

Selected plants from 'NC 5' and 'Florigiant', two cultivars of Virginia peanuts, were crossed in reciprocal during the summer of 1966. Approximately 100 F₂ plants from the cross and the reciprocal were grown during 1968. Twenty F₂ plants were chosen at random from each cross. The 20 F₂ families for each cross were bifurcated at random in the F₃ and F₄ generations to allow tests using plants in the F₅ and F₆ generations.

The F₅ and F₆ generation tests were conducted at the Peanut Belt Research Station at Lewiston, NC in randomized complete block designs during 1974 and 1976, respectively. Entries were nested to allow tests to be made among F₄ and families within F₃ families, among F₃ families within F₂ families, among F₂ families. The reciprocal crosses were tested separately but were planted in adjacent plots.

Each entry was replicated three times for both tests. Distance between plants within a row was 25.4 cm. Plots consisted of two rows of 35 plants each. Distance between rows was 91 cm. The F₅ generation test was planted 11 May and harvested 6 October, while the F₆ generation test was planted 6 May and harvested 30 September. Recommended cultural practices were used for growing the peanuts.

The yield of fruit (kg), the length of 20 two-seeded fruit (cm), fancy size pods (in-shell peanuts which ride a 1.35 x 2.54-cm screen), extra large kernels (seeds which ride a 0.85 x 2.54-cm screen), and sound mature kernels (seeds which ride a 0.60 x 2.54-cm screen) were measured for each plot.

Method of Analysis

The sources of variance and expectations of mean squares for an individual cross in a single environment, expressed both in terms of design components and genetic components of variance, are given (Table 1). The expectations in terms of genetic components were determined assuming only additive, σ_A^2 , and additive by additive epistatic, σ_{AA}^2 , variance and are the same for the F₅ and F₆ generation tests. The genetic variances are those among homozygous lines as described by Hanson and Weber (5) for late generations with dominance ignored. Data were collected from progeny in the F₅ and the F₆ generations so that dominance contributions should be small.

The genetic variances were estimated by the method of maximum likelihood assuming the relevant mean squares are distributed as multiples of

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independent chi-square random variables. This assumption is valid if the original observations are normally distributed. [A discussion of the properties of maximum likelihood estimators can be found in any statistical theory text; see, for example (9).]

The data for each cross and each generation were analyzed separately. The data were then combined over generations for each cross and finally over generations and crosses. Maximum likelihood estimates were computed for both σ_A^2 , σ_{AA}^2 , and when combined over generations, for the additive and additive x additive interactions with environments ($\sigma_A^2 \times E$ and $\sigma_{AA}^2 \times E$). The F₅ and F₆ generation tests were regarded as two environments for purposes of estimating $\sigma_A^2 \times E$ and $\sigma_{AA}^2 \times E$. Maximum likelihood estimates were also calculated for models ignoring σ_{AA}^2 and $\sigma_{AA}^2 \times E$. Differences

Table 1. Sources of variance and expectations of mean squares for both design and genetic components of variance for the F₅ and F₆ generation tests.

Source	d.f.	MS	Expectation of mean squares	
			Design components	Genetic components
Total	239			
Replications	2			
F ₂ families	19	M ₁	$\sigma_E^2 + 3\sigma_{F_4/F_3}^2 + 6\sigma_{F_3/F_2}^2 + 12\sigma_{F_2}^2$	$\sigma_A^2 + \frac{63}{8}\sigma_A^2 + \frac{351}{64}\sigma_{AA}^2$
F ₃ families in F ₂	20	M ₂	$\sigma_E^2 + 3\sigma_{F_4/F_3}^2 + 6\sigma_{F_3/F_2}^2$	$\sigma_A^2 + \frac{15}{8}\sigma_A^2 + \frac{159}{64}\sigma_{AA}^2$
F ₄ families in F ₃	40	M ₃	$\sigma_E^2 + 3\sigma_{F_4/F_3}^2$	$\sigma_A^2 + \frac{3}{8}\sigma_A^2 + \frac{39}{64}\sigma_{AA}^2$
Error	158	M ₄	σ_E^2	σ_E^2

between models, *i.e.*, $H_0: \sigma_{AA}^2 = \sigma_{AA}^2 \times E = 0$, were tested using the chi-square approximation, with appropriate degrees of freedom, of $-2 \ln \lambda$, where λ is the likelihood ratio for the two models.

Estimates of heritability were computed by the following formula using estimates from data combined over crosses and generations:

$$h^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_E^2/re + \hat{\sigma}_{AxE}^2/e + \hat{\sigma}_A^2}$$

where:

- $\hat{\sigma}_A^2$ = estimate of additive variance,
- $\hat{\sigma}_{AxE}^2$ = estimate of additive x environmental variance,
- $\hat{\sigma}_E^2$ = estimate of error,
- r = number of replications, and
- e = number of environments.

This heritability estimate applies to selection of a line based on its mean over r replications and e generations (environments).

Results and Discussion

The range of the F₂ family means for the reciprocal crosses of the two peanut cultivars, NC 5 and Florigiant, demonstrates the variability that might

be expected among progeny for an intercultivar peanut cross (Table 2). Means for the reciprocal crosses are very similar for all traits except for fancy size pods. The cross using Florigiant as the female has a higher percentage of fancy size pods than its reciprocal. No statistical test of this difference is valid but one would suspect that the difference is real because of the large number of observations involved in the means. Reciprocal cross differences for fruit characteristics have been previously reported (10).

Table 2. Range and means for F₂ families for traits measured on lines in F₅ and F₆ generations.

Parent or cross	Fancy size pods	Extra large kernels	Sound mature kernels	Fruit length (cm)	Yield/plot (kg)
NC 5	57	39	68	77.5	15.3
Florigiant	62	42	69	75.5	18.3
Florigiant x NC 5					
Mean	62.3	36.7	68.2	77.4	16.9
Range	41.4-81.9	23.4-46.1	64.2-72.0	73.9-80.9	15.2-18.3
NC 5 x Florigiant					
Mean	58.5	37.5	69.0	76.5	16.5
Range	40.7-77.1	24.7-44.0	64.1-73.8	72.9-81.4	15.6-18.0

An examination of F₂ family means indicates that all traits except yield have a large amount of variation. The F₂ family means range above and below the parental means for all traits except yield. The yield of some of the F₂ families was as large as the highest yielding parent, Florigiant.

Table 3. Maximum likelihood estimates of genetic variance components and their standard errors for traits of the cross NC 5 x Florigiant and its reciprocal for data combined over generations.

Trait	No. of parameters	Genetic parameters				
		σ_E^2	$\sigma_A^2 \times E$	$\sigma_{AA}^2 \times E$	σ_A^2	σ_{AA}^2
NC 5 x Florigiant						
Fancy size pods	5	29.01±2.30	10.21±33.96	44.13±34.35	132.98±96.50	0.00±75.64
	3	29.32±2.30	62.58±14.54	--	128.05±29.40	--
Extra large kernels	5	14.89±1.17	6.61±10.03	5.85±10.44	49.54±34.59	0.00±27.11
	3	15.02±1.16	12.73±3.70	--	48.99±10.51	--
Sound mature kernels	5	5.31±0.42	6.77±5.23	0.00±4.79	8.89±8.28	0.00±6.68
	3	5.31±0.41	6.77±1.77	--	8.89±2.60	--
Fruit length	5	4.17±0.33	0.00±1.51	1.28±1.85	6.37±5.11	1.06±4.33
	3	4.25±0.32	1.05±0.46	--	7.90±1.74	--
Yield/plot	5	2.58±0.20	0.46±0.78	0.00±0.93	0.58±0.92	0.17±0.95
	3	2.58±0.19	0.46±0.24	--	0.75±0.31	--
Florigiant x NC 5						
Fancy size pods	5	33.54±2.65	7.75±29.57	35.88±31.07	198.84±132.29	0.00±101.47
	3	34.01±2.65	47.26±12.11	--	194.56±38.90	--
Extra large kernels	5	13.76±1.09	0.31±11.91	17.70±12.88	36.84±28.23	0.00±23.06
	3	13.86±1.08	22.04±5.47	--	33.56±8.90	--
Sound mature kernels	5	4.85±0.38	1.93±6.28	8.35±6.27	8.50±8.71	0.00±7.42
	3	4.87±0.38	11.85±2.68	--	8.58±3.09	--
Fruit length	5	3.78±0.30	0.00±1.34	1.11±1.65	11.03±7.24	0.00±5.72
	3	3.85±0.29	0.90±0.41	--	11.15±2.24	--
Yield/plot	5	2.45±0.19	0.00±0.84	0.66±1.04	0.35±0.98	0.51±1.06
	3	2.53±0.19	0.48±0.24	--	0.91±0.35	--

Estimates of genetic variance components for the reciprocal crosses indicate that most of the genetic variance is σ_A^2 for all traits (Table 3). Variance estimates were similar for each cross. Neither σ_{AA}^2 nor $\sigma_{AA}^2 \times E$ was significantly different from zero for any trait when the data from the F₅ and F₆ generations were combined (5-parameter model).

Table 4. Maximum likelihood estimates of genetic variance components and their standard errors for data combined over crosses and generations.

Trait	No. of parameters	Genetic parameters				
		σ_g^2	$\sigma_{A \times E}^2$	$\sigma_{AA \times E}^2$	σ_A^2	σ_{AA}^2
Fancy size pods	5	31.27±1.75	8.68±22.47	40.37±23.17	166.38±81.04	0.00±62.73
	3	31.64±1.75	55.12±9.47	--	161.44±24.15	--
Extra large kernels	5	14.30±0.80	2.90±7.81	12.59±8.34	43.11±22.19	0.00±17.74
	3	14.43±0.79	17.41±3.26	--	41.25±6.85	--
Sound mature kernels	5	5.08±0.28	4.52±4.07	3.99±3.90	8.83±6.06	0.00±5.01
	3	5.10±0.28	9.23±1.57	--	8.77±2.01	--
Fruit length	5	3.98±0.22	0.00±1.01	1.19±1.23	9.46±4.50	0.00±3.62
	3	4.05±0.22	0.97±0.31	--	9.62±1.42	--
Yield/plot	5	2.54±0.14	0.00±0.59	0.63±0.74	0.60±0.67	0.15±0.72
	3	2.60±0.14	0.48±0.17	--	0.80±0.23	--

Reducing the model to three parameters by setting $\sigma_{AA}^2 = \sigma_{AA \times E}^2 = 0$ did not cause a significant reduction in the likelihood. Estimates of σ_A^2 and $\sigma_{A \times E}^2$ for the 3-parameter model (ignoring σ_{AA}^2 and $\sigma_{AA \times E}^2$) were significant for all traits measured on both crosses.

Combining the data over crosses (as well as generations) showed, by the chi-square test of the likelihood ratio, that the variances in the two crosses were not different. There was no indication from 5-parameter model estimates that σ_{AA}^2 was important. The chi-square test of the hypothesis that $\sigma_{AA}^2 = 0$ and $\sigma_{AA \times E}^2 = 0$ was nonsignificant in all variables except yield. Estimates of both σ_A^2 and $\sigma_{A \times E}^2$ for all traits were significant when σ_{AA}^2 and $\sigma_{AA \times E}^2$ were ignored (Table 4).

These data clearly show that additive genetic variance is important and provide no indication that additive by additive epistatic variance is of any importance for the cross of two Virginia cultivars. Similar results of significant additive genetic variance have been reported for most other self-pollinated crop plants when estimates are made for crosses between cultivars (1, 7, 8).

The results from this variance study do not agree with results from previous studies of combining ability (11, 12) for crosses among more genetically diverse peanut lines. Significant specific combining ability estimates for a diallel cross among six diverse peanut lines were found for the F_1 through F_5 generations (unpublished data). The significant specific combining ability estimates for crosses in late generation should result from additive x additive interactions since dominance contributions should be small. However, no indication of significant additive x additive epistatic variance was found for the cross used in this study.

Estimates of narrow sense heritability calculated with the mean for a progeny averaged over replications, generations and reciprocals being the appropriate selection unit are high for all traits including yield (Table 5). Since these heritability estimates are so large, selection among the progeny

Table 5. Estimates of heritability for an intercultivar cross of peanuts.

Trait	h^2^*
Fancy size pods	0.83
Extra large kernels	0.79
Sound mature kernels	0.62
Fruit length	0.89
Yield/plot	0.54

$$*h^2 = \sigma_A^2 / (\sigma_{E/re}^2 + \sigma_{A \times E/e}^2 + \sigma_A^2).$$

of this intercultivar peanut cross should be effective.

Additional variability studies are needed for peanuts. Not only are additional estimates of genetic variance needed for intercultivar crosses, the type and magnitude of genetic variance for important traits of both adapted and exotic intersubspecific crosses need to be characterized. Without this information efficient breeding procedures utilizing the range of diversity found for *A. hypogaea* cannot be implemented.

References

1. Brim, C.A. 1973. Quantitative genetics and breeding, pp. 155-186. In Soybeans: Improvement, production and uses. B.E. Caldwell (ed.), American Soc. of Agronomy, Madison, WI.
2. Brim, C.A., and C.C. Cockerham. 1961. Inheritance of quantitative characters in soybeans. Crop Sci. 1:187-190.
3. Hammons, R.O. 1973. Genetics of *Arachis hypogaea*, pp. 135-173. In Peanuts—Culture and uses. Amer. Peanut Res. and Educ. Asso., Stillwater, OK.
4. Hanson, W.D., A.H. Probst, and B.E. Caldwell. 1967. Evaluation of a population of soybean genotypes with implications for improving self-pollinated crops. Crop Sci. 7:99-103.
5. Hanson, W.D., and C.R. Weber. 1961. Resolution of genetic variability in self-pollinated species with an application to the soybean. Genetics 46:1425-1434.
6. Lin, H. 1966. Studies on the genetic behaviour of quantitative characters in the hybrid progenies of Virginia and Spanish peanut. J. Agric. Ass. China, N.S. 54:17-24.
7. Matzinger, D.F. 1963. Experimental estimates of genetic parameters and their applications in self-fertilizing plants. National Acad. Sci.-Nat. Res. Council, Publ. 982:253-279.
8. Moll, R.H., and C.W. Stuber. 1974. Quantitative genetics—Empirical results relevant to plant breeding. In Advances in Agronomy 26:277-313.
9. Mood, A.M., F.A. Grayhill, and D.C. Boes. 1974. Introduction to the theory of statistics. Third edition. McGraw-Hill Book Co., New York.

10. Wynne, J.C., and D.A. Emery. 1974. Response of intersubspecific peanut hybrids to photoperiod. *Crop Sci.* 14:878-880.
11. Wynne, J.C., D.A. Emery, and P.W. Rice. 1970. Combining ability estimates in *Arachis hypogaea* L. II. Field performance of F₁ hybrids. *Crop Sci.* 10:713-715.
12. Wynne, J.C., J.O. Rawlings, and D.A. Emery. 1975. Combining ability estimates in *Arachis hypogaea* L. III. F₂ generation of intra- and intersubspecific crosses. *Peanut Sci.* 2:50-54.