Heritabilities and Genetic Correlations for Yield and Quality Traits of Advanced Generations in a Cross of Peanut[1]

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ABSTRACT

The potential for selecting favorable early maturing virginia peanut (*Arachis hypogaea* L.) lines from advanced generations following a cross between an early maturing spanish (ssp. *fastigiata* var. *vulgaris*) and a large fruited virginia type (ssp. *hypogaea* var. *hypogaea*) was evaluated. Variability, broad and narrow-sense heritability and phenotypic and genetic correlations were estimated for the parents and 39 progeny lines in F_5 and F_6 generation grown over four location-year environments.

Substantial variability among the progenies was observed for yield, seed weight/20 fruits, meat content and protein content while less variability was observed for fruit length, 20-fruit weight, oil content and a maturity index. Heritability estimates obtained from variance component analysis and parent-offspring regression were highest for yield, meat content and protein content; intermediate for fruit length, 20-fruit weight, seed weight/20 fruits; and lowest for oil content and a maturity index.

Genotypic correlations generally were higher than phenotypic correlations. Low phenotypic correlations for the maturity index with yield and yield components suggested the possible recovery of favorable recombinants with early maturity and high yields. Fruit size was highly correlated with seed weight and both were significantly correlated with yield suggesting that selection for large fruit in this population would result in higher yield. Correlations between protein content and yield were low. Oil content was negatively correlated with yield indicating improvement in oil content could result in lower yield. Calculation of the relative efficiency of selection among traits indicated that (a) selection for yield components was not as effective as selection for yield itself, and (b) selection for yield could also increase protein content, several fruit and seed traits but would decrease meat and oil content.

Transgressive segregation was observed for all traits studied. Progeny means for all traits were distributed nearer the spanish parent than the virginia parent. However, a few favorable recombinants with early maturity, high yields and large fruits were observed among the progenies.

Key Words: *Arachis hypogaea*, yield, maturity, selection potential.

High yielding peanut (*Arachis hypogaea* L.) cultivars with large fruits and early maturity are desirable for use in the Virginia-North Carolina production area. Genotypes of the spanish type (ssp. *fastigiata* var. *vulgaris*) represent a source of early maturity, but they have small fruit size and are lower yielding than the virginia type. It would be advantageous to develop large fruited, high yielding, but early maturing peanut cultivars from the cross of a virginia with a spanish type.

Reviews of quantitative genetics as it relates to peanut breeding have been made (6, 18). Heritability and correlation estimates for yield and fruit and seed traits from populations derived after hybridization of virginia and

spanish peanuts have been reported by several workers (3, 11, 12). Lin (11) measured pod number and seed yield and found them to have low broad-sense estimates of heritability. Number of pods per plant, pod weight per plant and days to flowering were negatively correlated with each other. Pod number and pod weight per plant were positively and significantly correlated.

Coffelt and Hammons (3) obtained heritability and correlation estimates for nine yield traits in an F_2 population between 'Argentine' (spanish type) and 'Early Runner' (virginia type). They found high broad-sense heritability estimates for 100-seed weight, pod length, pod breadth and the pod length-to-breadth ratio. Significant positive correlations on a per-plant basis were obtained between pod number and pod weight, number of seeds and seed weight, pod weight and seed weight, pod weight and number of seeds, and number of pods and seed weight.

Mohammed *et al.* (12) using F_2 and F_3 populations from crosses between a virginia (NC 6) and two spanish lines (992 and R22) reported that considerable additive genetic variance existed for yield, fruit size, and maturity. Broad-sense heritability estimates over four environments (years and locations) were high for yield (.42 to .82) and fruit length (.79 to .92), but were lower for maturity. Heritabilities estimated from parent-offspring regression were generally lower than those estimated from variance components. Yield was positively correlated with fruit size and maturity for both crosses. Thus, selection for larger fruits or for earlier maturing plants at the time of harvest should increase yield. They concluded that selection for fruit size should be efficient in early generation. However, because of low narrow-sense heritabilities for yield and maturity, selection for these traits should be more effective in later generation.

This study was conducted to determine the potential for selecting large fruited, high yielding, and early maturing virginia peanut lines from late generations of a cross between an early maturing spanish and a large fruited virginia peanut line. Selection potential was determined by estimating variability, heritability and correlation coefficients for the following traits: yield, fruit size, maturity, oil content, and protein content.

Materials and Methods

The lines tested were in the F_5 and F_6 generations from the cross between NC 6 (17), a virginia cultivar, and 922, a spanish line. The spanish entry, 922, a breeding line from Texas A&M University, is early maturing but low yielding and small-seeded.

Thirty-nine families in the F_4 generation, each tracing to a separate randomly selected F_2 plant, were increased in 1978. In 1979, the 39 families and the two parents were evaluated at Lewiston and Rocky Mount, NC. At each location the 41 entries were grown in plots replicated three times in a randomized complete block design. Each plot consisted of two rows of 35 plants spaced 25 cm within and 91 cm between rows. The planting and harvesting dates were May 3 and October 5 for Lewiston, and May 9 and October 9 for Rocky Mount. All plants of each plot were machine-dug and combined at harvest.

The experiment was repeated in 1980 using randomly selected seeds of each entry harvested in 1979. The experiments were planted May 7 and May 8 and harvested October 5 and October 9 at Lewiston and Rocky Mount, respectively.

The following data were collected: yield of fruits (kg/plot), fruit length of 20 randomly selected fruits (cm), 20-fruit weight (g), seed weight/20 fruits (g), meat content (the ratio of seed-to-unshelled fruit weight of 20 fruits), maturity (as the percent of fruits with dark internal color of the hull of a 20-fruit sample), oil content and protein content. (Oil and protein contents were measured with a Neotec Model 21 Infrared Grain Quality Analyzer.)

Data collected were subjected to an analysis of variance for evaluation of the performance of the progeny lines (Table 1). In order to stabilize error variances across environments, transformation of data were conducted for the traits yield (Y) as log (Y + 1), meat content (MC) as log (MC + 1), and maturity (M) as M^2 as described by Hinz and Eagles (8).

Table 1. Relevant parts of the analysis of variance and the mean square expectations for traits measured on NC 6 x 922 lines grown in four location-year environments.

Source of variance	Degrees of freedom	Mean squares	Expectation of mean squares
Genotypes (G)	38	M_5	$\sigma_e^2 + 3\sigma_{g\ell y}^2 + 6\sigma_{g\ell}^2 + 6\sigma_{gy}^2 + 12\sigma_g^2$
G x Year (Y)	38	M_4	$\sigma_e^2 + 3\sigma_{g\ell y}^2 + 6\sigma_{gy}^2$
G x Location (L)	38	M_3	$\sigma_e^2 + 3\sigma_{g\ell y}^2 + 6\sigma_{g\ell}^2$
G x Y x L	38	M_2	$\sigma_e^2 + 3\sigma_{g\ell y}^2$
Error	312	M_1	σ_e^2

The following variance components were estimated:

$\hat{\sigma}_g^2$ = the component due to genotypic differences among the progeny lines

$\hat{\sigma}_{g\ell}^2$ = the component arising from interaction of progenies and locations

$\hat{\sigma}_{gy}^2$ = the component arising from interaction of progenies and years

$\hat{\sigma}_{g\ell y}^2$ = the component arising from interaction of progenies, locations and years

$\hat{\sigma}_e^2$ = the plot error variance.

The total phenotypic variance ($\hat{\sigma}_{ph}^2$) for progeny means was calculated as:

$$\hat{\sigma}_{ph}^2 = \hat{\sigma}_g^2 + \frac{\hat{\sigma}_{g\ell}^2}{\ell} + \frac{\hat{\sigma}_{gy}^2}{y} + \frac{\hat{\sigma}_{g\ell y}^2}{\ell y} + \frac{\hat{\sigma}_e^2}{r\ell y}$$

where r, l and y are the numbers of replications, locations and years, respectively.

Broad-sense heritability estimates (H) among progeny means were obtained as:

$$H = \hat{\sigma}_g^2 / \hat{\sigma}_{ph}^2 \times 100.$$

Narrow-sense heritability estimates (h^2) were computed using the regression coefficients of F_6 on F_5 generations means and corrected for parent-offspring relationship for continually self-pollinated populations as follows:

$$h^2 = \frac{b_{F_5 \cdot F_6}}{2r_{op}}$$

where: $bF_5 \cdot F_6$ is the regression coefficient and r_{op} is the coefficient of parentage with a value of 31/32 between F_5 and F_6 generations (13).

Covariance components were estimated from covariance analysis in an analogous manner to the variance components computed from the analysis of variance. Genetic correlations (r_g) between pairs of traits x and y were computed from the genetic variance and covariance estimates as the ratio of their covariance estimates [$Cov_{g(x,y)}$] over the prod-

uct of the square roots of their respective genetic variance estimates, $\hat{\sigma}_{g(x)}^2$ and $\hat{\sigma}_{g(y)}^2$ (7), as follows:

$$r_{g(x,y)} = \frac{\hat{COV}_{g(x,y)}}{\sqrt{\hat{\sigma}_{g(x)}^2 \hat{\sigma}_{g(y)}^2}}$$

Phenotypic correlations were obtained as the Pearson product moment coefficients of the trait means for each progeny line.

Under the assumption that all effects in the linear model were random, an approximate test was used for genotypic effects and the partitions of genotypic effects (15) as follows:

$$F_{(df_g, df_e')} = \frac{MSG}{MSE'}$$

where: MSG = mean squares for genotypic effect,

MSE' = $MS_{gy} + MS_{g\ell} - MS_{g\ell y}$; calculated from the corresponding mean squares in the analysis of variance.

The F table with df_g and df_e' degrees of freedom were used where

$$dfe' = \frac{(MSE')^2}{\left(\frac{(MS_{gy})^2}{df_{gy}} + \frac{(MS_{g\ell})^2}{df_{g\ell}} + \frac{(MS_{g\ell y})^2}{df_{g\ell y}} \right)}$$

and df is the number of degrees of freedom in the corresponding mean square.

To evaluate the relative performance of the progenies collectively, their means over environments for each trait were compared to each of the parental means and the midparental value using an adjusted t-test for comparing means of unequal variances and sample sizes (14).

The relative efficiency of indirect selection for one trait (x) as a result of selecting for another trait (y) was calculated by the method of Falconer (4) assuming the selection intensities for both traits were equal and expressed as a percentage of the response expected when selection was for the trait itself:

$$\frac{CR_x}{R_x} = \frac{h_y}{h_x} \cdot r_{g(x,y)} \times 100$$

where: h_x, h_y and $r_{g(x,y)}$ were the square roots of the heritabilities (narrow sense) and the genotypic correlation of x and y, respectively.

Results and Discussion

Significant differences were obtained between the two parents and between the parents and the progeny lines for fruit length, 20-fruit weight, seed weight/20 fruits and yield. The progenies significantly differed for seed weight/20 fruits, yield, meat content and protein content indicating that substantial amounts of variability existed for these traits. The progenies were not significantly different from each other for fruit length, 20-fruit weight, maturity and oil content.

With the exception of yield, the genotype x location interactions were generally not significant. The genotype x year interactions, however, were significant for six of the eight traits studied.

Genetic variance (σ_g^2) accounted for a substantial portion of the total phenotypic variance for seed weight/20 fruits, yield, meat content and protein content (Table 2). Consequently, the broad-sense heritability estimates for seed weight/20 fruits, yield, meat content and protein content were 0.45, 0.62, 0.54 and 0.75, respectively. A

smaller portion of genetic variance was recorded for fruit length, 20-fruit weight and oil content. Heritability estimates for fruit length, 20-fruit weight and oil content were 0.30, 0.36 and 0.09, respectively. A negative genetic variance estimate was obtained for maturity indicating that it has near zero value.

Mohammed *et al.* (12) estimated the heritability of fruit length, fruit weight, fruit maturity index, seed weight/20 fruits, shelling percentage and yield using F_2 and F_3 generation means of the same cross. The broad-sense heritability estimates of this study agreed with the average of the intraplot variance estimates over four year-locations obtained by Mohammed *et al* (12) for yield and shelling percentage (meat content) but were substantially lower for fruit length, 20-fruit weight and seed weight/20 fruits.

Estimates of heritabilities computed by offspring-parent regression were generally lower than those computed by the variance estimates. The results obtained by the two methods were comparable. Narrow-sense estimates of 0.24, 0.24 and 0.22 were obtained for yield, protein and meat content, respectively. Regression estimates were similar in magnitude for the three traits measuring fruit size, *i.e.*, fruit length (0.16), 20-fruit weight (0.19) and seed weight/20 fruits (0.17). Estimates of 0.17 and 0.05 were obtained for oil content and maturity index, respectively.

The magnitude of regression estimates from the F_2 and F_3 generations of the same cross obtained by Mohammed *et al.* (12) were lower than those estimated from F_5 and F_6 generations for yield (0.16) and meat content (0.05). They were comparable for fruit length (0.18) but were higher for 20-fruit weight (0.50) and seed weight/20 fruits (0.51). Regression estimates of heritability are less biased by genotype x environment interaction since the F_5 and F_6 generations were grown in different years. The relatively high regression estimates obtained for yield, meat content, protein content and for traits measuring fruit size indicated that selection for those traits should be effective.

Genotypic correlations, except for those involving the maturity index, were generally higher than phenotypic correlations for the traits measured (Table 3). Similar re-

Table 3. Phenotypic (r_p) and genotypic (r_g) correlation estimates among traits for NC 6 x 922 progeny lines.

		20 fruit weight	Seed wt/ 20 fruits	Yield	Meat content	Maturity	Protein content	Oil content
Fruit length	r_p	.70**	.70**	.25	-.13	-.01	-.11	-.26
	r_g	.30	.43**	.23	.71**	†	-.43	-1.80**
20-fruit wt	r_p		.98**	.28	-.34*	.03	.34*	-.14
	r_g		.98**	.50**	.02	†	.37*	-.67**
Seed wt/20 fruit	r_p			.22	-.15	.09	.37*	-.06
	r_g			.40**	.28	†	.39**	-.18
Yield	r_p				-.39*	-.23	.22	-.19
	r_g				-.36*	†	.20	-1.38**
Meat content	r_p					-.22*	-.06	.37*
	r_g					†	.01	1.73**
Maturity	r_p						.13	.30
	r_g							†
Protein content	r_p							.22
	r_g							.32*

*,**Denote significance at 5 and 1% probability levels, respectively.

†Unestimable because of negative genotypic variance estimate for maturity.

sults in peanut have been found by other workers (2, 10, 11, 12).

Phenotypic correlations of maturity with fruit weight, seed weight, or meat content were small although the correlation for meat content was significant. Genotypic correlations between maturity and other traits were not calculated due to a negative genetic variance estimate for the trait used to measure maturity. However, the low estimates for the phenotypic correlations suggest that selection for some favorable recombinants from among the progeny lines could be possible. Mohammed *et al.* (12) also found low, but significant, correlations between yield traits and maturity traits.

Positive and significant genotypic correlations were observed between fruit length, 20-fruit weight, seed weight/20 fruits, and yield. This was expected because any increase in fruit size and seed weight should result in a corresponding increase in yield. The negative correlation between yield and meat content, though significant, was small and should allow for selection of favorable recombinants in the progeny population.

Table 2. Estimates of variance components and heritability for 39 NC 6 x 922 lines from replicated trials over two years and two locations.

Traits	$\hat{\sigma}^2_g$	$\hat{\sigma}^2_{gy}$	$\hat{\sigma}^2_{g\ell}$	$\hat{\sigma}^2_{g\ell y}$	$\hat{\sigma}^2_e$	$\hat{\sigma}^2_{ph}$ **	$H^\dagger$ (%)
Fruit length	2.27	3.51	1.22	6.28	16.93	7.61	30
20-fruit weight	3.37	6.24	1.02	4.02	16.35	9.37	36
Seed wt/20 fruits	2.14	2.65	0.19	2.07	8.07	4.76	45
Yield	3.03×10^{-3}	2.17×10^{-3}	0.83×10^{-3}	0.13×10^{-3}	4.23×10^{-3}	4.97×10^{-3}	62
Meat content	1.17×10^{-5}	0.95×10^{-5}	0.26×10^{-5}	0.13×10^{-5}	4.24×10^{-5}	2.16×10^{-5}	54
Maturity	-0.06×10^{-2}*	0.17×10^{-2}	0.27×10^{-2}	0.25×10^{-2}	2.33×10^{-2}	0.48×10^{-2}	0
Protein content	0.73	0.24	-0.11*	0.18	1.01	0.98	75
Oil content	0.02	0.07	0.11	0.06	1.29	0.23	9

*Negative estimates for which the most reasonable values should be zero and zero values were used in the calculations.

$$**\hat{\sigma}^2_{ph} = \hat{\sigma}^2_g + \hat{\sigma}^2_{gy}/y + \hat{\sigma}^2_{g\ell}/\ell + \hat{\sigma}^2_{g\ell y}/\ell y + \hat{\sigma}^2_{e}/r\ell y.$$

$$^\dagger H = \left(\hat{\sigma}^2_g/\hat{\sigma}^2_{ph}\right) \times 100.$$

Fruit length and 20-fruit weight were significantly and highly correlated both phenotypically and genotypically with seed weight/20 fruits. The values suggested that phenotypic selection for larger and heavier fruits could result in higher seed yield. Coffelt and Hammons (3) have also reported highly significant positive correlation between fruit and seed weight.

Fruit length and 20-fruit weight were highly correlated phenotypically but not genotypically indicating that pod-filling was dependent upon environmental conditions. Seed weight accounted for the major portion of the total fruit weight as evident by the high meat content values (70-82%) obtained in this study. Godoy and Norden (5) have suggested that fruit and seed size traits in segregating peanut populations are controlled by different genes.

Correlations between protein content and seed weight and fruit weight were low, although significant (Table 3). Layrisse et al. (10) recorded similar results among the segregating progeny of 10 diverse peanut lines.

Negative correlations were obtained between oil content and all yield traits. Improvement for oil content could therefore result in a negative selection for the other traits.

We found protein and oil content to be positively correlated. This finding disagrees with the negative correlation between protein and oil content measured by Holley and Hammons (9) and Tai and Young (16). This disagreement is not surprising since the previous studies used many different genotypes while this study used progenies from a single cross.

The relative efficiency of selection using a secondary trait, expressed as a percentage of the progress expected when selection was for the trait itself, suggested that selecting for increased fruit length, high 20-fruit weight, high seed weight/20 fruits or lower meat content would not be as effective as selection for yield itself (Table 4). Therefore, even though these traits were genetically correlated with yield, selection for yield can best be achieved by selecting for yield itself verifying the earlier conclusions of Bernard (1).

Table 4. Relative efficiency of indirect selection of trait x due to selection for trait y.

Trait y	Relative efficiency of selection for trait x[†]						
	Fruit length	20-fruit weight	Seed wt/ 20 fruits	Yield	Meat content	Protein content	Oil content
Fruit length	--	--	42	29	60	--	--
20-fruit weight	--	--	105	44	--	33	(-)87
Seed wt/20 fruits	--	--	--	44	--	43	(-)23
Yield	53	64	58	--	(-)50	20	(-)69
Meat content	--	--	--	(-)44	--	--	--
Protein content	--	--	--	20	--	--	47
Oil content	--	--	--	(-)94	--	--	--

[†]Relative efficiency of selection expressed as percentage of the progress expected when selection was for trait x itself and (-) indicates negative association.

Selection for increased fruit length would result in a higher meat content and selection for high 20-fruit weight would result in improvement of seed weight/20 fruits as efficiently as selecting directly for seed weight/20 fruit. This would be an advantage as fruit length and weight are more easily measured than seed weight and meat content.

The estimates of progress expected in oil content from selecting for 20-fruit weight, seed weight/20 fruits and the estimate of the expected progress in yield by selecting for oil content were negative. Positive selection for those traits would reduce the oil content, especially if higher 20-fruit weight was used as the criterion for selection.

A positive response of oil content to selection for protein content was found due to the higher estimate of heritability for protein content. Thus, if simultaneous improvement of protein and oil contents were desired in this population, protein would serve as the best indicator for the advancement of both traits.

In most breeding programs yield is the decisive factor when other traits for selection are comparable. It is interesting to note that if yield had been the criterion for selection, it would result in substantial correlated improvement in fruit length, 20-fruit weight, seed weight/20 fruits and protein content.

The range of means for fruit length, 20-fruit weight, seed weight/20 fruits and yield, and range extended from just below the higher parent (NC 6) to beyond the lower spanish parent (922) while values for meat content, maturity, oil and protein contents ranged beyond both parental means (Table 5). Progeny means were not significantly different from the spanish parent 922. However, they were significantly different from the virginia parent and the midparent for yield, fruit length, 20-fruit weight and seed weight/20 fruits. Protein content of the progeny lines was also significantly lower than that of the virginia parent. Therefore, when the parents differed substantially for the traits, as in the case of yield, fruit length, 20-fruit weight, seed weight/20 fruits and protein content, the spanish type was the dominant parent. Godoy and Norden (5) have also reported progenies from crosses of parents distinct for fruit/seed sizes approached the small size parents.

As expected, when the parents did not differ significantly in meat content, maturity, oil content and protein content, the progenies did not deviate significantly from either the parents or the midparent. Nevertheless, a substantial number of transgressive segregants, mostly in the direction of the spanish parent, were observed for these traits. This again indicates dominance of the spanish traits.

A large proportion of the 39 progeny lines higher in protein, oil or meat contents and with earlier maturity than the progeny midparent could be recovered from the progeny population. Thirteen to 36 percent of the progenies, depending on the traits, performed better than the high parent. None of the progenies outyielded NC 6, but three of the lines were not significantly different from the virginia parent. All three lines were intermediate in maturity to the two parents and two of the lines had pod sizes only slightly smaller than NC 6.

Only a small proportion of the progeny lines performed better than the lower spanish parent for the fruit and seed traits measured. However, this may not be a problem because selection for yield would also bring about a substantial correlated response for these traits in the selected population.

Table 5. Range, means and their standard errors for traits measured on NC 6 x 922 lines in the F_5 and F_6 generations.

Parental or progeny line	Fruit length (cm)	20-fruit wt (g)	Seed weight/ 20 fruits (g)	Yield[†] (kg)	Meat[†] content	Maturity[†]	Oil content	Protein content
NC 6	73.53±1.26**	45.22±1.61**	33.41±1.40**	0.75±0.03**	0.24±0.00	0.52±0.07	44.46±0.58	30.53±0.26*
922	50.88±2.71	24.30±2.54	18.33±1.75	0.56±0.03	0.25±0.00	0.65±0.05	45.58±0.51	30.38±0.44
Midparent	62.20±2.78*	34.76±2.63**	25.87±1.92**	0.67±0.03**	0.24±0.00	0.58±0.05	45.02±0.40	30.45±0.25
NC 6 x 922 lines:								
Mean	55.32±0.26	27.05±0.27	20.43±0.19	0.54±0.01	0.25±0.00	0.62±0.01	45.18±0.09	29.82±0.10
Range	48.14-65.00	20.76-34.47	16.13-25.50	0.36-0.75	0.23-0.26	0.41-0.72	43.07-46.01	27.93-32.92

[†]Values based on transformed data.

*,**Denote significant difference from the mean of NC 6 x 922 lines at 5 and 1% probability levels, respectively, using an adjusted t-test (Snedecor and Cochran, 1967).

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