Multidirectional Selection for Fiber Strength in Upland Cotton[1]

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ABSTRACT

Selection experiments are usually conducted in one or two directions, whereas studies involving multidirectional selection are rare. This multidirectional selection experiment for T_1 fiber strength was conducted through five cycles within a genetically variable population of upland cotton (*Gossypium hirsutum* L.) to investigate the direct and correlated responses to selection for that trait. The original population was a mixture comprised of equal amounts of mature F_2 seed from 45 crosses. The stronger-fibered 10% of the plants, as well as the weaker-fibered 10%, were selected within each population in each cycle. Selfed seed from selected plants were used to form new populations for testing and further selection. Analyses of variance detected significant differences among populations for all traits in selection cycles 3, 4, and 5, except for fiber fineness in cycle 4. No genotype × environment interactions were detected for T_1 fiber strength. Selection for fiber strength was effective. After four cycles of selection under enforced self-pollination, half the populations still possessed sufficient genetic variability to show a significant selection response in the fifth selection cycle. One generation of reverse selection for fiber strength was often followed by dramatic increases in variability and in subsequent selection response; however, two or more low-strength selections had a detrimental effect on later selections for high fiber strength. Selection for stronger fiber tended to result in lower picked and pulled lint percents; increased 2.5 and 50% span lengths, uniformity index, T_0 fiber strength, and earliness; and variable response for lint yield and fiber fineness.

Additional index words: Gossypium hirsutum L., Selection response, Correlated response, Realized heritability, Lint yield, Lint percent, Fiber length, Fiber length uniformity, Fiber fineness, Earliness.

A LLAN and Robertson (1964) developed a theoretical basis for interpreting selection experiments where several generations of reverse selection were followed by renewed forward selection to the limit using constant selection intensities and population sizes. Their model was idealized in that it used a population that guaranteed symmetrical responses for the two-way selections during early generations. They found that resumption of forward selection in the reverse line would converge on the line continuously selected forward if the initial gene frequency were greater than 0.5 and diverge if less than 0.5. They also demonstrated that it would be impossible after *n* generations (the actual number based primarily upon population size) to return to the original starting point using the same population size and selection intensity.

The Illinois oil and protein selection study in corn (*Zea mays* L.), begun in 1896, has set the standard for long-term, two-way selection studies in crop plants. Winter (1929), reporting on the first 28 yrs of selection in that study, indicated that the high protein and high oil lines appeared to have no limit to their future progress. The low protein line had remained fairly constant for the last 20 yrs, and the low oil line was apparently approaching a physiological limit to further decline.

After 50 generations of selection, Woodworth et al. (1952) reported that progress was still being made in the low protein and high oil lines, while the high protein and low oil lines had failed to respond for some 15 generations. Two generations of reverse selection indicated that especially the high oil line, but also the high and low protein lines, still possessed a considerable amount of genetic variability. After 65 generations of selection, Dudley and Lambert (1969) detected a significant amount of genetic variability in all populations, indicating that additional progress should be possible in each, but that the low oil line may have reached its physiological limit. Oil and protein contents displayed small, but positive, correlated responses; the magnitude of those responses varied with direction of selection.

Ceccarelli et al. (1980a) conducted a divergent selection study, including reverse selection, in an ecotype of perennial ryegrass (*Lolium perenne* L.) for dry matter yield (DMY). Selection for high DMY was more effective than for low. Reverse selection for low DMY in the high population produced no significant response, while selection for high DMY in the low population was effective. Taking cumulative selection differentials as the reference point, a symmetrical response pattern was obtained in both directions. The authors interpreted the symmetrical response patterns as indirect evidence that inbreeding depression was negligible. A subsequent paper by Ceccarelli et al. (1980b) showed that selection for DMY did not affect leaf size and produced asymmetrical correlated responses on the rates of tiller production and leaf appearance. Selection for high DMY increased the rate of tiller production without changing the rate of leaf appearance, while selection for low DMY decreased both.

Altukhov et al. (1976) studied the effects of modal vs. directional selection in cotton (*Gossypium hirsutum* L.) and concluded that modal selection in general reduced variability within the population. It improved the population relative to the control and improved the two selected populations for a number of economic traits, especially "suitability for mechanized harvest" and "wilt resistance".

The objectives of our experiment were to investigate the direct and correlated responses to multidirectional selection for T_1 fiber strength through five cycles within a genetically variable population of upland cotton. Verhalen and Murray (1967, 1969) and Verhalen et al. (1971) reported genetic analyses for the seed source used to construct the initial population of this study. A narrow-sense heritability for T_1 fiber strength of 0.62 was estimated in the F_2 with gene action in the partial dominance range. Fiber length had a narrow-sense heritability of 0.49 in the F_2 with long fiber being partially dominant over short, while fiber fineness displayed a narrow-sense heritability of 0.19 and overdominant gene action. Lint yield, lint percent, and earliness were governed by overdominance in the F_2 with no epistasis; and estimates of heritability ranged from 0.15 to 0.31.

Relative stability for fiber strength of cotton over years, locations, or both in Oklahoma has been reported by Murray and Verhalen (1970). The only significant genotype × environment (GE) interaction found was for cultivars × years; however, that variance component was only 14% as large as the cultivar component. A confounded GE study (one location, 2 yrs) of the parental material used in this study was unable to demonstrate a significant years × parents mean square for fiber strength (Verhalen and Murray, 1969).

Miller et al. (1958) reported genotypic correlations in cotton between fiber strength vs. lint yield (−0.01 to −0.34), lint percent (−0.24 to 0.07), fiber length (−0.23 to 0.33), and fiber fineness (−0.31 to 0.06) with similar phenotypic correlations. Woodward and Malm (1976) did not detect significant phenotypic correlations between fiber strength vs. lint yield, lint percent, fiber length, or fiber fineness. Quisenberry et al. (1975) showed fiber strength and length to be unrelated in their populations; whereas, fiber strength and fineness were closely and positively related. A recurrent selection program by Miller and Rawlings (1967b) for increased lint yield demonstrated a decline in fiber strength as yield increased and a general decline in genetic variances for most unselected traits. Results presented by Scholl and Miller (1976) agree with previous determinations that lint yield and fiber strength were negatively correlated in cotton. Strength was also negatively correlated with lint percent and fiber fineness, but positively related to fiber length. Miller and Rawlings (1967a) obtained results suggesting linkage as contributing to that negative association. Six generations of intermating in an isolation block with approximately 50% self-fertilization changed the genetic correlation between lint yield and fiber strength within their population from −0.69 to −0.35. Similar results by Meredith and Bridge (1971) and by Culp et al. (1979) corroborate their findings.

MATERIALS AND METHODS

During the winter of 1964–1965, crosses were made among the entries 'Paymaster 101', 'Gregg', 'Western Stormproof', 'Lankart 57', 6-77, 'Deltapine 45', 'Coker 100A WR', 'Acala 44', 'Stoneville 7', and 'Auburn M' (Verhalen and Murray, 1967, 1969; Verhalen et al., 1971). All entries were cultivars of cotton except 6-77, which was a selection for bacterial blight [*Xanthomonas campestris* pv. *malvacearum* (Smith) Dye] resistance in the cultivar 'Stormproof No. 1'. All 45 possible F_1s (ignoring reciprocals) among the 10 entries were subsequently self-pollinated to produce F_2s.

In 1968, a mixture of 100 mature, undamaged F_2 seed from each of the 45 populations was planted in a block at Perkins, OK, on a Teller loam soil (fine-loamy, mixed, thermic Udic Argiustoll). Rows were spaced 1.0 m apart, and plants within rows were thinned to 30 cm apart. All competitive plants (i.e., plants not bordering alleys or skips within the row) were selfed, and those plants (approximately 100) that retained one or more selfed bolls at the end of the season were individually harvested after frost. Fiber strength was measured with the stelometer as T_1 on lint from mature, open-pollinated bolls in the Oklahoma State University Cotton Quality Research Laboratory at Stillwater. Ten percent of the harvested plants were chosen from each end of the population distribution, resulting in a high (H) and a low

(L) selected population. The selfed seed from the selected F_2 plants within each population were then bulked, delinted, and planted in 1969 at Perkins. After frost (and using the same criteria as before), approximately 100 F_3 plants were harvested; and those from the upper and lower 10% of the distribution were again selected for fiber strength within each population. This resulted in four populations (i.e., HH, HL, LH, and LL); and as before, the selfed seed from the selected plants within each group were bulked. The same selfing, selection, and bulking pattern was followed in 1970 (F_4), 1971 (F_5), and 1979 (F_8), which resulted in 8, 16, and 32 populations, respectively. In 1973, F_6 seed from the fourth selection cycle (16 populations) were planted, selfed, and harvested without selection to increase the seed supply. Remnant F_7 seed from that 1973 increase were again planted, selfed, and harvested without selection in 1976 for the same reason.

All replicated field trials were planted at Tipton, OK, on a Tipton silt loam soil (fine-loamy, mixed, thermic Pachic Argiustoll) in a randomized complete block experimental design with single row plots 9.1 m in length and 1.0 m apart. Plants within rows approximated a commercial spacing. The first trial evaluating the third selection cycle (i.e., HHH, HHL,. . ., LLL) was conducted in 1973 with five replications and repeated in 1974 with four. The fourth selection cycle (i.e., HHHH, HHHL,. . ., LLLL) was evaluated in 1975 with five replications and again in 1979 with four. The fifth selection cycle (i.e., HHHHH, HHHHL,. . ., LLLLL) was evaluated in 1980 with six replications.

Lint weights per plot from the replicated tests were converted into kilograms per hectare. Fifteen mature bolls, from the midportion of the plant, were randomly sampled from each plot. Those samples were ginned on an eight-saw gin, and their lint properties were measured in the Cotton Quality Research Laboratory. From data collected while ginning, picked lint percent (lint weight as a percentage of seed cotton weight) and pulled lint percent (lint weight as a percentage of the combined weights of seed cotton and bur) were calculated. In the Cotton Quality Research Laboratory, the digital fibrograph was used to measure 2.5 and 50% fiber span lengths converted to millimeters. Uniformity index was computed as the ratio of 50 to 2.5% span length expressed as a percentage. Fiber fineness was measured on the micronaire in standard curvilinear micronaire units. Fiber strength was estimated with the stelometer using 0-inch (0.0 mm) gauge (T_0) and also 1/8-inch (3.175 mm) gauge (T_1) measurements converted into kilonewton meters per kilogram. The experiments in 1973 and 1974 were harvested twice (all others were harvested once); therefore, estimates of earliness measured as percent first harvest [(lint weight from the first harvest/combined lint weights from both harvests) × 100] were calculated in those experiments.

Response to selection for fiber strength in a population was measured as the difference between the mean performance (estimated from a replicated trial) of the high vs. low selections from that population. Correlated response to selection was measured in the same manner; but it refers to traits for which selection was not practiced. Realized heritability estimates for fiber strength were calculated using Falconer's (1981) formula: R/S, where R represents the actual response to selection (estimated from replicated trials) and S represents the selection differential (i.e., the difference between the means of the high vs. low selection groups obtained from a population at the time selections were made).

Analyses of variance were conducted for all traits in each replicated trial. Selection cycles 3 and 4 were each evaluated in 2 yrs. Sums of squares attributable to populations were partitioned into a set of orthogonal contrasts to evaluate

differences between high vs. low selections within a population. A nonorthogonal set of contrasts was also made in the T_1 fiber strength analyses to investigate possible differences within a selection cycle among populations having an equal number of high (H) selections in their pedigree (ignoring order). All contrasts were appraised for statistical significance using an F test, assuming a fixed model.

RESULTS AND DISCUSSION

Analyses of variance over years for selection cycle 3 (Table 1) showed significant differences among populations for T_1 fiber strength and for all other traits investigated. The variation attributable to years was likewise significant for all traits. The populations $\times$ years interaction was used as an indicator of GE interaction, though the term is confounded with a location effect. Using that criterion, the relative performance of T_1 fiber strength, the trait for which selection was practiced, was stable over the 2 yrs of testing. Among the other traits investigated, only lint yield and pulled lint percent exhibited significant interaction terms in selection cycle 3.

Table 1 also contains the analyses for selection cycle 4 populations over years. Highly significant differences were detected among populations for all traits except fiber fineness, while the effects due to years were significant for all but pulled lint percent and fiber fineness. The significant interactions in the cycle 4 analyses included lint yield and all of the fiber properties except T_1 fiber strength. Analyses of variance for the cycle 5 selections (not shown) exhibited significant differences among populations for all traits studied.

The data used to construct Fig. 1 were adjusted for year effects in the manner described by Patterson (1950). Data in cycles 0 through 2 were estimated by assuming that high-low selections within a population were equally effective and by averaging all succeeding populations that originated from that point within each cycle (3 through 5), then averaging over cycles. The data in cycles 3 through 5 are adjusted means from replicated field trials, with cycles 3 and 4 being averaged over two environments each. Single values are shown in the figure because the interaction terms with environments for the selected trait were not significant.

Previous work in this germplasm indicated that fiber strength was primarily additive, but that some dominant alleles increased strength while others decreased it (Verhalen and Murray, 1969). Continuous forward selection in a population with unidirectional dominance would be expected to decrease genetic variability by increasing the frequency of genes favorable to the direction of selection. Conversely, in a population without unidirectional dominance, we speculate that the variability gained through practicing reverse selection and shifting gene frequency in the opposite direction could allow subsequent forward selections in those populations to approach or exceed the magnitude of the continuously forward-selected populations. This situation appears to have occurred in the third cycle with the LHL and LLL populations (Fig. 1). The continuously high selected population was apparently not affected in this manner until the fourth cycle when the HHLH, HLHH, HLHL, and HHHL populations were near, or greater than, HHHH. Reverse selection practiced in HH and HHH were followed by dramatic increases in variability and selection response. Large responses were also observed in LH, LHHL, and LLHL. One explanation for these observations may be that effective selection was being practiced in a variable population that contained numerous genes governing large dominant effects for both strong and weak fiber, but that homozygosity was rapidly being approached in many of the dominant loci involved. A reverse selection may have shifted the gene frequency back toward a point of higher selection effectiveness. A single generation of reverse selection could increase genetic variability in the same manner as relaxation of selection pressure for several generations in *Drosophila* (Falconer, 1981). Subsequent selections would display increased effectiveness.

The general slope of the line formed by the continuously high selected populations is approximated by that connecting the L population to the LHHHH. This suggests that variability for high strength was not drastically decreased by one generation of low selection. The line connecting the LL and LLHHH populations exhibits a flatter slope while that connecting the LLL and LLLHH is flatter still. These trends imply that the frequency of genes for high strength declined

Table 1. Analyses of variance for T_1 fiber strength selections for selection cycles 3 and 4.

				Mean squares							
Source	df	T_1 fiber strength	Lint yield	Lint percent		Fiber span length		Uniformity index	Fiber fineness	T_0 fiber strength	Earliness
				Picked	Pulled	2.5%	50%				
Cycle 3 (1973 and 1974)											
Reps in years	7	5.79**	6 222	4.67	12.03†	0.4091	0.4158†	4.04**	0.31**	6.09†	304.49**
Populations (P)	7	24.80**	30 460**	21.93**	17.75**	7.4919**	2.6660**	7.68**	0.20*	29.12**	769.21**
Years (Y)	1	15.90**	2 423 829**	112.17**	276.50**	75.4490**	29.8921**	28.93**	1.41**	19.60*	8 671.06**
P × Y	7	1.31	47 816**	5.16	16.36*	0.6396	0.1760	1.52	0.12	1.47	106.90
Error	49	1.75	6 031	4.36	5.86	0.6286	0.2102	1.04	0.09	3.27	83.93
Cycle 4 (1975 and 1979)											
Reps in years	7	6.36**	10 736	3.81	0.92	1.0076**	0.7389**	7.59**	0.10†	15.85**	–‡
Populations (P)	15	41.16**	35 662**	23.20**	16.30**	15.8089**	5.4032**	10.83**	0.04	37.97**	–
Years (Y)	1	15.55**	293 508**	10.78†	0.83	189.4365**	55.0572**	18.45**	0.09	3 127.08**	–
P × Y	15	2.12	17 424*	3.59	1.95	1.1481**	0.4284**	2.31†	0.16**	5.83**	–
Error	105	1.48	8 716	3.11	2.13	0.3235	0.1894	1.47	0.06	2.23	–

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Significant at the 0.10 probability level.
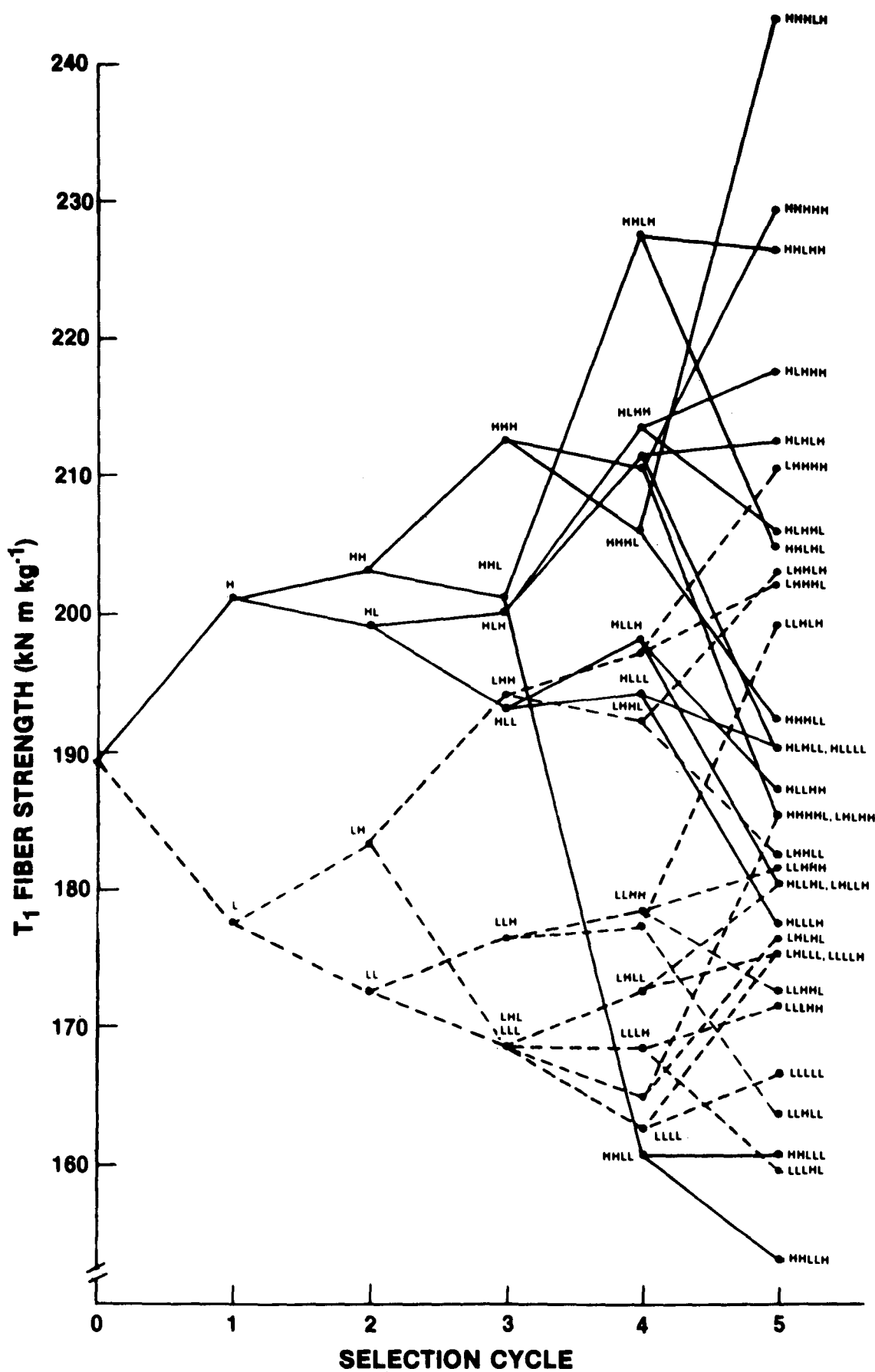‡ Trait not estimated in 1975 or 1979.

Fig. 1. Response to five cycles of multidirectional selection for high (H) and low (L) T_1 fiber strength.

Table 2. Direct and correlated responses to selection for high (H) and low (L) T_1 fiber strength within the second selection cycle populations.

| Popula-tions | T_1 fiber strength | Lint yield | | Lint percent | | | Fiber span length | | Uniformity index | Fiber fineness | T_0 fiber strength | Earliness |
| | | 1973 | 1974 | Picked | Pulled | | 2.5% | 50% | | | | |
					1973	1974						
	kN m kg^{-1}	— kg ha^{-1} —			%		— mm —		%	units	kN m kg^{-1}	%
HH‡	10.8†	160**	117*	−1.9†	−2.2*	−1.5	−0.26	0.45*	2.1**	−0.05	9.8	8.5*
HL	6.9	164**	1	0.2	0.3	0.8	0.78*	0.36	−0.1	−0.19	5.9	−5.8
LH	24.5**	−114*	219**	−1.6†	−3.2**	−3.3	0.62†	0.73**	1.7**	0.28*	−2.0	18.1**
LL	6.9	−200**	61	−3.0**	−3.2**	−1.9	−0.04	0.33†	1.5**	−0.02	−17.7†	10.8*

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Significant at the 0.10 probability level.
‡ Responses in population HH in cycle 2 are measured by differences in populations HHH and HHL in cycle 3, etc.

Table 3. Direct and correlated responses to selection for high (H) and low (L) T_1 fiber strength within the third selection cycle populations.

| Popula-tions | T_1 fiber strength | Lint yield | | Lint percent | | Fiber span length | | | | Uniformity index | | Fiber fineness | | T_0 fiber strength | |
| | | 1975 | 1979 | Picked | Pulled | 2.5% | | 50% | | 1975 | 1979 | 1975 | 1979 | 1975 | 1979 |
						1975	1979	1975	1979						
	kN m kg^{-1}	— kg ha^{-1} —		— % —				mm		— % —		— units —		— kN m kg^{-1} —	
HHH‡	3.9	−77	−15	−0.9	−0.9	0.58†	0.38	0.03	0.15	−1.0	−0.1	0.14	0.00	12.8	27.5*
HHL	65.7**	24	−46	−4.1**	−3.4**	3.53**	4.55**	2.21**	2.36**	2.2**	0.9	0.18	−0.02	60.8**	73.6**
HLH	2.0	−40	161*	0.1	0.5	0.61*	−0.10	0.25	−0.05	−0.1	0.0	−0.08	0.13	11.8	21.6†
HLL	3.9	77	−37	1.8*	1.8**	−0.13	−1.12*	0.05	−0.25	0.4	1.0	0.24†	0.00	7.8	32.4**
LHH	4.9	−28	−80	−0.5	−0.3	−0.41	−0.20	0.18	−0.28	1.4†	−0.7	0.08	−0.08	9.8	−14.7
LHL	−8.8	92†	−89	−4.3**	−2.0**	0.86**	0.51	0.31	0.41	−0.3	0.6	0.06	0.22	27.5**	−8.8
LLH	1.0	26	104	1.5†	0.5	0.08	0.25	0.41	0.31	1.7*	0.7	−0.10	−0.05	−13.7	−6.9
LLL	6.9	123*	25	0.4	−0.3	0.97**	−0.91†	0.61*	−0.13	0.6	1.1	−0.06	0.02	20.6*	23.5*

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Significant at the 0.10 probability level.
‡ Responses in population HHH in cycle 3 are measured by differences in populations HHHH and HHHL in cycle 4, etc.

as two or more selections for weaker fiber were practiced. Similar trends were not detected in the populations selected initially for strong fiber.

The nonorthogonal partition of the populations sum of squares for fiber strength (not shown) indicated that the order in which the high and low selections were made in constructing the populations of selection cycle 3 affected a population's performance in 1973, but not in 1974. Both evaluations of cycle 4 and the single evaluation of cycle 5 indicated that the order in which high and low selections were made in a pedigree, in general, affected the performance of the populations.

Phenotypic correlations with T_1 fiber strength in the original, unselected population were calculated for all traits upon which data were available. Positive correlations ($P < 0.01$) were found for T_1 vs. 2.5 and 50% span lengths and uniformity index (0.32, 0.51, and 0.30, respectively), while a value of -0.17 ($P < 0.05$) was found for T_1 vs. fiber fineness.

Values in Table 2 are shown as high minus low mean deviations and are presented within or over years as indicated by the interaction mean squares in the analyses of variance (Table 1). The data indicate that effective selections in cycle 2 for T_1 fiber strength were made in the HH and LH populations, but not in HL or LL. The 1973 data of cycle 3 show that selections for higher strength positively influenced the direction of yield response in two populations, but had a negative effect in the other two. The trend was the same for HH in 1974, but reversed for LH. Picked lint percent declined with high strength selections in three of four populations as did pulled lint percent in 1973. No significant differences were detected for pulled lint percent in 1974. Selection for stronger fiber also ex-

hibited a tendency to increase 2.5% span length in two populations and 50% span length in three of four populations. Uniformity index increased in the HH, LH, and LL populations, while fiber fineness was significantly affected in only one. The T_0 fiber strength changed significantly only in the LL population, and it was in the negative direction. This negative response in T_0 was unexpected because T_0 and T_1 are both measures of fiber strength. Selection for stronger fiber favored earliness in three of four populations.

Selections practiced for T_1 fiber strength in the third cycle populations (Table 3) were effective only in the HHL population. Correlated responses for lint yield were largely nonsignificant, although three significant increases were detected over the 2 yrs. Both picked and pulled lint percents showed significant decreases in HHL and LHL. A positive correlated response was detected in HLL for both lint percents, while only picked lint percent displayed that response in LLH. The 2.5% span length showed five increases with stronger fiber selection in 1975, but only one increase and two declines in 1979. The 50% span length exhibited two positive, significant responses in 1975 and one in 1979. Three positive responses in 1975, but none in 1979, were detected for uniformity index. Fiber fineness was relatively unaffected although one significant, positive response was found in 1975. The T_0 fiber strength significantly increased in three populations in 1975 and in five of eight in 1979.

Data from T_1 fiber strength selections made in the fourth selection cycle populations (Table 4) indicate that considerable genetic variability remained in the populations. Significant increases were found in eight populations, while a significant decline was noted in

Table 4. Direct and correlated responses to selection for high (H) and low (L) T₁ fiber strength within the fourth selection cycle populations.

Populations	T₁ fiber strength	Lint yield	Lint percent		Fiber span length		Uniformity index	Fiber fineness	T₀ fiber strength
			Picked	Pulled	2.5%	50%			
	kN m kg⁻¹	kg ha⁻¹	%		mm		%	units	kN m kg⁻¹
HHHH‡	44.1**	−130**	−2.8**	−4.1**	0.71†	1.55**	4.5**	0.25	−10.8
HHHL	52.0**	−75*	−1.8†	−2.9**	0.69	0.89**	2.2**	−0.12	25.5*
HHLH	21.6**	−57†	−1.8†	−2.7**	0.33	0.33	0.6	−0.10	18.6†
HHLL	−7.8	−6	0.7	0.2	0.38	0.33	0.8	−0.23	11.8
HLHH	11.8†	−75*	−1.4	−1.8†	−0.03	0.36	1.3	0.03	77.5**
HLHL	22.6**	61†	1.9*	0.8	1.04*	1.25**	2.8**	0.22	−6.9
HLLH	6.9	70*	−0.3	0.1	0.51	0.13	−0.4	0.08	−3.9
HLLL	−12.8†	29	0.2	0.3	−1.70**	−0.53†	1.2	0.05	23.5*
LHHH	8.8	−45	−0.5	0.2	0.46	0.13	−0.4	0.07	20.6*
LHHL	20.6**	−110**	−2.0*	−1.6	0.74†	0.25	−0.4	−0.01	−5.9
LHLH	8.8	−9	−0.4	1.4	0.46	0.69*	1.8*	0.45*	−3.9
LHLL	5.9	64†	−4.3**	−2.2*	1.32**	0.79**	0.7	0.03	37.3**
LLHH	8.8	3	1.3	0.4	−0.74†	−0.08	1.1	0.10	16.7
LLHL	35.3**	26	−0.7	0.3	1.30**	0.97**	1.5†	−0.20	10.8
LLLH	11.8†	14	−0.5	−1.9*	0.94*	0.10	−1.4†	−1.04**	−7.8
LLLL	8.8	7	−2.5**	−1.4	0.99*	0.46	0.1	0.10	7.8

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Significant at the 0.10 probability level.
‡ Responses in population HHHH in cycle 4 are measured by differences in populations HHHHH and HHHHL in cycle 5, etc.

Table 5. Realized heritability estimates and standard errors for T₁ fiber strength.

Cycle 0	Cycle 1	Cycle 2		Cycle 3		Cycle 4
		1973	1974	1975	1979	1980
Base 0.89‡	H 0.00	H 0.11 ± 0.10§	0.23 ± 0.16	H −0.13 ± 0.17	0.35 ± 0.13**	H 0.74 ± 0.11** L 0.87 ± 0.11**
				L 0.70 ± 0.10**	0.80 ± 0.08**	H 0.30 ± 0.09** L −0.22 ± 0.18
		L 0.12 ± 0.09	0.07 ± 0.16	H 0.11 ± 0.15	−0.04 ± 0.12	H 0.22 ± 0.13† L 0.43 ± 0.13**
				L 0.10 ± 0.20	0.07 ± 0.17	H 0.13 ± 0.12 L −0.30 ± 0.16†
	L 0.41	H 0.29 ± 0.10*	0.50 ± 0.17†	H 0.24 ± 0.16	−0.05 ± 0.13	H 0.18 ± 0.14 L 0.43 ± 0.14**
				L −0.37 ± 0.21†	−0.02 ± 0.17	H 0.26 ± 0.20 L 0.13 ± 0.15
		L 0.03 ± 0.12	0.22 ± 0.20	H 0.00 ± 0.18	0.06 ± 0.15	H 0.19 ± 0.15 L 0.77 ± 0.15**
				L 0.23 ± 0.17	0.02 ± 0.13	H 0.28 ± 0.16† L 0.20 ± 0.16

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Significant at the 0.10 probability level.
‡ Response in the heritability formula in cycle 0 is measured by the difference in populations high (H) and low (L) in cycle 1, etc.
§ SE = [(2 error mean square)/r]½/S where r = no. of reps and S = selection differential.

one. Eight of the 16 populations showed significant changes in lint yield due to selection for fiber strength; five were negative, three positive. Six of seven populations showing significant differences in picked lint percent were negative, while all six significant changes in pulled lint percent were negative. Seven of the nine significant changes in 2.5% span length were increases in fiber length with selection for stronger fiber while six of seven significant deviations in 50% span length were increases. Uniformity index significantly increased in five populations and decreased in another. Only two significant responses were detected for fiber fineness; one was positive, the other negative. All six significant differences for T₀ fiber strength were in the positive direction.

Falconer (1981) indicates that the validity of the heritability estimates presented in Table 5 is based on the assumptions that observed selection response is not confounded with systematic changes in generation means due to environment or to the effects of inbreeding and that maternal effects are absent. However, Fal-

coner (1981) does indicate that regardless of the validity of the estimates as narrow-sense heritabilities, the values obtained provide excellent descriptions of selection effectiveness. Therefore, the best use of these realized heritabilities may be to evaluate selection effectiveness because severe inbreeding in the form of self-pollination was imposed throughout the study.

The estimates in Table 5 follow the trends exhibited in Fig. 1 and in Tables 2 through 4. In cycle 2, the LH estimate is the only one differing from zero at the 0.10 or lower probability level, and it is the population exhibiting the most response to selection. The same can be said of the HHL population in cycle 3. The HHH and the LHL populations were each significant in 1 of the 2 yrs. The HHHH, HHHL, HHLH, HLHH, HLHL, HLLL, LHHL, LLHL, and LLLH populations in cycle 4 were significant. In two populations (i.e., LHL and HLLL) the responses were in the negative direction. Both were significant at only the 0.10 probability level and could well represent Type I errors.

Half the populations derived in this study still

showed a significant response to selection for T_1 fiber strength in the fifth selection cycle. Normally, plant breeders would not select that many times for a trait that is primarily additive in inheritance and does not display GE interaction. Perhaps, fiber strength could be improved in other populations by more numerous selections. After one generation of reverse selection for fiber strength, a very large response often followed in subsequent selections. An explanation for this unexpected response could be that the original population possessed some dominant alleles that increased and some that decreased fiber strength (Verhalen and Murray, 1969). Reverse selection could retard genetic fixation caused by inbreeding, thus allowing following selections to be more effective. Two or more low-strength selections appeared to decrease the number of genes for strong fiber since later selections for high fiber strength were detrimentally affected. Selection for stronger fiber tended to result in lower picked and pulled lint percents; increased 2.5 and 50% span lengths, uniformity index, T_0 fiber strength, and earliness; and variable response for lint yield and fiber fineness.

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