

Progress and Variability After Four Cycles of Recurrent Selection in Peanut

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ABSTRACT

Recurrent selection procedures are becoming more popular as a means of population improvement in self-pollinated crops. Four cycles of recurrent selection for yield in a broad-based peanut (*Arachis hypogaea* L.) population have been completed. The objectives of this study were to determine (a) progress made after four cycles of recurrent selection for fruit yield and (b) if sufficient variability remained in the population to permit further improvements in yield from additional cycles of selection. The 40 highest yielding lines from 100 random-paired matings, were intercrossed to produce each successive cycle, resulting in a selection intensity of 40%. Bulk seed of the parental lines from each cycle were evaluated for yield to determine progress made after four cycles of selection. The observed variation in yield among entries was mainly due to differences among cycle means. Differences among cycle means were also detected for pod length, but not for any of the other fruit traits measured. The response to selection for yield was linear with a significant ($p = 0.01$) and positive regression coefficient ($b = 190.7 \text{ kg ha}^{-1}$). Selection based on fruit yield did not

significantly change the means for any of the fruit traits measured. Significant estimates of genetic variability among entries within the cycle 4 population for yield and all fruit traits measured suggest that continued progress from additional cycles of selection should be expected in this population. Greater progress from selection may have resulted had a higher selection intensity been applied. However, estimates of genetic variability would be expected to decrease with each cycle of selection as the selection intensity increases and as the genetic base of the original population narrows. In the use of a broad-based population and a relatively low selection intensity, we chose to accept a lower rate of progress/cycle for yield in order to maintain a greater level of genetic variability within the recurrent selection population.

Key Words: Genetic variability, groundnut, peanut, *Arachis hypogaea*.

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The pure line breeding methods traditionally used in peanut (*Arachis hypogaea* L.) improvement programs impose severe restrictions on the amount of recombination among linked genes during the rapid approach to homozygosity (14). Branch (1), Norden (10), and Wynne and Isleib (15) reported on the use of a number of multiple crossing systems

aimed at increasing variability in the population prior to selection. One such system is that of recurrent selection for population improvement.

Recurrent selection procedures trace back to a common breeding scheme proposed for population improvement in open-pollinated species (12). The scheme was later expanded toward utilization for hybrid breeding with the expectation that a gradual increase in frequency of favorable alleles would occur, thus avoiding rapid fixation of genes that takes place with selfing. By the late 1970s, the definition of recurrent selection had been extended to encompass any cyclical method of intra- or interpopulation improvement in which selection is alternated with recombination. The objective is to find an optimum allocation of available resources and a reasonable compromise between selection intensity and effective population size (12). Recurrent selection programs are now being used as long-term breeding strategies for the development of hybrids, synthetics, homozygous lines, and clones (12). Population improvement *per se* has become the central point of many breeding programs with selection for cultivar development occurring after each cycle.

The two basic concerns of plant breeders using recurrent selection schemes are (a) whether progress is being made in the improvement of a given trait (i.e., short-term objective) and (b) whether adequate levels of genetic variation remain to permit continued progress from selection (i.e., long-term objective) (5). Rawlings (11) demonstrated that reasonably sized recurrent selection programs very nearly satisfy the objectives of maximizing both short- and long-term gains from selection.

Although the use of recurrent selection programs in self-pollinated species increases the opportunity for recombination and expression of new blocks of genes, allowing the breeder to maximize selection progress (6), its application to the improvement of self-pollinators has been limited until recently. The major objections to using recurrent selection in self-pollinated crops have been the number of pollinations required during the recombination phase and the length of time needed to complete a cycle of selection (2). This is especially true in peanut where an average of two seeds are obtained from each pollination. Compton (3) proposed a recurrent selection procedure for self-pollinated species in which a genetically broad-based population is generated by random-mating a number of selected lines and single seed descent procedures are used to extract one random line from each of the crosses. Wynne (13) modified the procedure proposed by Compton and adapted it to peanut, including it as part of a comprehensive breeding program initiated in 1974 at North Carolina State University (9). The base population (cycle 0) of a recurrent selection program was developed by randomly crossing 40 diverse virginia-type peanut cultivars or breeding lines that had been selected for high yield in preliminary yield trials. Each line was used as a parent five times, producing 100 single crosses. After three cycles of recurrent selection, Monteverde-Penso and Wynne (8) reported a significant and linear response to selection for fruit yield. They concluded that the recurrent selection procedure is simple, cost effective, and increased the mean yield of the population. They proposed the use of this procedure as a systematic approach to developing high yielding peanut cultivars with a broader genetic base.

While recurrent selection for fruit yield resulted in gains of approximately 1% per year through three cycles of recurrent selection in the Monteverde-Penso and Wynne study (8), another consideration for effective recurrent selection schemes is the maintenance of adequate variability in the population to allow for continued improvements. The objectives of this study were to use the populations developed by Monteverde-Penso and Wynne (8) to determine (a) progress made after four cycles of recurrent selection for fruit yield and (b) if sufficient variability remained in the population to permit further improvements in yield from additional cycles of selection.

Materials and Methods

Four cycles of recurrent selection for yield in a broad-based peanut population have been completed. The 40 highest yielding lines from 100 random-paired matings were intercrossed to produce each successive cycle, resulting in a selection intensity of 40%.

Bulked seed of the parental lines from each cycle of recurrent selection were evaluated to determine additional progress made from a fourth cycle of selection. The cultivar Florigiant was used as the check genotype as consistent with previous evaluations of cycle progress (8). The experiment was planted in a randomized complete block design with 10 replications at two locations—the Peanut Belt Research Station in Lewiston, NC and the Upper Coastal Plain Research Station in Rocky Mount, NC—in 1989. The traits measured included:

- Yield, in kg ha⁻¹;
- Pod length, in cm (length of 20 random pods);
- Pod weight, in g (weight of 20 random pods);
- Seed number (number of seed from 20 random pods); and
- Seed weight, in g (weight of seed from 20 random pods).

The analysis of variance was computed from cycle means for all traits measured. Two orthogonal contrasts from the partition of the entries sum of squares to compare the check vs. the mean of the cycles (1 df) and among cycle means (3 df) were obtained. In addition, linear and nonlinear contrasts were obtained from the among-cycle sum of squares to test the response to selection over cycles. The means of each variable over environments were regressed on cycles to estimate progress from selection. Estimates of realized heritability were obtained by regression of cumulative response on cumulative selection differential (4). Standard errors of the estimates were obtained by the procedure proposed by Hill (7).

In a separate study the cycle 4 population was evaluated for genetic variability remaining for yield and fruit characters. One hundred entries representing the cycle 4 crosses in the S_{1,3} generation were planted in a randomized complete block design with four replications at two locations, Lewiston and Rocky Mount, in 1988. Two commercial cultivars, Florigiant and NC-V11, were included as checks. The traits measured were the same as for the evaluation of cycle bulks described above. Analyses of variance and Waller-Duncan K-ratios were computed from the entry means for each trait.

Results and Discussion

From the evaluation of cycle bulks, it is apparent that recurrent selection for fruit yield effectively increased the mean yield of the population through two cycles of selection (Table 1). Most of the variation among entries was attributable to differences among cycle means, which showed a highly significant linear response to selection (Table 2). While in this study population yields appear to level off after the second cycle of selection, that was not the case when the first three cycles were evaluated by Monteverde-Penso and Wynne (8). In their study, evaluations were made over 2 years, whereas a single year's evaluation was used in the present study. Such a limitation may have contributed to our failure to detect significant differences in yield among cycles 2, 3, and 4, in spite of the significant linear response observed over all cycles of selection.

The mean yields of cycles 2 and 4 were significantly greater than the mean of the check cultivar Florigiant, while

Table 1. Check vs. cycle means for yield and traits from the first four cycles of recurrent selection in a broad-based population.

Entry	Yield (kg ha ⁻¹)	Pod length (cm)	Pod weight (g)	No. seed 20 pods ⁻¹	Seed weight (g)
Cycle 0 (bulk)	3764.0bc†	73.8ab	48.5a	40a	35.2a
Cycle 1 (bulk)	3458.8c	72.4bc	46.8a	39a	33.8a
Cycle 2 (bulk)	4238.8a	73.3ab	46.5a	39a	34.0a
Cycle 3 (bulk)	4170.9ab	73.8ab	46.5a	40a	34.0a
Cycle 4 (bulk)	4374.4a	74.3a	48.5a	39a	35.6a
Florigiant	3730.1bc	71.1c	47.6a	39a	34.7a
b-value‡	190.7**±71.4	0.24±0.20	-0.04±0.25	-0.08±0.11	0.11±0.20

†Means followed by the same letter are not significantly different from each other.

‡Linear coefficient for regression of trait means across environments on cycles.

the mean yield of cycle 3 was greater but not significantly different from the mean of Florigiant (Table 1). Differences among cycle means were detected for pod length, with all cycles except cycle 1 having a mean pod length significantly greater than that of Florigiant (Table 1). No significant differences were detected among cycle means or between cycle means and the check for any of the other traits measured—pod weight, seed number, or seed weight (Table 1).

The response to recurrent selection for yield was linear across four cycles of selection. The regression coefficient was positive and significantly different from zero ($P = 0.01$)

(Table 1). The estimate of progress from selection was 190 kg ha⁻¹ per cycle. Selection based on fruit yield did not result in significant changes in the means for the other variables measured. The regression coefficients across cycles for pod length, pod weight, seed number, and seed weight were not significant (Table 1). This suggests that recurrent selection for fruit yield has not significantly altered fruit or seed size or the number of seed per pod in this population.

The estimate of realized heritability based on the regression of cumulative response on cumulative selection differential was 0.49 ± 0.36 . This estimate seems reasonable when compared with previous reports for peanut of estimates of

Table 2. Mean squares and variance component estimates for yield and fruit characters over four cycles of recurrent selection.

Source	df	Yield	Pod length	Pod wt	Seed no.	Seed wt	Expected mean square†
Locations (Loc)	1	424.13**	65.21**	19.99	0.26	64.95**	
Rep (Loc)	18	4.10	4.68	7.63	2.73	4.25	
Entries	5	21.90**	26.83**	17.08	2.47	8.59	$\sigma_e^2 + r\sigma_{gl}^2 + rl\sigma_g^2$
Check vs. cycles	1	11.88	92.24**	1.07	1.25	0.16	
Among cycles	4	24.41**	41.92	21.40	2.78	10.70	
Linear	(1)	65.47**	11.49	0.79	1.49	1.87	
Nonlinear	(3)	10.72	10.14	28.26	3.21	13.64	
Loc * Entries	5	4.19	12.35	26.52*	3.52	14.55*	$\sigma_e^2 + r\sigma_{gl}^2$
Loc*(Check vs. cycles)	1	0.63	0.24	0.96	1.44	0.71	
Loc*(Among cycles)	4	5.09	15.37	32.91*	4.04	18.01*	
Error	90	4.73	7.57	10.84	1.87	6.37	σ_e^2
Variance component estimates†							
σ_g^2		0.89	0.72	-0.48(0)	-0.05(0)	-0.30(0)	
σ_{gl}^2		-0.05(0)	0.48	1.57	0.17	0.82	
σ_{Ph}^2		1.10	1.34	0.85	0.12	0.43	

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

† $\sigma_g^2, \sigma_{gl}^2, \sigma_{Ph}^2$ = estimates of genotypic, genotype x location, and phenotypic variation, respectively; $r = \text{no. reps} = 10$; $l = \text{no. locations} = 2$.

Table 3. Mean squares and components of genetic variance for yield and fruit characters in the cycle 4 population.

Source	df	Yield	Pod length	Pod wt	Seed no.	Seed wt	Expected mean square†
Location (Loc)	1	876.84**	204.79**	122.44**	130.92**	82.68**	
Set (Loc)	2	111.38**	26.89*	143.52**	6.13	78.55**	
Rep [Set (Loc)]	12	10.25**	11.64	20.71	4.18	10.68	
Entries (Set)	100	7.96**	68.65**	107.85**	4.85**	56.73**	$\sigma_e^2 + rs\sigma_{gl}^2 + rsl\sigma_g^2$
Loc *Entries (Set)	100	4.61**	13.90	17.92*	3.06	11.50*	$\sigma_e^2 + rs\sigma_{gl}^2$
Error	590	3.34	9.70	13.61	2.87	8.47	σ_e^2

Variance component estimates†

σ_g^2	0.21	6.84	11.24	0.22	5.65
σ_{gl}^2	0.16	1.05	1.08	0.05	0.76
σ_{Ph}^2	0.50	8.58	13.48	0.61	7.09

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

† $\sigma_g^2, \sigma_{gl}^2, \sigma_{Ph}^2$ = estimates of genotypic, genotype x location, and phenotypic variation, respectively; r = no. reps = 4; s = no. sets = 2; l = no. locations = 2.

realized heritabilities for yield of 28 and 32% (8) and narrow-sense heritabilities for yield of 54% (16).

While recurrent selection for fruit yield resulted in gains of approximately 1% per year through three cycles of recurrent selection in the Monteverde-Penso and Wynne (8) study, another consideration for effective recurrent selection schemes is the maintenance of adequate genetic variability in the population to allow for continued improvements to be made. A fourth cycle of recurrent selection was completed since the report by Monteverde-Penso and Wynne (8). When the cycle 4 population was evaluated, significant levels of variability were detected ($P \leq 0.01$) among entries for yield and all fruit traits measured (Table 3). This suggests that adequate variability is present in the recurrent selection population for continued progress from further cycles of recurrent selection, as additional cycles of recombination take place. In the use of a genetically broad-based population to initiate the first cycle of recurrent selection and a relatively low selection intensity, we chose to accept a lower rate of progress/cycle for yield (1%) in order to maintain a greater level of genetic variability within the recurrent selection population.

A greater selection intensity—40% of the lines are retained in the present scheme—may result in a greater response to selection, especially for those fruit characters such as pod length and weight, and seed length and weight, which are typically associated with fruit yield but did not respond to selection for yield in this study. A greater selection intensity would most likely lead to a reduction in variability in the population as fewer lines are retained. If a higher selection intensity is applied to future cycles of recurrent selection leading to declining levels of variability, the inclusion of more diverse genotypes—perhaps of spanish or valencia botanical type—in the subsequent recombination phase would increase the variability present in the population.

While slight decreases in yield may result initially, the opportunity for producing new gene combinations should compensate for the temporary yield decline when the long-term objective of maintaining variability in the population is considered.

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