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Effects of Recurrent Seed Irradiation on Genetic Variability and Recombination in Cotton (*Gossypium hirsutum* L.)[1]

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ABSTRACT

The effect of five cycles of seed irradiation with 10 kr of γ-rays per cycle on the means, variances, and covariances of a synthetic variety of cotton (*Gossypium hirsutum* L.) was studied.

Means were lower after the treatment for the traits previously selected for high values and were higher for the traits previously selected for low values. Means of traits previously selected for intermediate values remained unaffected. Variances were generally but moderately increased. The effect on correlations between traits was rather small. Expected gains from selection were higher in the treated population, but the increased gain could hardly, if at all, compensate for the lower means of that population.

The changes effected by the treatment are deemed rather small. The reason is thought to be the low doses of radiation used.

***Additional index words:* Mutation, γ-rays.**

PROGRESS from selection in a population is very often limited by lack of sufficient genetic variability and negative correlations between traits under selection. The possibility of increasing the genetic variance of a population by means of ionizing radiations or chemical mutagenic agents has received considerable attention in the last 3 or 4 decades. The implications of the results obtained thus far on the role of induced mutations in plant breeding are discussed by Brock (1971).

In the case of quantitative traits, the general effect of ionizing radiations is a lowering of the mean of the irradiated population and a considerable increase of its genetic variance. Within certain limits that vary with the plant species, the response to the treatment increases with the dose of the applied radiation. Very high doses produce many gross mutations and chromosomal aberrations, however, and reduce the value of the material for plant breeding purposes. It would be only reasonable, therefore, to try to accumulate many small mutations by recurrently using small amounts of radiation. The general conclusion from such experiments is that additional cycles of irradiation give diminishing returns in terms of induced variability and selection potential to the point that many authors feel that the returns from a second cycle of treatment do not compensate for the amount of time and labor required (Khadr and Frey, 1965; Brock, 1966). Nevertheless, as Brock (1966) points out, more than one cycle may give rewarding results in the case of polyploid species.

Regarding the problem of negative correlations among traits in cotton (*Gossypium hirsutum* L.), Al-Jibouri, Miller, and Robinson (1958) indicated that the most likely causes for the observed correlations are linkage or pleiotropism. Miller et al. (1958) reported that lint yield was positively associated with lint percentage and bolls per plant and was negatively associated with seed index and weight per boll. Selection for increased lint yield resulted in decreased weight per boll, seed index, fiber length, and fiber strength (Miller and Rawlings, 1967b). The same authors (1967a) found that intermating may reduce correlation between traits, which implies that linkage may be at least a partial cause for some of these associations. The same conclusion was reached by Meredith and Bridge (1971).

The purpose of the present study was to ascertain the effect of five cycles of recurrent γ-irradiation on the means, variances, and covariances of several quantitative traits in a synthetic variety of cotton.

MATERIALS AND METHODS

The experimental material used in this study was a synthetic variety composed of nine strains or varieties derived from 'Empire.' Equal amounts of seed from each component were mixed in 1953 and grown in an isolated plot at Knoxville, Tenn., an area of high natural crossing. Each year isolated increase plantings were made from seed of the preceding increase generation. The seed lots thus producd in 1954-61 were designated as K1 to K8. More details regarding this synthetic are given by Duncan, Pate, and Porter (1962).

A five-cycle irradiation treatment was initiated with seeds of synthetic K8. In each 1-year cycle 10 kr of γ-rays from a Cobalt 60 or Cesium 137 source were used. The seeds were treated from a few days to 2 weeks before planting. In the time between treatment and planting they were stored at room temperature. The seed moisture during the treatment was different for each generation and ranged from 9.4 to 12.26%. The treated seeds of each generation were planted in an isolated field of 0.05 ha, and a single lock was harvested from each plant to make sure that all plants were sampled and to reduce the effect of natural selection. The last treatment was in March 1968, and the treated seeds were put in cold storage until it was planted in the spring of 1969. A sample of the seeds thus treated and one of the parental stock K8 were kindly made available to the authors by E. N. Duncan and are designated as irradiated and control material, respectively.

Two populations of about 1000 plants, one each from the irradiated and control material, were grown at Clayton, N. C. in 1969. No abnormal plants were observed. Within each population the plants were randomly intermated by artificial cross pollination in order to reduce the inbreeding coefficient to 0 and thus avoid any confounding of the differences in means and variances induced by the treatment with the differences that would be produced by a different inbreeding coefficient for each population. Bolls from intermatings were obtained from about 300 plants in each population. The two seed lots thus produced were planted in Mexico during the winter of 1969, and 180 randomly selected plants from each population were selfed. The seed from each plant was harvested separately. Out of the 180 seed lots of each population, 120 were selected. The criterion used was the amount of seed produced. Only lots consisting of 300 or more seeds were retained.

In 1970, part of each seed lot was used to plant 240 nursery rows consisting of 20 hills with two or three plants per hill for a seed increase at Clayton, N. C., and the remainder was used for a replicated progeny test at Rocky Mount, N. C. In each nursery row two to three bolls per plant were selfed to produce seed for the 1971 tests at Rocky Mount and Lewiston, N. C.

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To decrease the effects of soil heterogeneity the 240 entries were randomly allocated to eight sets of 30 entries, 15 from each population. The allocation was the same for both years and both locations. A randomized complete block design with two replications was used for each set. Plots were single rows 2.44 m long for the 1970 trial and 7.62 m long for the 1971 trials. Distance between rows was 101.6 cm for Rocky Mount in both years and 91.4 cm for Lewiston. Stands were thinned to 1 plant/10 cm in all three trials. Uniform stands were obtained.

A random sample of 25 bolls was harvested from each plot for the determination of lint percentage, weight per boll in grams, seed index (weight of 100 seeds in grams), seeds per boll, and lint index (weight of the lint from 100 seeds in grams). Lint yield values were calculated by multiplying seed cotton yield per plot by the lint percentage value for the same plot. The number of bolls per plot was obtained by dividing seed cotton yield by the weight per boll.

Fiber data were recorded only for the 1970 trial at Rocky Mount. A lint sample of 10 to 15 g from each plot was analyzed by the USDA Fiber Laboratory at Knoxville, Tenn. The 50 and 2.5% span lengths were measured on the Digital Fibrograph. Fiber strength (T1) expressed in grams force per tex and fiber elongation (El) were measured on the .32-cm (1/8-in) gauge Stelometer. Fiber fineness was measured on the Micronaire and expressed in standard (curvilinear scale) Micronaire units.

The effect of the recurrent irradiation was studied by comparing the means, variances, and covariances of the treated and untreated populations. Estimates of the components of variance and covariance were obtained from separate analyses of the two populations. A combined analysis over both populations was used to obtain a pooled error for mean comparisons. The analysis was combined over locations for the 1971 data. Combining over years was impossible, because of the heterogeneity of the experimental error variances due to the difference in growing conditions, plot size, and generation of inbreeding of the seed used for the 2 years. The pertinent portion of the analysis of variance or covariance and the mean square or product expectations are given in Table 1.

The genotypic components of covariance or variance were estimated as:

$$\sigma_{gij} = (M1_{ij} - M2_{ij})/r \text{ (one year, one location)}$$

$$\sigma_{gij} = (M1_{ij} - M2_{ij})/rp \text{ (one year, two locations)}$$

These components were used to estimate the genotypic correlations,

$$\text{Genotypic } r_{ij} = \sigma_{gij}/(\sigma_{gii}\ \sigma_{gjj})^{1/2}$$

Standard errors for the estimated genotypic components of variance and correlation coefficients were computed as outlined by Mode and Robinson (1959). The significance of the difference between corresponding genotypic components of the two populations was tested by treating the two components as normally distributed variables.

Genetic advance from selection was estimated as $k\sigma_{gii}/\sigma_{phi}$, where σ_{phi} is the phenotypic standard deviation and k is the standardized selection differential. When 5% of the progenies are saved, as it will be assumed in this paper, k has the value 2.06. The expected change in trait j when trait i is selected was estimated as $k\sigma_{gij}/\sigma_{phi}$, where k, σ_{gij} and σ_{phi} are as defined previously.

RESULTS

Means

Performance data for the two populations are shown in Table 2. Means for yield and yield components except lint percentage are significantly lower in the treated population. This holds true for both years. Among fiber trait means, those for 50% span length and fiber strength remained unchanged, the one for 2.5% span length is significantly lower, while those for fiber elongation and fiber fineness are significantly higher in the treated population.

The range of the entry means is generally wider for the irradiated than for the control population. The left margin of the range is lower for the treated population for all traits except fiber elongation and fiber fineness. The right margin is higher in the treated population for the traits seed index, lint index, 50% span length, 2.5% span length, and fiber elongation in the case of the 1970 trial, and for all traits except bolls per plot in the case of the 1971 trial.

The distribution of the entry means is essentially symmetric in both populations, although the left tail is longer in the treated than in the untreated population for some traits.

Table 1. Pertinent portion of the analysis of covariance between traits i and j (analysis of variance if i = j).

Source	df	Mean product (square)	Mean product (square) expectation
a) One location, one year			
Entries in blocks	b (g-1)	$M1_{ij}$	$\sigma_{ij} + r\sigma_{gij}$
Pooled error	b (g-1) (r-1)	$M2_{ij}$	σ_{ij}
b) Two locations, one year			
Entries in blocks	b(g-1)	$M1_{ij}$	$\sigma_{ij} + r\sigma_{gpij} + rp\sigma_{gij}$
Entries by locations in blocks	b(g-1) (p-1)	$M2_{ij}$	$\sigma_{ij} + r\sigma_{gpij}$
Pooled error	pb (g-1) (r-1)	$M3_{ij}$	σ_{ij}

σ_{ij} = pooled error covariance (variance), σ_{gpij} = interaction covariance (variance) of entries by locations, σ_{gij} = genotypic covariance (variance) among entries, b = number of blocks, g = number of entries, r = number of replications, p = number of locations.

Table 2. Lowest entry mean, population mean, and highest entry mean for the irradiated (I) and control (C) populations.

		1970 data (one location)			1971 data (two locations)		
		Mean			Mean		
Trait	Population	Lowest entry	Population	Highest entry	Lowest entry	Population	Highest entry
Lint yield, q/ha	I	9.9	17.1±.2	25.2	4.3	6.4±.1	9.4
	C	11.8	19.0±.2**	26.1	4.5	7.0±.1**	9.3
Lint percentage	I	29.4	34.3±.1	38.3	32.5	38.2±.1	42.6
	C	29.6	34.3±.1	38.6	34.3	38.2±.1	42.0
Weight per boll, g	I	5.58	7.14±.02	8.92	5.69	7.30±.02	9.24
	C	6.32	7.64±.02**	8.98	6.66	7.67±.02**	9.05
Seed index, g/100 seeds	I	10.7	12.99±.03	15.8	11.3	13.41±.03	16.5
	C	11.0	13.13±.03*	15.2	11.4	13.71±.03**	16.3
Seeds per boll	I	26.3	36.2±.1	42.7	28.9	33.7±.1	38.8
	C	33.3	38.3±.1**	43.3	30.9	34.7±.1**	37.7
Lint index, g/100 seeds	I	4.97	6.79±.02	8.68	6.33	8.27±.02	10.01
	C	5.72	6.86±.02*	8.02	6.70	8.46±.02**	9.99
Bolls per plot	I	106	173±1	236	103	170±1	244
	C	118	180±1**	246	107	177±1**	250
50% span length, in.	I	0.50	0.538±.001	0.58			
	C	0.51	0.541±.001	0.57			
2.5% span length, in.	I	1.02	1.113±.001	1.19			
	C	1.03	1.119±.001**	1.17			
Fiber strength, T1	I	15.1	17.60±.05	20.2			
	C	15.7	17.70±.05	20.6			
Fiber elongation, E1	I	6.70	8.12±.05**	9.88			
	C	6.41	7.92±.05	9.28			
Fiber fineness, Mic.	I	3.17	4.02±.01**	4.67			
	C	3.13	3.92±.01	4.77			

*, ** Significantly higher than the corresponding mean of the other population at the 0.05 and 0.01 levels of significance, respectively. (Student's t-test).

Variances

The genotypic components of variance for the 1970 trial as well as the genotypic and genotypes by locations components of variance for the 1971 trial are presented in Table 3. All genotypic components of variance are significantly different from 0 (larger than twice their standard error). Only one of the genotypes by locations components is significantly different from 0, that for lint percentage in the irradiated population.

All genotypic components of variance are higher for the irradiated than for the control population. The difference is statistically significant, however, in only a few cases (Table 3). The genotypic components of variance for lint yield are different in the two populations only for the 1971 trial. There are no significant differences between populations with respect to genotypic variances for fiber characteristics.

It should be kept in mind that genotypic components of variance estimated from the 1970 experiment also contain the genotypes by environments component of variance, while those estimated from the 1971 experiment contain the genotypes by years components of variance (see footnotes, Table 3).

Correlations

The genotypic correlations among the various traits measured are presented in Table 4. Coefficients were quite consistent over years and are presented only for 1970.

Lint yield is highly positively correlated with lint percentage and bolls per plot, and negatively correlated with seed index, in agreement with the findings of Miller et al. (1958).) The correlation between lint yield and weight per boll is negative in the control population, although not significantly different from 0, but positive in the irradiated one. Miller et al. (1958) found a rather strong negative correlation between those traits. There is a considerable reduction in the correlations of lint yield with fiber fineness and fiber strength in the treated material as compared to the control material. Among the other correlations presented in Table 4 meriting attention are the correlations of weight per boll with seed index and bolls per plot, which have been considerably reduced after the treatment.

Table 3. Estimates of genotypic (σ^2_g) and genotypes by locations (σ^2_{gp}) variance components for the irradiated (I) and control (C) populations. Standard errors in parentheses.

Trait	Population	1970 data (one location) $\hat{\sigma}^2_g$‡		1971 data (two locations) $\hat{\sigma}^2_g$§		$\hat{\sigma}^2_{gp}$¶	
Lint yield, q/ha	I	6.43	(1.31)	0.58**	(.12)	-.004	(.09)
	C	3.47	(0.97)	0.19	(.09)	.19	(.11)
Lint percentage	I	3.07	(.47)	2.57	(.41)	.32	(.14)
	C	2.44	(.38)	1.77	(.29)	.12	(.11)
Weight per boll, g	I	0.37*	(.06)	0.33*	(.05)	-.02	(.02)
	C	0.20	(.03)	0.19	(.03)	-.002	(.02)
Seed index g/100 seed	I	1.08	(.16)	1.07	(.16)	.04	(.03)
	C	0.74	(.11)	1.02	(.15	.03	(.03)
Seeds per boll	I	7.83**	(1.27)	3.46**	(.63)	-0.20	(.38)
	C	1.74	(0.42)	1.40	(.36)	-0.14	(.36)
Lint index g/100 seed	I	0.39**	(.06)	0.40	(.06)	.03	(.02)
	C	0.19	(.03)	0.35	(.05)	-.005	(.01)
Bolls per plot	I	444	(104)	484	(94)	13	(63)
	C	302	(86)	274	(73)	50	(71)
50% span† length, in.	I	0.14	(.03)				
	C	0.12	(.03)				
2.5% span† length, in.	I	0.92	(.14)				
	C	0.81	(.12)				
Fiber strength, T1	I	0.70	(.14)				
	C	0.52	(.11)				
Fiber elongation, E1	I	0.27	(.05)				
	C	0.17	(.04)				
Fiber fineness, Mic.	I	0.08	(.01)				
	C	0.06	(.01)				

*, ** Component of variance significantly higher than the corresponding component of the other population at the 0.05 and 0.01 levels of significance, respectively. † 50% and 2.5% span length × 1,000. ‡ $\hat{\sigma}^2_g$ (1970 data) also contains $\sigma^2_{gp} + \sigma^2_{gy} + \sigma^2_{gpy}$, where y = years. § $\hat{\sigma}^2_g$ (1971 data) also contains σ^2_{gy}.
¶ $\hat{\sigma}^2_{gp}$ also contains σ^2_{gpy}.

Expected Progress from Selection

The expected genetic advance from selecting the superior 5% of the lines for a particular trait in the treated and control populations as well as the predicted mean of the progeny of the selected individuals are presented in Table 5. Although the expected gain is always higher for the irradiated than for the control population, the difference is not always large enough to compensate for the lower mean of the treated population. It should be noted, however, that

Table 5. Expected gain from selecting the superior 5% of the entries and predicted mean of the progeny of the selected entries in the irradiated (I) and control (C) populations.

Trait	Population	1970 data (one location) Expected gain Units	%	Predicted mean	1971 data (two locations) Expected gain Units	%	Predicted mean
Lint yield, q/ha	I	4.3	25.1	21.4	1.3	20.3	7.7
	C	2.8	14.7	21.8	0.5	7.1	7.5
Lint percentage	I	3.4	9.9	37.7	3.0	7.9	41.2
	C	3.0	8.7	37.3	2.5	6.5	40.7
Weight per boll, g	I	1.16	16.2	8.30	1.12	15.3	8.42
	C	0.82	10.7	8.46	0.79	10.3	8.46
Bolls per plot	I	34	19.7	207	38	22.4	208
	C	26	14.4	206	25	14.1	202
2.5% span length, in.	I	0.06	5.4	1.17			
	C	0.05	4.5	1.17			
Fiber strength, T1	I	1.4	7.9	19.0			
	C	1.2	6.8	18.9			
Fiber elongation, E1	I	0.89	11.0	9.01			
	C	0.66	8.3	8.58			
Fiber fineness, Mic.	I	0.55	13.7	4.57			
	C	0.47	12.0	4.39			

Table 4. Genotypic correlations between traits for the irradiated (I) and control (C) populations. Standard errors in parentheses. (Values estimated from 1970 data).

Traits	Population	Lint percentage	Weight per boll	Seed index	Seeds per boll	Lint index	Bolls per plot	50% span length	2.5% span length	Fiber strength	Fiber elongation	Fiber fineness, Mic.
Lint yield, q/ha	I	0.62 (0.08)	0.34* (0.11)	-0.30 (0.11)	0.46 (0.11)	0.24 (0.11)	0.75 (0.06)	-0.09 (0.15)	-0.09 (0.12)	-0.24 (0.14)	0.07 (0.14)	0.24* (0.12)
	C	0.79 (0.09)	-0.14 (0.15)	-0.62 (0.12)	0.37 (0.18)	0.22 (0.14	0.71 (0.08)	-0.19 (0.18)	-0.18 (0.14)	-0.46 (0.15)	0.02 (0.18)	0.62 (0.12)
Lint percentage	I		0.08 (0.11)	-0.31 (0.09)	0.08 (0.11)	0.57 (0.07)	0.29 (0.12)	-0.31 (0.12)	-0.30 (0.10)	-0.40 (0.11)	-0.01 (0.12)	0.45 (0.09)
	C		-0.07 (0.11)	-0.54 (0.08)	0.23 (0.13)	0.51 (0.08)	0.37 (0.13)	-0.27 (0.13)	-0.41 (0.09)	-0.24 (0.12)	-0.08 (0.13)	0.51 (0.08)
Weight per boll, g	I			0.45* (0.08)	0.59 (0.07)	0.45 (0.09)	-0.28* (0.12)	0.23 (0.13)	0.22 (0.10)	0.14 (0.12)	0.05 (0.12)	-0.06 (0.11)
	C			0.72 (0.06)	0.38 (0.12)	0.67 (0.07)	-0.73 (0.10	0.37 (0.13)	0.19 (0.11)	0.33 (0.12)	-0.13 (0.14)	0.17 (0.11)
Seed index, g/100 seeds	I				-0.41 (0.09)	0.60 (0.07)	-0.53 (0.10)	0.39 (0.11)	0.35 (0.09)	0.15 (0.12)	0.12 (0.12)	0.02 (0.11)
	C				-0.28 (0.12)	0.44 (0.09)	-0.81 (0.10)	0.45 (0.12)	0.30 (0.10)	0.44 (0.11)	0.04 (0.13)	-0.15 (0.11)
Seeds per boll	I					-0.29 (0.10)	0.14 (0.14)	-0.04 (0.14)	-0.02 (0.11)	0.12 (0.13)	-0.05 (0.13)	-0.21 (0.11)
	C					-0.02 (0.14)	0.02 (0.19)	-0.07 (0.17)	0.03 (0.13)	-0.12 (0.16)	-0.24 (0.16)	0.21 (0.13)
Lint index, g/100 seeds	I						-0.23 (0.13)	0.09 (0.13)	0.05 (0.11)	-0.20 (0.12)	0.09 (0.12)	0.38 (0.09)
	C						-0.43 (0.14)	0.19 (0.14)	-0.12 (0.11)	0.20 (0.13)	-0.06 (0.14)	0.40 (0.10)
Bolls per plot	I							-0.09 (0.17)	-0.12 (0.13)	-0.19 (0.15)	0.03 (0.15)	0.16 (0.13)
	C							-0.30 (0.18)	-0.12 (0.14)	-0.57 (0.15)	0.17 (0.18)	0.31 (0.14)
50% span length, in.	I								0.78 (0.06)	0.63 (0.11)	-0.24 (0.15)	0.06 (0.13)
	C								0.68 (0.08)	0.59 (0.12)	-0.39 (0.16)	0.02 (0.14)
2.5% span length, in.	I									0.41 (0.11)	-0.19 (0.12)	-0.32 (0.10)
	C									0.28 (0.12)	-0.22 (0.13)	-0.49 (0.09)
Fiber strength, T1	I										-0.43 (0.12)	-0.07 (0.13)
	C										-0.23 (0.14)	-0.22 (0.12)
Fiber elongation, E1	I											-0.24 (0.12)
	C											-0.21 (0.13)

* Difference between coefficients of the two populations larger than twice the standard error of their difference.

Table 6. Predicted changes in lint yield and fiber characteristics in the irradiated (I) and control (C) populations from selecting the superior 5% of the entries on the basis indicated (Values estimated from 1970 data).

Basis of selection	Population	Lint yield	2.5% span length	Fiber strength	Fiber elongation	Fiber fineness, Mic.
Lint yield, q/ha	I	4.3	-0.005	-0.4	0.06	0.12
	C	2.8	-0.008	-0.5	0.01	0.23
Lint percentage	I	3.0	-0.02	-0.6	-0.01	0.25
	C	2.8	-0.02	-0.3	-0.06	0.25
Weight per boll, g	I	1.6	0.01	0.2	0.05	-0.04
	C	-0.5	0.01	0.4	-0.10	0.07
Bolls per plot	I	3.1	-0.01	-0.3	0.02	0.07
	C	2.0	-0.005	-0.6	0.10	0.11
2.5% span length, in.	I	-0.5	0.06	0.7	-0.18	-0.18
	C	-0.7	0.05	0.4	-0.17	-0.23
Fiber strength, T1	I	-1.1	0.02	1.4	-0.38	-0.04
	C	-1.5	0.01	1.2	-0.16	-0.09

the treated material will probably maintain a higher genetic variance after the first cycle of selection. Thus, after a second cycle of selection means would be expected to be higher in the treated than in the control population.

Yield and fiber properties are the primary traits of economic interest in cotton. The predicted correlated effects of selection on these traits when selection is based on certain individual traits are presented in Table 6. The predicted increase in lint yield is maximum when lint yield itself is the basis of selection. However, this increase in yield is accompanied with a reduction in fiber length and strength and an increase in fiber diameter. Similar results would be expected if the basis of selection were lint percentage or bolls per plot. Selection on the basis of weight per boll would not adversely affect fiber length or strength, but would give a small increase in lint yield in the treated population and would decrease the yield in the control. Selection for either fiber length or strength would result in stronger and longer fiber, but also in reduced yield of finer and less elastic fiber. If realistic economic weights can be assigned to yield and fiber properties, a selection index optimizing net worth of the selections should be more appropriate than any single criterion of selection.

DISCUSSION

Assumptions

It is appropriate to examine to what extent other factors besides mutations may have contributed to the observed changes in means, variances, and covariances. Some selection for radioresistance may have occurred. Emery (1972), however, found no association between yield and radiosensitivity in peanuts (*Arachis hypogaea* L.). The same could well be true for cotton. It is also possible that selection for fertility and productivity has taken place during the process of selecting the entries to be included in the tests. Any such selection, however, should have been in the same direction for both populations so that comparisons between populations are not expected to have been vitiated considerably.

As shown by Miller and Rawlings (1967b) and Meredith and Bridge (1971), intermating within a population derived from the cross of two inbred lines may reduce correlations between traits. On the other hand, Hanson (1959) showed that in a random mating population derived from intermating p homozygous lines in all possible ways, the reduction in average segment length per chromosome proceeds rapidly in the first eight generations and becomes very slow later. Thus, it is unlikely that the additional intermating in the treated population (subsequent to the original eight generations of intermating) had any important effect on the linkage relationship within the material. Nevertheless, it is recognized that the use of genetically uniform material for an experiment of this type would be more desirable, and that the control population should also be grown in an isolated lot every time that the treated population was grown in the field.

Means

Brock (1965) hypothesized that random mutation in a population will shift the mean away from the direction of the previous selection. The results of this experiment lend support to his hypothesis. Past selection favored directly or indirectly higher values for lint yield, weight per boll, seed index, seeds per boll, lint index, bolls per plot, span length, and fiber strength. The means for all these traits are lower in the treated than in the control population. On the contrary, means for fiber fineness and elongation are shifted upwards. These traits are negatively correlated with fiber length and strength. Thus, past selection for long and strong fiber may have been associated with a shift toward finer and less elastic fiber. The observed direction of the shift of the means for these latter two traits might therefore be expected.

The behavior of the mean for lint percentage, which remained unchanged through five cycles of irradiation, is puzzling at first sight. Brock (1965) expressed the opinion that characters previously selected for an intermediate mean would be expected to respond to a mutagenic treatment with an increase in variance, but no shift in the mean. This might be the present case. Lint percentage is positively correlated with lint yield and negatively correlated with fiber length and strength. Simultaneous selection for higher yield as well as longer and stronger fiber in the past apparently resulted in intermediate values for lint percentages. Hence, its mean did not shift in either direction after the treatment.

From the agronomic point of view, the shift of the means in an undesirable direction is of no particular importance, since the aim of a mutagenic treatment is the creation of new variability rather than the development of a new variety. The important question here is whether the best lines of the treated population are superior to the best lines of the control population for any one particular trait. It is rather disappointing that in this study the mean difference between the best lines of the two populations was generally small for almost all traits.

Variances

Although genetic variances were always higher in the irradiated than in the control population, the increase in variability was considerably smaller than the four- or fivefold increase after a single irradiation treatment reported by many authors.

The most reasonable explanation for this small increase in genetic variance appears to be the low dose of radiation used. This point cannot be decided from the results of this experiment, since only one radiation dose was used in each cycle. There is, however, some indirect evidence supporting this hypothesis. Constantin (1964), studying the effect of a single treatment of cotton seed with γ-rays, found that reduction in plant height and yield occurs only when the radiation dose is 10 kr or higher. The 50% growth reduction dose for all three varieties used in the experiment was 38 kr, whereas the 50% yield reduction dose was 23 kr. Similarly, Osborne and Bacon (1960) found that the lowest γ-ray dose reducing growth below that of the unirradiated control after a single treatment is 10 kr in the case of cotton.

Correlations

There is no test available that would allow one to decide whether there is a significant difference between two correlation coefficients calculated as in this experiment. If we assume that there is a real difference between two correlation coefficients only when their estimates differ by more than twice the standard error of their difference, then there are only four correlations that have been affected (Table 4). This is about the number of changes that would be expected to be significant at the 5% probability level if the null hypothesis that the treatments has no effect on correlations were true. There are, however, several other coefficients whose value has been changed substantially so that a treatment effect is suspected.

In most cases where correlations have been affected, they are lower after the treatment. We might hypothesize that radiation treatment by randomly changing the allelic form of the genes would tend to establish a linkage equilibrium and move correlation values toward 0.

Expected Progress from Selection

The genetic variances estimated from the 1970 data also contain genotype by locations, genotype by years, and the second-order interaction components, while the genetic variances estimated from the 1971 data contain a genotype-by-years component. Therefore, these estimates may be inflated and estimated gains from selection are also inflated. It is likely, however, that the interaction components constitute the same proportion of the estimated genetic variance in the two populations, so that comparisons of expected gains in the two populations are not invalidated. In fact, most genotype-by-locations interaction components were not different from 0 for both the treated and the control populations (Table 3). Also, the experimental errors for the two populations were homogeneous.

The existence of additive genetic variance is prerequisite to progress from selection in a population. Therefore, the higher expected gains in the irradiated population can be realized only to the extent that the additional variance induced by the treatment is additive. The nature of the induced variance cannot be ascertained from the results of this experiment. Generally, additive effects appear to predominate in cotton populations. Besides, the material tested in this experiment was selfed for one generation in the case of the 1970 trial and for two generatitons in the case of the 1971 trial. Any dominance variance that might be present originally should be considerably reduced after the selfing. It is probably safe to conclude that most of the induced variance is also additive, and, consequently, the calculated higher gains from selection are realizable.

Notwithstanding the degree to which the induced variability is susceptible to selection, the superiority of the treated population over the untreated remains small. The reason for this small response to the treatment cannot be determined from the results of this experiment. It might be that the radiation dose was very low. Or that the population could not tolerate more variability. A much larger experiment with more than one dose of radiation and with all treated generations included in the test would be necessary to provide answers to these questions.

REFERENCES

Al-Jibouri, H. A., P. A. Miller, and H. F. Robinson. 1958. Genotypic and environmental variances and covariances in an upland cotton cross of interspecific origin. Agron. J. 50:633-636.

Brock, R. D. 1965. Induced mutations affecting quantitative characters. Radiat. Bot. 5 (Suppl.):451-464.

———. 1966. Second cycle of mutation and selection for quantitative variation in *Trifolium subterraneum*. Radiat. Bot. 6: 357-369.

———. 1971. The role of induced mutations in plant improvement. Radiat. Bot. 11:181-196.

Constantin, M. J. 1964. Feasibility of producing F_1 hybrid cotton seed through radiation induced pollen sterility. Crop Sci. 4:299-302.

Duncan, E. N., J. B. Pate, and D. D. Porter. 1962. The performance of synthetic varieties of cotton. Crop Sci. 2:43-46.

Emery, D. A. 1972. Effects of reirradiation on radioresistance in peanuts (*Arachis hypogaea* L.) Radiat. Bot. 12:137-150.

Hanson, W. D. 1959. The breakup of initial linkage blocks under selected mating systems. Genetics 44:857-868.

Khadr, F. H., and K. J. Frey. 1965. Recurrent irradiation for oat breeding. Radiat. Bot. 5:391-402.

Meredith, W. R., Jr., and R. R. Bridge. 1971. Breakup of linkage blocks in cotton, *Gossypium hirsutum* L. Crop Sci. 11: 695-698.

Miller, P. A., and J. O. Rawlings. 1967a. Breakup of initial linkage blocks through intermating in a cotton breeding population. Crop Sci. 7:199-204.

———, and ———. 1967b. Selection for increased lint yield and correlated responses in upland cotton, *Gossypium hirsutum* L. Crop Sci. 7:637-640.

———, J. C. Williams, Jr., H. F. Robinson, and R. E. Comstock. 1958. Estimates of genotypic and environmental variances and covariances in upland cotton and their implications in selection. Agron. J. 50:126-131.

Mode, C. J., and H. F. Robinson. 1959. Pleiotropism and the genetic variance and covariance. Biometrics 15:518-537.

Osborne, T. S., and J. A. Bacon. 1960. Radiosensitivity of seeds. I. Reduction or stimulation of seedling growth as a function of γ-ray dose. Radiat. Res. 13:686-690.