Selection for Increased Lint Yield and Correlated Responses in Upland Cotton,

Gossypium hirsutum L.[1]

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ABSTRACT

Three cycles of recurrent selection for increased lint yield in Upland cotton (*Gossypium hirsutum* L.) have been completed. Yield of the third cycle selections exceeded that of the base population by 29.7%. Response to selection was linear and is predicted to continue at approximately the same rate of gain for an additional cycle.

Correlated responses to selection for yield were observed for the majority of the unselected traits measured. As selection increased lint yield, simultaneous increases were observed for lint percentage, number of seed per boll, earliness, fiber elongation, and fiber coarseness. Boll size, seed size, and fiber length and strength decreased. Weight of lint per seed showed little change.

There was generally close agreement between predicted and observed responses to selection. This suggests that dominance effects were lacking or of relatively minor importance. Additive genetic effects would appear to predominate in this population, although additive $\times$ additive effects cannot be excluded.

Additional index words: recurrent selection, gene action, linkage, pleiotropy.

ESTIMATES of genotypic variances and covariances in three cotton populations were reported by Miller et al. (1958) and their implications on selection in breeding populations were discussed. Sufficient genetic variability appeared to be present in all populations to realize substantial genetic advance through selection for each of the traits studied. The estimated genotypic covariances also indicated that selection for any one trait would result in correlated responses for many of the unselected traits. Subsequently, selection for lint yield was initiated in the 'Coker 100' $\times$ 'Acala 1517' population in order to evaluate the validity of the original predictions and the adequacy of the genetic interpretation upon which they were based. Three cycles of selection have been completed. We will present the observed and predicted responses in each of the three cycles of selection and discuss the genetic interpretation of the results.

MATERIALS AND METHODS

The population used in this study stemmed from the cross of two inbred lines designated as G-4 and H-1. The former line was selected from the variety Coker 100, a rain-belt Upland cotton having high lint yield but relatively poor quality fiber. The latter was selected from Acala 1517, a western high-quality variety, with low yield under North Carolina conditions. Six generations of a pedigree system of inbreeding preceded the original cross. The base population consisted of 81 lines each of which traced to a randomly chosen F_2 plant and had been increased by bulk self-pollination in the F_3 and F_4 generations.

A recurrent selection scheme based on performance of progenies grown in replicated tests was initiated. Populations grown and the selections made were as follows:

Base population — The F_4 and F_5 generations of the 81 lines were grown in two replicates at each of two environments (an "environment" refers to any single year-location combination).

First cycle selections — The six highest yielding lines, based on their average performance in the F_4 and F_5 generation tests, were selected from the base population. Remnant seed was planted in the nursery and the 15 possible crosses among the six lines (bulking reciprocals) were produced. Flowers from at least 10 plants were used from each line to represent that line in any particular cross.

Second cycle population — Approximately six plants were chosen at random from each of the 15 crosses produced above and self-pollinated to produce seed for progeny tests. A total of 86 progenies were obtained and tested in three or four replicates at each of three environments.

Second cycle selections — The six highest yielding lines were selected and intercrossed as described above to form the third cycle population.

Third cycle population — 90 random plants (six from each of the 15 crosses) were self-pollinated and the progeny tested in two or three replicates at each of three environments.

Third cycle selections — The six highest yielding lines were selected and intercrossed to form the fourth cycle population.

Fourth cycle population — 90 random plants (six from each of the 15 crosses) were self-pollinated and the progeny tested in two or three replicates at each of three environments.

Progeny plots for the base population were single rows, 3.7 m in length and those for subsequent cycles were single rows, 4.6 m in length. A randomized complete block design was used for all tests. Data were recorded on seed cotton yield from all plots. A random sample of 25 bolls was harvested from each plot to provide material for determination of lint percentage and various seed and fiber properties. Lint yield values were calculated by multiplying the total weight of seed cotton per plot by the lint percentage value for that plot. Fiber analyses were made on only a portion of the material, i.e. base population, two replicates from one environment; cycle 2, none; cycle 3, two replicates from each of the three environments; and cycle 4, two replicates from each of two environments. Fiber length was measured on the fibrograph and the data are presented for the upper half mean length (U.H.M.) in millimeters. Fiber fineness, measured by the micronaire (Mic.), represents an approximate ratio of weight per unit length; the larger the value, the coarser the individual fiber. Fiber strength was measured on the Pressley instrument (0 gauge) in the base population and the data are presented in Pressley index units. All subsequent fiber strength evaluations were measured with 3.2 mm (1/8-inch) gauge length on the Stelometer and expressed as grams per tex (T_1). Fiber elongation (E_1) is the measure of elongation at the time of break-loading compared to the initial length; this is expressed as a percentage. Data on seed index (weight in grams of 100 seed), lint index (weight in grams of lint from 100 seed), and number of seed per boll were obtained only on the base population.

Estimates of pertinent variance components, genetic correlation coefficients, and expected response to selection for each cycle were obtained from analyses of variance of the progeny tests described above. Form of analyses, mean square expectations, and appropriate estimation formulae have been previously described by Al Jibouri, Miller, and Robinson (1958). Predicted effects from selecting a superior portion of the progenies were calculated from the formula $k\sigma^2_g / \sigma_{ph}$, where k is

the selection differential in multiples of σ_{ph}, and σ^2_g and σ_{ph} are the estimated genetic component of variance and phenotypic standard deviation, respectively. Variance components for "among progenies" were used as the estimate of the genetic variance (σ^2_g). Expected change in a trait other than the one used as the criterion for selection was calculated from the formula $k\ \sigma_{g_{1.2}} / \sigma_{ph_1}$, where k is as above, $\sigma_{g_{1.2}}$ is the estimated genetic covariance between the selected and unselected traits, and σ_{ph_1} is the estimated phenotypic standard deviation of the selected character. Selection differentials (k values) were 1.89 for selection in the base population (6 of 81 lines selected), 1.92 for selection in the second cycle population, and 1.94 in the third and fourth cycles.

Data on the change in mean performance due to each cycle of selection could not be obtained directly from the above tests because of the confounding effects of years. Thus, observed effects of selection on mean performance were obtained from a second and separate experiment. The six selected progenies from each of the first three cycles had been maintained by bulk self-pollination of a 75-plant progeny row representing each selected line and all had reached at least the F_6 generation of inbreeding. These three sets of six lines, the two original parental lines (G-4 and H-1), and a commercial check variety, Coker 100A, were tested in a randomized complete block design with four replicates at five environments. Plots were single rows, 15.2 m in length. Weight of seed cotton was recorded for all plots, and 50-boll samples harvested from each plot provided the lint and seed material for yield component and fiber property measurements. Fiber analyses were made on only two replicates at each of three environments. Percentage first pick data were recorded in four replicates at each of two environments.

RESULTS

Selection for Yield

The six lines selected from each of the three cycles and the two original parental lines, G-4 and H-1, were compared in the second experiment to evaluate the effectiveness of the selection practiced. The average of the two original parental lines was used as an estimate of the yield of the base population. This assumes additive gene effects. Data for yield are presented in column 1 of Table 1. Significant increases in yield were recorded for each cycle of selection. Yield of the third cycle selections exceeded that of the base population by 29.7% and the high parent (G-4) by 13.0%. The response over the three cycles of selection appeared to be linear (Fig. 1). Yields of the individual third cycle lines ranged from 1055 to 1172 kg/ha, all out-yielding the higher yielding parent (G-4) of the original cross.

Predicted increases in yield computed from the original experiments for each cycle of selection agreed very closely with the observed response (column 1 of Table 2). Further progress from selection for yield might be expected as indicated by the predicted response of 6.1% for selection in the fourth cycle population.
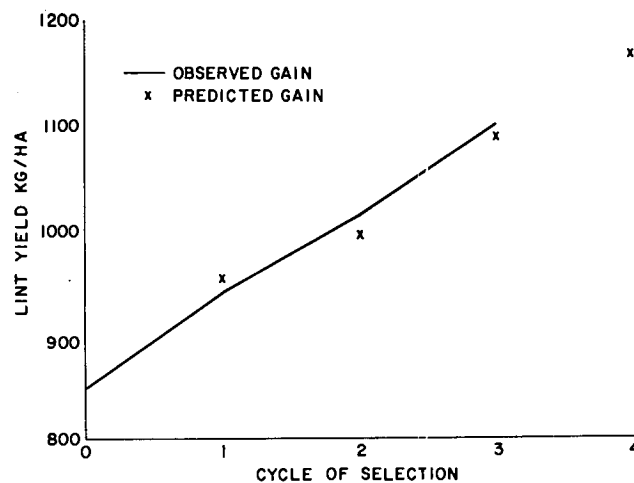

Fig. 1. Observed and predicted response to recurrent selection for increased lint yield.

Genetic variance components for lint yield were estimated from the original experiments for each cycle of selection and are presented in column 1 of Table 3. Values fluctuated rather widely. While there was no evidence of a trend from cycle to cycle, the estimation was not sufficiently precise to be informative on this point.

Estimated genotype $\times$ environmental variance components for yield (Table 3) also fluctuated widely. The estimates are generally of sizeable magnitude relative to the genetic component of variance, indicating the necessity for evaluating lint yield in such material over an adequate sample of environments within the breeding area.

Correlated Response to Selection

As pointed out previously, selection in this population was restricted to a single trait, lint yield. Concurrent with the increase in lint yield, however, substantial changes occurred in the unselected traits (see Table 1). Lint percentage increased. Weight per boll and seed index decreased. Number of seed per boll showed some fluctuation but tended to increase. Lint index showed little change. As measured by the percentage of the total crop harvested at the first picking, the selections became progressively earlier during the successive cycles of selection. Fiber length and strength decreased while fiber elongation increased. There was a slight tendency for micronaire values to increase. All changes from the base population, except for seed per boll, were in the direction of the higher yielding

Table 1. Response to three cycles of recurrent selection for increased lint yield as measured by the performance of the selected strains.

Material	Lint, kg/ ha	Lint, %	Wt./ boll, g	Seed index	Seed/ boll no.	Lint index	1st pick, %	Fiber Length, U.H.M., mm	Fiber Strength, T_1	Fiber Elonga-tion, E_1	Fiber Fine-ness, Mic.
Base population†	849d*	35.2e	6.92b	12.8b	34.6d	7.10ab	80.8ab	30.5b	19.9b	8.2bc	3.97c
Cycle 1 selections‡	941c	35.9d	6.82b	12.0c	36.1b	6.81d	79.3bc	30.2b	19.9b	7.8c	4.13b
Cycle 2 selections‡	1015b	37.5bc	6.71c	11.5d	36.4ab	6.98abc	81.6ab	29.5c	19.0c	8.5b	4.24ab
Cycle 3 selections‡	1101a	38.1a	6.43d	11.2e	35.6c	6.95bc	87.5a	29.5c	18.6d	9.0a	4.16b
Parent, G-4	974bc	36.8c	6.04e	11.8c	32.0e	6.99abcd	83.4ab	29.0c	17.0e	9.4a	4.44a
Parent, H-1	725e	33.7f	7.79a	13.9a	37.3a	7.20a	78.2ab	32.0a	22.8a	6.9d	3.50d
Coker 100A (check)	1077ab	38.1ab	6.53cd	11.3de	35.0cd	7.07ab	71.7bc	30.2b	18.6cd	8.1bc	4.28ab

* Means followed by the same letter cannot be considered significantly different at the 5% level of probability. (Duncan's New Multiple Range Test with adjustments for unequal replication).   † Estimated as mid-parent value of G-4 and H-1.   ‡ Mean of 6 lines.

Table 2. Predicted and observed responses to selection for increased lint yield.[†]

Population	Lint, kg/ha	Lint, %	Wt./ boll, g	Seed index	Seed/ boll, no.	Lint index	Length, U.H.M., mm	Strength, T₁	Elongation, E₁	Fineness, Mic.
Base population: Predicted response, %	+12.4	+6.6	-3.2	-8.4	+1.4	0.0	-1.7	-2.5‡	-	-
Observed response, %	+10.8*	+2.0*	-1.4	-6.3*	+4.3*	-4.1*	-1.0	0.0	-4.9	+4.0*
Cycle 2: Predicted response, %	+ 6.1	+2.9	-0.9	-	-	-	-	-	-	-
Observed response, %	+ 7.9*	+4.5*	-1.6*	-4.2*	+0.6	+2.5*	-2.3*	-4.5*	+9.0	‡2.7
Cycle 3: Predicted response, %	+ 7.4	+1.7	-1.4	-	-	-	+0.8	-2.1	+3.5	-2.8
Observed response, %	+ 8.5*	+1.6*	-4.2*	-2.6*	-2.2*	-0.4	0.0	-1.4*	+5.9*	-1.9
Cycle 4: Predicted response, %	+ 6.1	+0.7	+0.5	-	-	-	-0.7	+0.2	-0.6	+2.3

* Observed response significantly different from 0 at 5% level of probability.   † Predicted responses are expressed as a percentage of the mean of the population in which selection was to be made. Observed responses were computed from the data presented in Table 1 and are expressed as the percentage change observed in the mean performance of the selections from one cycle to the next.   ‡ Pressely index units.

Table 3. Estimates of genetic (σ^2_g) and genetic-environmental interactions (σ^2_{gn}) components of variance and their standard errors.

Population		Lint, kg/ha	Lint, %	Wt./ boll, g	Length, U.H.M., mm	Strength, T₁,(× 100)	Elongation, E₁	Fineness Mic.
Base	σ^2_g	3249± 943	3.49±.65	0.088±.021	1.032±.206	13.7± 2.8*	-	-
	σ^2_{gn}	-137±987	0.70±.19	0.009±.015	-	-	-	-
Cycle 2	σ^2_g	1305± 529	1.62±.26	0.158±.027	-	-	-	-
	σ^2_{gn}	1188± 664	0.14±.04	0.019±.007	-	-	-	-
Cycle 3	σ^2_g	1933± 867	1.62±.28	0.074±.015	0.858±.155	66.8±12.0	0.365±.067	0.0544±.0107
	σ^2_{gn}	6374±1098	0.41±.07	0.036±.008	0.110±.065	6.4± 5.2	-0.023±.036	0.0194±.0060
Cycle 4	σ^2_g	3391±1227	0.71±.12	0.154±.024	0.413±.071	32.4± 7.4	0.199±.046	0.0488±.0086
	σ^2_{gn}	2238±1533	0.08±.04	-0.002±.004	-0.032±.032	4.9± 5.3	-0.020±.036	-0.0004±.0030

* Pressley index units

parent of the cross (G-4). It is of interest to note that for two unselected traits, lint percentage and seed index, the mean values of the six lines selected from the third cycle population were more extreme than either of the two original parental inbreds.

Predicted changes in unselected traits were computed from the original experiments for each cycle of selection and were generally in good agreement with observed response (Table 2). Estimates of genetic variances for the unselected traits (Table 3) show considerable fluctuation in successive cycles, but with the exception of weight per boll show a general tendency to decrease in magnitude with each additional cycle of selection. In contrast to lint yield, genotype × environment interaction variance components are generally very small relative to the corresponding components of genetic variance.

Genetic correlations observed between lint yield and certain of the unselected traits in each of the four cycles of the population are presented in Table 4. In the base population, lint yield was positively correlated with lint percentage and negatively correlated with weight per boll, fiber length, and fiber strength. The magnitude of these correlation coefficients tended to decrease with each additional cycle of intercrossing and selection.

DISCUSSION

The recurrent selection procedure based on replicated progeny tests grown at two or three environments was very effective in increasing lint yield in this population. It should be pointed out that the base population was rather poorly adapted, as measured by lint yield, to North Carolina conditions. This is not surprising, since the H-1 parent of the base population was extracted from material developed in New Mexico under a cotton growing environment which is somewhat different from the Southeast. As noted by comparison with a commercial variety, Coker 100A, the

Table 4. Estimates of genetic correlations between lint yield and various other traits.

Population	Lint, %	Wt./ boll, g	Length U.H.M., mm	Strength T₁	Elongation E₁	Fineness Mic.
Base	0.87	-0.46	-0.33	-0.34*	-----	-----
Cycle 2	0.69	-0.12	-----	-----	-----	-----
Cycle 3	0.43	-0.27	0.21	-0.26	0.39	-0.46
Cycle 4	0.25	0.08	-0.28	0.05	-0.10	0.40

* Pressley index units.

three cycles of selection have increased the mean yield of the selected lines up to or slightly above the yield of this adapted variety. A substantial amount of residual genetic variance for lint yield persists in the population, as indicated by the estimated genetic variance component for the fourth cycle material. Response to the first three cycles of selection was linear and the response to selection in the fourth cycle population is predicted to continue at approximately the same rate of gain. These observations agree with Manning (1963), who reported on a selection index technique for yield in cotton which was used in self-fertilized material for 12 generations. The magnitude of the genetic variability which persisted in this material was sufficient to lead to continued appreciable yield improvement.

Correlated responses to selection for yield were observed for all of the unselected traits measured. Furthermore, these responses were generally of sizeable magnitude. Plant breeders must be concerned with the total array of economic characteristics, not just one trait. Thus the importance of knowing how change in one character by selection may cause simultaneous changes in other economic traits is self-evident. The close agreement betweeen the predicted changes in the unselected traits and the changes actually observed indicate the utility of the prediction formula for such plant breeding situations.

Almost all changes from the base population for unselected traits were in the direction of the higher

yielding parent. This suggests linkage and pleiotropy as possible causal factors for the correlated responses. Selection for "high-yield genes" contributed by the G-4 parent could also result in selection of linked genes affecting the unselected traits, or, as an additional possibility, the "high-yield" genes themselves might have pleiotropic effects. There appeared to be some tendency for the genetic correlations between traits to decrease in magnitude with successive cycles of intercrossing (Table 4). To this extent, linkage would be indicated as a factor contributing to the initial correlated responses. Miller and Rawlings (1967) reported decreased genetic correlations in a cotton population following several cycles of intercrossing, suggesting that intercrossing tends to break up initial linkage blocks following a cross between inbred lines. A similar response may be operating in this population.

Since the only selection applied was for increased lint yield, we might also suppose that the unselected traits would tend to move towards optimum values for maximum yields, especially those traits which are components of lint yield. Lending support to this hypothesis, which might be considered as pleiotropy, is the observation that the characteristics of the third cycle selections tended to be more similar to the adapted and high yielding variety, Coker 100A, than to the high-yielding parent, G-4 (Table 1). Coker 100A was developed from repeated selection within a varietal type over a number of generations with major emphasis on increased yield. Perhaps similar selection pressure in the two populations has resulted in an array of unselected traits with similar values approaching an optimum for high lint yield. Observations that lint percentage and seed index of the third cycle selections were significantly more extreme than either of the parents lends further support to this hypothesis.

There was generally close agreement between predicted and observed responses to selection in this experiment. Predicted reponses from each cycle were based on the total genetic variance among progeny of randomly chosen plants which could include additive, dominance, and epistatic effects. Observed responses were measured by comparing the performance of lines selected from successive cycles and which had then been bulk inbred without further selection to at least the F_6 generation. Superiority (or change in the case of traits other than yield) of these selected inbred progenies over the mean of the population from which they were selected could be due to only the additive and a portion of the additive $\times$ additive effects of the original total variance. Any superiority or change

of the original selections due to dominance or dominance interaction effects would have been lost as the selections were inbred. Close agreement between predicted and observed responses thus suggests that dominance effects were lacking or of relatively minor importance. Additive genetic effects would appear to predominate in this population, although additive $\times$ additive effects cannot be excluded.

The relatively large magnitude of the estimated genetic - environmental interaction variance components for lint yield indicates the importance of evaluating material at more than one environment before making selections. Undoubtedly the agreement between predicted and observed response would have been much poorer if the material had been tested at only one environment. The estimated genetic variance components used in the predictions were unbiased with respect to genotype $\times$ environment interactions. Genotype $\times$ environment interactions would appear to be of only minor importance for traits other than yield.

The extent to which the results observed in this particular population might also apply to other breeding populations is not known. Estimated variance and covariance components of this base population were generally similar to estimates reported for two additional cotton populations of independent origin (Miller et al., 1958). Moll and Robinson (1966), using models based on genetic interpretations similar to those used here, reported good agreement between observed and expected response for yield in maize. Certainly a considerable amount of additional information is needed, however, before generalizations can be made.

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