The Effectiveness of Early Generation Testing as Applied to a Recurrent Selection Program in Peanut[1]

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ABSTRACT

The effectiveness of early generation testing for yield improvement in peanut (*Arachis hypogaea* L.) was evaluated in an attempt to increase the efficiency of an on-going recurrent selection program by reducing the time required for evaluation and selection. The objectives of the study were to (1) determine if the number of years required per cycle of selection could be reduced; and (2) estimate the amount of genetic variability remaining in the population for yield and four agronomic traits after four cycles of recurrent selection. Sixty-eight random-mated crosses, among the 40 highest yielding lines from the cycle 3 population, were evaluated for yield and agronomic traits in 1985 ($S_{0:1}$), 1986 ($S_{0:2}$), and 1987 ($S_{0:3}$). The results were compared to determine if early generation performance accurately predicts the performance of cross bulks in later generations. No significant correlations were found for yield of entries in the $S_{0:3}$ and $S_{0:2}$ or in the $S_{0:3}$ and $S_{0:1}$; however, there was a significant correlation between yield of entries in the $S_{0:2}$ and $S_{0:1}$ generations. No correlations were found between yield and any of the agronomic traits measured in the $S_{0:3}$; however, significant correlations were found in the $S_{0:2}$ between yield and most traits measured. Significant correlations were also found for entries in the $S_{0:3}$ and $S_{0:2}$ generations for each agronomic trait measured except number of seed per 20 pods. Early generation testings appears to be useful for selection of certain agronomic traits, but of limited value when selecting for yield. A decrease in genetic variation for yield in the population from the $S_{0:1}$ to the $S_{0:3}$ generation was observed; however, the number of crosses equal to or exceeding the yield of the check cultivar increased in later generations. All agronomic traits measured, except number of seed per 20 pods, showed significant genetic variation remaining in the population in both the $S_{0:2}$ and $S_{0:3}$ generations. The greater the genetic variation remaining in the population for a given trait, the more likely it is that further improvement of that trait will be realized with additional cycles of selection.

Key Words: Early generation testing, recurrent selection, genetic correlations.

A recurrent selection procedure based on the evaluation of late generation bulk families has been effective in improving yield in peanut (*Arachis hypogaea* L.) (14); however, each cycle of selection requires approximately 3 years to complete. If performance of hybrid progenies in early generations accurately reflects the genetic potential of the cross, then the identification and selection of superior crosses in early generations would reduce the number of years required per cycle of recurrent selection, resulting in a more efficient selection program.

One of the advantages of using early generation testing is the early elimination of undesirable material. This is especially important when resources are limited and/or a large number of lines must be evaluated. However, the effectiveness of early generation testing in self-pollinated crops has been disputed. Harlan *et al.* (8) and Immer (10), working with barley (*Hordeum vulgare* L.); Harrington (9), with wheat (*Triticum aestivum* L.); and Leffel and Hanson (12), with soybeans (*Glycine max* L., Merrill), concluded that early generation testing could be used effectively in self-pollinators to identify crosses from which segregates with high yielding ability could be selected. However, the value of early generation testing for predicting yield potential in later generations has been questioned by Fowler and Heyne (7), working with wheat; Atkins and Murphy (2), working with oats (*Avena sativa* L.); and Weiss *et al.* (15), with soybeans. Boerma (4) concluded that pure lines of soybeans developed by early generation testing did not differ significantly in yielding ability from lines developed by testing in late generations using either pedigree selection or single seed descent procedures. These results agree with previous reports indicating that, in soybeans, genes governing yield tend to stabilize in early generations.

In peanut, Wynne (16) concluded that, although early generation testing appeared to be effective for fruit length, sound mature kernels, and fancy size pods, yield in the S_1 generation was ineffective in predicting the yield of the same cross grown in bulk in the S_4 generation. He suggested that the failure to effectively select among crosses for yield in early generations could be explained in part by the diversity of the original parents used to generate the crosses and that a significant portion of the variance among crosses was nonadditive, as evidenced by low general combining ability estimates. Similarly, Mohammed *et al.* (13) found that early generation selection for yield in segregating peanut populations originating from crosses among genetically diverse

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parents would be ineffective, based on low regression estimates for heritability of yield. However, they did observe significant positive correlations between yield and both fruit size traits and maturity estimates, suggesting that selection for larger fruit size and/or plant maturity may result in increased yields of the cross progeny.

Iroume and Knauft (11) investigated early generation selection methods for the identification of peanut crosses with both high yields and leafspot resistance. Their results suggest that, in the S_1, selection among crosses for all traits would be advantageous over individual plant selection or within family selection, with selection of genotypes within crosses being the poorest strategy for selection in early generations. Negative correlations observed between yield and leafspot severity led the researchers to conclude that selection for yield under disease pressure in early generations may be effective in the development of high yielding genotypes with leafspot resistance. The effectiveness of early generation testing procedures in peanut appears to be enhanced by limiting its use to traits of high heritability or to indirect selection for yield, based on selection for correlated traits.

The objectives of this study were to (a) determine whether early generation testing could be utilized effectively as part of an on-going recurrent selection program to reduce the number of generations required before cross evaluation, and (b) estimate the amount of genetic variation remaining in the cycle 4 population in the $S_{0:1}$, $S_{0:2}$, and $S_{0:3}$ generations.

Materials and Methods

Sixty-eight random-mated crosses among the 40 highest yielding lines selected from a cycle 3 recurrent selection population (14) were evaluated for yield and agronomic traits in the $S_{0:1}$ and $S_{0:2}$ generation in replicated tests at the Peanut Belt Research Station in Lewiston, NC in 1985 ($S_{0:1}$) and 1986 ($S_{0:2}$). In 1987, the same crosses were evaluated for yield and agronomic traits in the $S_{0:3}$ generation, in replicated tests at Lewiston and at the Upper Coastal Plain Research Station in Rocky Mount, NC. The experimental design used was a randomized complete block with entries randomly assigned to sets, in both 1986 and 1987, for additional blocking effect. The commercial cultivar Florigiant was included as a check. A plot consisted of two rows, 91 cm apart, with 28 plants per row. Each plot was dug and harvested using commercial equipment. Fruit were dried to approximately 8% moisture, weighed, and sampled. Yield (fruit weight in kg/ha) was measured in all three generations.

The following agronomic traits were measured in the $S_{0:2}$ and $S_{0:3}$ generations:

(a) fruit length of 20 random pods, in cm;
(b) fruit weight of 20 random pods, in g;
(c) number of seed per 20 random pods; and
(d) weight of seed from 20 random pods, in g.

Correlation coefficients were calculated for the following:

(a) fruit yield of entries in the $S_{0:1}$, $S_{0:2}$, and $S_{0:3}$ generations,
(b) fruit yield and four agronomic traits in the $S_{0:2}$ and $S_{0:3}$ generations, and
(c) four agronomic traits for entries in the $S_{0:2}$ and $S_{0:3}$ generations.

Plots of the correlations of entry means for yields in the $S_{0:1}$ vs. $S_{0:2}$, $S_{0:1}$ vs. $S_{0:3}$, and $S_{0:2}$ vs. $S_{0:3}$ were obtained.

In addition, the total amount of genetic variation for yield and four agronomic traits remaining in the population each generation was estimated from the analysis of variance. Estimates of broad-sense-heritability were calculated as the ratio of total genetic variance to phenotypic variance. The number of lines equal to or exceeding the yield of Florigiant (the check cultivar) in each generation was also noted.

Results and Discussion

Entry yields in the $S_{0:1}$ generation were significantly correlated with yield of the entries in the $S_{0:2}$ generation; however, no correlation was found for yield of entries in the $S_{0:2}$ and $S_{0:3}$ or $S_{0:1}$ and $S_{0:3}$ generations (Table 1). Plots of entry means for yield in the $S_{0:1}$ vs. the $S_{0:3}$ and the $S_{0:2}$ vs. the $S_{0:3}$ generations confirmed the lack of correlation observed for yield of entries based on correlation coefficients. There was no indication that the highest yielding lines were consistently highest yielding over generations, with lines at the lower end of the yield range fluctuating to account for the lack of correlation observed. Instead, all entries were dispersed over the range of yield observed across generations and contributed to the nonsignificant estimates obtained for the correlation coefficients for fruit yield of entries in the $S_{0:1}$ and $S_{0:3}$ and in the $S_{0:2}$ and $S_{0:3}$ generations.

Thus, pod yields in early generations were ineffective in predicting the yield potential of crosses grown in bulk in later generations.

One problem with the use of early generation testing procedures in bulk populations is that average yields of the cross bulk are identified, rather than the yield of superior segregates from specific crosses (5). Wynne (16), in determining the value of early generation testing in peanut from a diallel cross among six diverse lines representing three botanical varieties, found that, although the average performance of a parental line in crosses in the F_2 was correlated with its average performance in crosses in the F_5 generation, yields of the highest yielding lines selected from the crosses using a modified pedigree system were not correlated with the yield of the crosses grown in bulk in either the F_2 or F_5 generations. These results and the results of the present study point to a limitation which may occur when selecting for yield among bulk progenies in early generations.

Table 1. Coefficients of correlation between entries in the $S_{0:1}$, $S_{0:2}$, and $S_{0:3}$ generations for yield.

	Yield ($S_{0:3}$)	Yield ($S_{0:2}$)	Yield ($S_{0:1}$)
Yield ($S_{0:3}$)	--	-0.04 NS	-0.12 NS
Yield ($S_{0:2}$)		--	0.31 **
Yield ($S_{0:1}$)			--

**Indicates significance at the 0.01 level.

Among entries in the $S_{0:2}$, significant correlations were found between yield and all agronomic traits measured except number of seed per 20 pods; however, no significant correlations were observed in the $S_{0:3}$ generation (Table 2), indicating that selection based on agronomic characters would not consistently predict the yield potential of the bulk crosses in this population. Therefore, indirect selection for yield, based on the selection of correlated traits with higher heritabilities, would be ineffective in this population. Significant correlations were found for each agronomic trait measured, except number of seed per 20 pods, for entries in the $S_{0:2}$ and $S_{0:3}$ generations (Table 3), suggesting that early generation selection may be effective in the improvement of traits with high heritability among bulk crosses from a diverse peanut population. These results are consistent with those obtained by Wynne (16) who found that, although F_2 generation cross means for yield were not correlated with F_5 cross means, several agronomic characters measured for the bulk crosses in the F_5 generation were correlated with similar measures in the F_2 generation. Mohammed *et al.* (13) in evaluating the potential for selection of large fruited, early maturing, high yielding genotypes among crosses between very early spanish lines and a large fruited, high yielding virginia line, concluded that, because of low estimates of heritability, selection for yield and maturity would be more efficient in later generations. However, selection for fruit size and other traits with higher heritabilities should be effective even in early generations.

Table 2. Coefficients of correlation between yield and four agronomic traits in the $S_{0:2}$ and $S_{0:3}$ generations.

Agronomic trait	Pod yield	
	$S_{0:2}$	$S_{0:3}$
Fruit length	0.36 **	-0.08 NS
Fruit weight	0.39 **	-0.02 NS
No. seed	0.13 NS	-0.07 NS
Seed weight	0.35 **	0.01 NS

**Indicates significance at the 0.01 level.

Table 3. Coefficients of correlation between entries in the $S_{0:2}$ and $S_{0:3}$ generations for four agronomic traits.

Trait ($S_{0:2}$)	Trait ($S_{0:3}$)			
	Fruit length	Fruit weight	No. seed	Seed weight
Fruit length	0.50 **			
Fruit weight		0.58 **		
No. seed			0.08 NS	
Seed weight				0.51 **

**Indicates significance at the 0.01 level.

In contrast, Coffelt and Hammons (6), based on yield tests involving high yielding F_2 lines in the F_3, F_4, F_5, and F_6 generations, concluded that early generation testing for yield should be an acceptable procedure for peanuts. In their study, selection was practiced each generation with only those lines that outyielded the parental cultivars being advanced each generation, rather than advancing the population in bulk, as was practiced by Wynne (16), by Mohammed *et al.* (13), and in the present study. This could account for much of the difference in opinion as to the usefulness of early generation yield tests in peanuts. The effectiveness of such tests appears limited to those cases in which selection is practiced as each generation is advanced. For example, in 1985, Bandyopadhyay *et al.* (3) evaluated the genetic potential of F_2 progeny from single and three-way crosses using both physiological traits and components of yield. They found that F_3 families derived from the top 25% of F_2 plants provided a higher frequency of selections for increased pod number than those derived from the top 50, 75, or 100%. In addition, they found the frequency of superior selections to be higher in three-way than single crosses; and a selection index based on physiological and yield components to be more effective than an index based on yield components alone. The researchers concluded that, with appropriate selection intensities and the use of a selection index based on both physiological and yield components, effective selection for yield improvement in peanut can be made as early as the F_2 generation. The recurrent selection scheme practiced in peanut improvement programs (14) does not produce sufficient early generation material to allow adequate testing and selection to take place as early generations are advanced. Thus, the effectiveness of early generation testing, coupled with appropriate selection intensities indicated by the results of a number of studies (3, 6, 11), is not realized when crosses are advanced in bulk as they are in the recurrent selection scheme.

A high level of genetic variation for yield was estimated for the $S_{0:1}$ and a moderate level was estimated for the $S_{0:2}$; however, estimates of genetic variation for yield remaining in the population in the $S_{0:3}$ generation were not significant. Estimates of broad-sense heritability for yield in the $S_{0:1}$, $S_{0:2}$, and $S_{0:3}$ generations were 0.39, 0.29, and 0.00, respectively. A broad-sense heritability estimate of zero for yield in the $S_{0:3}$ was the result of an estimate of genetic variance equivalent to zero. The $S_{0:3}$ generation yield trials were conducted at two locations which may account, in part, for the decrease observed in estimates of genetic variation compared to the $S_{0:1}$ and $S_{0:2}$ generations, which were evaluated at a single location. A trait such as yield, with low heritability, can be influenced to a great extent by environmental conditions causing estimates of genetic variance in the $S_{0:1}$ and $S_{0:2}$ to be biased upward by genotype x environment interactions. When analyzed over locations, yield of entries in the $S_{0:3}$ generation gave a highly significant effect due to location ($p = 0.0001$) while differences among entries were not significant.

Three of the four agronomic traits measured (fruit length, fruit weight, seed weight) showed significant levels of genetic variation remaining in the population in both the $S_{0:2}$ and $S_{0:3}$ generations, indicating that continued progress from recurrent selection can still be made for such traits in this population (Table 4). Relative to yield, the higher heritabilities associated with these traits should reduce the impact of genotype x environment interactions on the estimates of genetic variance obtained from a single location.

Although estimates of genetic variation for yield decreased in later generations, the number of lines that were not significantly different in yield from Florigiant, the check cultivar, increased from 69.6% in the $S_{0:1}$, to 82.9% in the $S_{0:2}$, to 94.4% in the $S_{0:3}$. The large number of lines equal to or exceeding Florigiant in yield each generation suggests that recurrent selection has been effective in improving yield of this diverse peanut population through the fourth cycle of recurrent selection. The cycle 5 crosses are currently under evaluation to determine whether there is enough genetic variation left in the recurrent selection population to continue making progress in yield improvement with further cycles of selection.

Some inherent problems with this study arose from the limited number of seed produced in early generations. The limited quantity of seed resulted in the use of a single location for yield tests in the $S_{0:1}$ and $S_{0:2}$. Yield tests conducted at a single location cannot adequately estimate genotype x environment interactions and may have introduced a bias into the results. In addition, when generations are tested in

Table 4. Mean squares and variance component estimates for yield and four agronomic traits in the SO:1, SO:2 and SO:3 generations of the cycle 4 recurrent selection population.

Source	df[b]	Yield	Pod length	Pod weight	Seed no.	Seed weight	Expected mean squares[a]
$S_{0:1}$ generation:							
Rep	3	30.48**					
Entries	68	5.03**					$\sigma_e^2 + r\sigma_g^2$
Error	192	3.05					σ_e^2
Variance component est.[a]:							
σ_g^2		0.50					
σ_{Ph}^2		1.26					
H		0.39					
$S_{0:2}$ generation:							
Set	1(1)	83.84**	160.71**	330.18**	1.61	111.61**	
Rep (set)	6(2)	8.21**	0.19	2.02	0.35	1.58	
Entries (set)	68(68)	3.28*	32.76*	22.98**	4.60	15.18**	$\sigma_e^2 + rs\sigma_g^2$
Error	200(139)	2.32	18.41	9.20	3.32	6.17	σ_e^2
Variance component est.[a]:							
σ_g^2		0.12	3.59	3.45	0.32	2.25	
σ_{Ph}^2		0.41	8.19	5.75	1.15	3.80	
H		0.29	0.44	0.60	0.28	0.59	
$S_{0:3}$ generation:							
Location (loc)	1	1327.73**	4.66	873.95**	69.23**	1070.06**	
Set (loc)	2	3.79	98.74**	320.12**	8.43	130.75**	
Rep [set (loc)]	12	32.45**	12.37	21.35*	3.98	22.01**	
Entries (set)	70	3.02	55.86**	61.60**	2.65	31.22**	$\sigma_e^2 + rs\sigma_{gl}^2 + rsl\sigma_g$
Loc • entries (sets)	70	4.03	9.47	13.60	2.71	10.62	$\sigma_e^2 + rs\sigma_{gl}^2$
Error	412	3.59	7.78	11.37	2.91	8.36	σ_e^2
Variance component est.[a]:							
σ_g^2		-0.06[c]	2.90	3.00	-0.004[c]	1.29	
σ_{gl}^2		0.06	0.21	0.28	-0.03[c]	0.28	
σ_{Ph}^2		0.19	3.49	3.85	0.17	1.95	
H		0	0.83	0.78	0	0.66	

*,**Indicates significance at the 0.05 and 0.01 probability levels, respectively.

[a] σ_g^2, σ_{gl}^2, σ_{Ph}^2, H = estimates of genotypic, genotype x location, phenotypic variances, and broad-sense heritability for yield, respectively; r = no. reps, s = no. sets, l = no. locations.

[b] Degrees of freedom in parentheses correspond to fruit traits.

[c] Equivalent to zero.

successive years, the individual populations are subjected to different selection pressures which could lead to genetic shifts in the population that vary from generation to generation. Interactions among crosses, generations, and years may be confounded, thus reducing the accuracy with which later generation performance can be predicted based on early generation testing (1). This problem cannot be overcome with the recurrent selection procedure currently in use in peanut.

Early generation testing was not consistently effective in selecting high yielding bulk crosses from this diverse peanut population and, therefore, may not be an efficient procedure for reducing the time required for evaluating bulk families in a recurrent selection program. However, even without the benefit of early generation testing, recurrent selection has proven to be effective for improving both yield and agronomic characters in this broad-based peanut population.

Literature Cited

1. Allard, R. W. 1960. Principles of Plant Breeding. John Wiley and Sons, Inc., New York.
2. Atkins, R. E. and H. C. Murphy. 1949. Evaluation of yield potentialities of oat crosses from bulk hybrid tests. Agron. J. 41:41-45.
3. Bandyopadhyay, A., V. Arunachalam, and K. Venkaiah. 1985. Efficient selection intensity in early generation index selection in groundnut (*Arachis hypogaea*. L.). Theor. Appl. Genet. 71:300-304.
4. Boerma, H. R. 1973. The effectiveness of three breeding procedures in selecting superior yielding pure lines in soybeans. Unpubl. PhD. Diss., Univ. of Illinois.
5. Briggs, F. N. and P. F. Knowles. 1967. Introduction to Plant Breeding. Reinhold Publ. Corp., Davis, CA.
6. Coffelt, T. A. and R. O. Hammons. 1974. Early generation yield trials of peanuts. Peanut Sci. 1:3-6.
7. Fowler, W. L. and E. G. Heyne. 1955. Evaluation of bulk hybrid tests for predicting performance of pure line selections in hard red winter wheat. Agron. J. 47:430-434.
8. Harlan, H. V., M. L. Martini, and H. Stevens. 1940. A study of methods of barley breeding. USDA Tech. Bull. No. 720.
9. Harrington, J. B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Canad. J. Res. 18:578-584.
10. Immer, F. R. 1941. Relation between yielding ability and homozygosis in barley crosses. J. Amer. Soc. Agron. 33:200-206.
11. Iroume, R. N. and D. A. Knauft. 1987. Heritabilities and correlations for pod yield and leafspot resistance in peanut (*Arachis hypogaea* L.): Implications for early generation selection. Peanut Sci. 14:46-50.
12. Leffel, R. C. and W. D. Hanson. 1961. Early generation testing of diallel crosses of soybeans. Crop Sci. 1:169-174.
13. Mohammed, J., J. C. Wynne, and J. O. Rawlings. 1978. Early generation variability and heritability estimates in crosses of virginia and spanish peanuts. Oleagineux 33:81-86.
14. Monteverde-Penso, E. J. and J. C. Wynne. 1988. Evaluation of three cycles of recurrent selection for fruit yield within a population of virginia-type peanut. Crop Sci. 28:75-78.
15. Weiss, M. G., C. R. Weber, and R. R. Kalton. 1947. Early generation testing in soybeans. J. Amer. Soc. Agron. 39:791-811.
16. Wynne, J. C. 1976. Evaluation of early generation testing in peanuts. Peanut Sci. 3:62-66.

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