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Some Sources of Variability in Boll and Fiber Properties of Cotton (*Gossypium hirsutum* L.)[1]

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ABSTRACT

Sources of variability in cotton fiber quality were studied by a series of experiments carried out over a period of several years. Homozygosity or heterozygosity of the individual plants or of the strain had only a small effect on variability. Environmental fluctuations were a major cause of variability within each variety, inbred line, or doubled haploid studied. Varieties differed in homeostasis, or buffering against environmental fluctuation, and homeostasis was not the same for all properties studied. It is suggested that cotton breeders can minimize the effects of environmental fluctuation on fiber quality, either by breeding and selection for buffering systems effective over a wider range of environments, or by breeding plants with a shorter season, so that they will not require adjustment to the unfavorable environment which lowers fiber quality of bolls developed just before frost.

Additional index words: **Homeostasis, Doubled haploids, Environment.**

LARGE variations in fiber properties make it more difficult and less profitable for a farmer to market his cotton crop. We carried out a series of experiments at Stoneville, Mississippi, to study the relative importance of some of the factors which were known or suspected to cause variation in fiber development. *(1)* Variation between plants in a row (heterogeneity) might be large because ancestral plants with a wide range of properties contributed to the strain, and genetic segregation would produce plants with different assortments of properties. We used doubled haploid strains of cotton as a standard to test the significance of this source of variability. Except for the extremely rare exceptions of gene mutations and chromosome aberrations, all gametes produced by any one haploid plant or strain should be genetically identical. *(2)* heterozygosity or homozygosity might have important effects on variability. According to one theory (Lerner, 1954) a pair of dissimilar genes would be better able to buffer environmental fluctuations during development than would a pair of identical genes; the result would be less variability for heterozygotes. According to another hypothesis, however, (Gustafsson, 1948), a pair of dissimilar genes could respond to a wider range of environments; the result would be more variability for heterozygotes. To test these two theories, we compared different populations, each composed of genetically identical plants – homozygous populations from selfed doubled haploids, and heterozygous F_1 populations from crossing two doubled haploids. *(3)* A general physiological balance or "tuning" within the plants might be a major factor affecting variability. If this is the case, one would expect the greatest differences in variability between strains from different varieties; strains from the same variety should be quite similar, because plants that make up a variety would have nearly identical combinations of genes which act harmoniously with each other and the environment to produce a good phenotype. Genotypes from different varieties would have harmonious, but different, combinations of genes. If this is the case, then strains from the same variety would not be expected to differ very much, and they would have little more variability than strains derived from doubled haploids. *(4)* Most variation might be from responses to variable weather, and independent of the plants' inherited properties. If this is the case, we would expect the same amount and kind of change for all varieties grown at the same time under the same conditions. *(5)* Nonrandom variation could be due to factors which we have not discovered or cannot measure.

MATERIALS AND METHODS

We carried out all of the experiments reported in this paper at the Delta Branch, Mississippi Agricultural Experiment Station, Stoneville, Miss. All plants were grown in field plots with the standard row spacing of about 1 m; unless other specific spacings are noted, plants within rows were grown approximately 30 cm apart.

The 1953 Variability Experiment used the doubled haploid 'Z106' and seven commercial varieties: 'Bobshaw 1A,' 'Coker 100W,' 'Delfos 9169,' 'Deltapine 15,' 'Deltapine Fox,' 'Empire WR,' and 'Stoneville 2B.' Samples for each entry were taken from 25 consecutive non-border plants in each of the four replications. Analysis of variance was by standard methods [Snedecor, 1956 (237-250)]. The F test was performed by dividing the within-plot variance thus obtained, for each property within each variety, by the corresponding variance for Z106.

In the 1955 experiment, the doubled haploids 'M8' and 'Z106' were used as female parents. Both were selfed and crossed with each other and the following doubled haploids: 'Z99,' 'Z112,' 'Z104,' 'Z108,' and 'Z109.' Also, long-term inbreds from 'Stoneville 5' (13 selfed generations) and 'Stoneville 5A' (15 selfed generations) were used as male parents. Individual plots consisted of 25 hills at 30-cm spacing. Plots were sampled by taking one boll from each plant. Analysis of variance was by Snedecor's method for unequal numbers (1956, pp 268-274). Four replications of each entry were grown, except for three crosses of Z106 which had only enough seed for three replications. Differences in variability within crosses or selfed populations were tested by Chi-Square tests based on $\log_e$ of variance (Steel & Torrie, 1960, pp. 347-349).

In the 1960 Heterosis Experiment, seven entries were grown in three replications at two spacings (1 and 2 plants per hill).

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Entries grown in this experiment were the doubled haploids 'M8' and 'M11' the highly inbred strain of 'Stoneville 5A', their three F_1 hybrids, and the commercial variety 'Deltapine 15' as a check.

In a 1962 experiment the doubled haploids M8 and M11 and their two reciprocal F_1 hybrids were grown in five randomized replications. The fourth replication had poor stands, and its data were used only for stand count. In the other four replications 5-boll samples were taken from 10 plants in each row.

Only the M8 doubled haploid was used in the 1965 sampling experiment. Six replications consisted of eight rows each, with a 4-row "wet" and a 4-row "dry" plot assigned at random within each replication. For nine successive Wednesdays the center furrow of the four rows of the wet plot was filled with water. Freshly opened flowers were tagged in the center rows of each plot before each irrigation. The plots were harvested whenever a set of tagged bolls was entirely open. The data were analysed as a randomized complete block, with dates representing split plots [Snedecor, 1956 (366 ff.)] Steel and Torrie's test (1960, pp. 347-349) for homogeneity of variance was used to detect differences in error mean squares.

For Homeostasis Experiment I, grown in 1967 and 1968, the five selected strains were planted in 3-row plots, 6.1 m long, 2 seeds per hill, hills 30 cm apart. Flowers were tagged each Wednesday during July and August. Bolls were harvested from the center row of each plot whenever a set of tagged bolls had opened. The varieties in Homeostasis Experiment II were grown in two replications during 1968. Boll properties were determined from samples of just-opened bolls harvested at weekly intervals throughout the harvest season. Statistical analysis was by the methods described above.

The strains of cotton selected for Homeostasis Experiment I were: M8 and 'Stoneville 213 DH-1,' doubled haploids from 'Deltapine 14' and 'Stoneville 213,' respectively; the locally adapted commercial variety 'Deltapine 16;, the western variety 'Acala SJ-1;' and the South Carolina variety 'FTA 263-20.'

In the 1968 Homeostasis Experiment II, 15 additional varieties (see Table 5), plus the M8 doubled haploid, were grown in two replications, and samples were harvested weekly for 7 weeks. Fiber properties were not determined, but analysis of variance was carried out on data for grams lint per plant, grams seed cotton per boll, seed index, lint index, and lint %.

RESULTS AND DISCUSSION

Doubled haploids compared with commercial varieties: In the 1953 Variability Experiment, we compared variances of seven commercial varieties with the variances for the same properties in the doubled haploid 'Z106'. Table 1 presents F values calculated by dividing the variance for each property within each variety by the corresponding variance for Z106. These data show that for nearly every property measured the doubled haploid Z106 varies significantly less than the varieties studied in the same experiment. Perhaps even more interesting, the contrast between the F values for Deltapine 15 and Delfos 9169 reflects significant differences in the variability of commercial varieties grown under the same experimental conditions.

Doubled haploids compared with their F_1 hybrids: Variability of selfed doubed haploids was compared with variability of their F_1 hybrids in three different years. There were no highly significant differences in variability in any of these experiments. Analyses of variance for the 1955 experiment comparing doubled haploids and their F_1 hybrids showed highly significant effects of female parents for mean values of every property measured, highly significant effects for male parent for all properties except weight of seed cotton per plant, and highly significant interaction for male and female parents for every property except seed index. Nevertheless, Chi-square tests based on $\log_e$ of variance for each cross showed no significant differences in variability, whether the 18 crosses were taken separately, grouped by female parent, or grouped by doubled haploid vs. highly inbred male parent (Table 2). In the 1960 experiment, data were taken on grams seed cotton per plot, height per plant, leaf area and dry weight of vegetative parts. In no case was there a significant difference in variance of the seven entries tested; spacing had no significant effect on variability. In the 1962 experiment the Chi-square test for the lint percent data indicated a difference in variance significant at the .05 probability level. This was due to the great variability in lint % of the M11 samples. Variance for lint % for the M8 samples was between the variances for the two F_1 hybrids. There were no significant differences in variance for number of seeds per boll, seed index, stand count, boll weight, lint index, fiber length, fiber strength, or micronaire.

This group of experiments was carried out during three different growing seasons, used different experimental designs each time, and was based on doubled haploids which originated from a very wide range of genetically different cotton varieties. Only the seed size of the M11 doubled haploid, and this in only one experiment, varied significantly more than the same property in other entries of that experiment. Examination of the data showed that some of the individual plant samples from M11 had bolls with fewer and larger seeds than usual. Taken as a whole, the data from these three experiments comparing doubled haploids and their F_1 hybrids indicate that differ-

Table 1. F values comparing variances of seven commercial varieties of cotton with variance of the doubled haploid Z106.

	Variety						
Property	Empire WR	Bob-shaw	Delta-pine 15	Delta-pine Fox	Delfos 9169	Coker 100 W	Stone-ville 2B
No. seeds/5 bolls	2.35**	1.79**	2.24**	2.61**	1.87**	2.90**	2.28**
Grams seed/5 bolls	1.86**	1.69**	1.17	1.46**	0.93	1.50**	2.19**
Grams lint/5 bolls	2.07**	1.16	2.17**	1.67**	1.26	1.85**	2.07**
Seed index	2.66**	2.15**	2.32**	1.15	1.16	1.32	2.22**
Lint index	2.52**	1.63**	3.41**	1.85**	1.41*	1.40*	2.01**
Lint %	1.76**	2.69**	4.34**	2.95**	1.35	1.96**	2.69**
Fiber length, upper half mean	1.74**	1.89**	2.67**	1.25	1.44*	2.75**	2.05**
Fiber strength, T_1	1.39	1.93**	2.31**	1.43*	1.12	1.90**	1.38
Fiber elongation, E_1	2.29**	1.37	4.75**	3.38**	1.94**	3.50**	2.86**
Fiber fineness, A	1.91**	1.95**	1.92**	1.00	1.08	1.50*	2.51**
Fiber roundness, D	2.14**	2.07**	1.76**	1.00	1.13	1.47*	3.01**

* Significant at .05 probability level. ** Significant at .01 probability level. df = 96, 96.

Table 2. 1955 Variability Experiment. Means and Chi-square values testing differences in between-plant variability for selfed doubled haploids and F_1 hybrids from doubled haploids.

	Kilograms/plot				
Cross	Seed cotton	Lint	Lint %	Seed index	Lint index
M8, selfed	5.0	1.8	36.8	10.9	6.3
Z106 × M8	6.2	2.1	34.1	12.8	6.7
M8 × Z106	6.6	2.3	34.0	12.8	6.6
Z106, selfed	5.2	1.6	31.5	14.0	6.4
M8 × Z99	6.2	2.1	34.5	12.4	6.5
Z106 × Z99	5.5	1.7	31.2	13.7	6.2
M8 × Z112	6.6	2.3	34.2	12.8	6.7
Z106 × Z112	4.8	1.5	30.9	13.7	6.2
M8 × Z104	6.6	2.4	35.8	13.1	7.3
Z106 × Z104	5.8	1.9	32.0	14.1	6.7
M8 × Z108	6.0	2.0	34.8	12.9	6.8
Z106 × Z108	5.5	1.8	32.4	14.1	6.7
M8 × Z109	5.8	2.0	34.3	12.9	6.7
Z106 × 109	6.0	2.0	33.3	14.2	7.1
M8 × Stoneville 5	5.5	2.0	35.9	12.6	7.0
Z106 × Stoneville 5	5.9	2.0	33.3	13.6	6.8
M8 × Stoneville 5A	6.5	2.3	35.9	11.3	6.3
Z106 × Stoneville 5A	6.2	2.3	33.0	13.4	6.6
χ^2 testing significant difference† in variability	24.14ns	18.39ns	19.86ns	17.99ns	13.69ns

† A χ^2 of 27.59 < is required for significance at the .05 probability level.

ences between cotton plants within a progeny row are not controlled in any important way by the homozygous or heterozygous condition of the plants' allelic genes.

Doubled haploids compared with their parent varieties: Meredith, Bridge, and Chism (1970) describe and discuss a comparison of doubled haploids with their parent commercial varieties of cotton, as measured in diallel crosses. Kohel (1969) studied other aspects of haploid variability with genetically different plant material, and with somewhat different techniques. Because these authors have covered the subject well, it needs only brief treatment here. In both cases the overall genetic background of the plant material proved far more important to variability than did the presence or absence of doubled haploids among the ancestors of the plants. An obvious conclusion from these data would be that breeding and selection of a successful cotton variety involves collecting together genes which cooperate to maintain a favorable physiological balance or "tuning", and eliminating any genes which interfere with this balance. Although other advantages or disadvantages might result from the use of doubled haploids in cotton breeding or experiments, their effect on variability seems negligible.

Environmental effects on variation of doubled haploids and commercial varieties: Only the M8 doubled haploid was used in the 1965 experiment, which was designed to determine the relative importance of non-genetic sources of variability in fiber samples. Soil and water variations caused only minor differences in the properties studied. For every property measured, except E_1, analysis of variance showed highly significant differences between sample means from bolls matured on different dates (Table 3). Since environment produced such highly significant differences between samples from a doubled haploid, it seemed desirable to see if any other doubled haploids and varieties would show a similar response.

We decided to study variability in response to environment as it occurs within quite different strains of cotton. Doubled haploids were included because they lack genetic variability. Locally grown varieties were included because they have been selected for yield performance within the environmental range usual in the field plots at Stoneville. Commercial varieties from other areas were included because they have been selected for performance under another set of environmental conditions. There were significant differences in variability of the varieties for the properties measured, but the differences did not follow any consistent pattern (Table 4). Neither genetic homozygosity nor adaptation to the local environment had any predictable effect on variability in this experiment. It should be pointed out that in this experiment we measured a different kind of variability than in some earlier experiments. These differences were between bolls matured on different dates, not between individual plants.

In the 1968 Homeostasis Experiment II, 15 additional varieties, plus the M8 doubled haploid, were grown. Analysis of variance was carried out on data for grams lint per plant, grams seed cotton per boll, seed index, lint index, and lint percent (Table 5). Variety × date interactions were significant for lint index, and highly significant for lint percent (Table 6). This indicated that the effect of weather on lint production was not the same for all varieties in the experiment.

Table 3. Environmental effects on fiber properties of a doubled haploid cotton, M8, grown under 2 treatments (irrigated and dry) in 6 replications, and harvested weekly as bolls opened on 9 harvest dates in 1965.

	F values					Coefficient of variation	
Property	Replication (Soil)	Treatment (Water)	Harvest date†	Treatment × Date	Chi square‡	Wet	Dry
Yield/plot	ns	ns	28.19**	ns	27.71**	14.24	5.68
Boll size	ns	ns	68.73**	6.01**	12.06**	5.52	7.58
Seeds/boll	7.19*	ns	27.35**	2.40*	5.61*	6.75	8.28
Seed index	ns	22.47**	30.45**	2.68*	none	5.07	6.31
Lint index	ns	11.49**	4.87**	ns	none	5.11	6.30
Lint %	8.05*	22.17**	37.62**	3.96**	none	1.84	2.16
UHM	ns	12.12**	42.09**	3.10**	none	2.44	2.10
T	ns	ns	15.97**	4.33**	none	4.40	4.04
E	ns	ns	ns	ns	none	4.87	3.20
Micronaire	5.57*	ns	7.01**	ns	7.39**	6.16	8.82

* Significant at .05 probability level. ** Significant at .01 probability level. † Overall climate variations. ‡ For significant difference in error ms wet plots vs dry.

Table 4. Homeostasis Experiment I: Variability within 5 varieties, 3 replications, 9 harvest dates in 1967, 10 harvest dates in 1968.

	F values					χ^2 for significant difference between varieties	
Property	Year	Variety	Var. × year	Harvest date	Date × variety	Total s^2	Error ms
Yield/plot	32.49**	ns	ns	--	--	--	ns
Boll size	35.45**	19.80**	ns	27.38**	ns	ns	18.91**
Seed index	65.80**	118.88**	6.78**	16.47**	ns	9.53*	14.50**
Lint index	ns	26.21**	ns	6.84**	ns	12.37*	15.51**
Lint %	258.10**	100.03**	6.43**	14.36**	ns	14.50**	ns
Fibrograph	106.51**	59.46**	ns	12.24**	ns	ns	ns
T_1	--	543.93**	--	16.68**	3.23**	38.42**	27.19**
E_1	--	756.44**	--	8.83**	2.72**	ns	16.07**
Micronaire	--	ns	ns	10.52**	ns	14.95**	ns

* Significant at .05 probability level. ** Significant at .01 probability level.

Table 5. Homeostasis Experiment II, 1968. Means and significant differences* for 16 varieties.

	Grams lint/plant	Lint index	Seed index	Lint %	Grams seed cotton/boll
Variety	Mean	Mean	Mean	Mean	Mean
Ak Djura	14.3 cd	4.99 c	9.37 efg	34.79 cde	3.28 gh
Del Cerro 169	21.4 bcd	5.36 bc	12.91 ab	29.41 fg	4.22 e
Hopi	11.3 cd	2.90 d	8.26 fg	25.78 g	1.24 i
Coker 201	24.1 bcd	6.27 ab	10.46 cde	37.55 bcd	5.40 abc
Samson 217	21.8 bcd	5.83 abc	10.46 cde	35.94 bcd	4.31 e
Stv. 508	30.8 bcd	5.75 abc	10.01 de	36.43 bcd	4.80 cde
Del Cerro 180	13.8 cd	6.00 abc	13.63 a	31.34 efg	4.58 de
DPL 5540	31.1 bcd	6.09 abc	9.32 efg	39.58 b	4.20 f
Acala 4-42	41.3 abc	6.19 abc	11.42 bcd	35.22 cde	5.82 ab
Acala 4447	41.3 abc	6.39 ab	12.19 abc	34.42 def	6.08 a
Acala 9999	46.2 ab	5.52 abc	12.44 ab	30.72 efg	5.65 ab
PD 2165	22.5 bcd	6.81 a	12.02 abc	36.11 bcd	5.35 abc
Mo. 565	49.6 ab	6.55 ab	11.39 bcd	36.25 bcd	5.14 bcd
Samson 197	29.1 bcd	6.52 ab	7.94 g	44.93 a	3.45 g
M8	64.6 a	6.21 abc	9.86 def	38.66 bc	5.20 bcd
Yugoslav	10.1 d	3.03 d	7.93 g	27.56 fg	2.66 h

* Means followed by the same letter do not differ significantly at the 0.01 level of probability.

Table 6. Homeostasis Experiment II, 1968. Significant F values for 16 varieties, 2 replications, 7 harvest dates.

Character	Replication	Variety	Date	Var. × Date
Grams lint per plant	ns	5.03**	-	-
Grams seed cotton per boll	ns	14.14**	26.13**	ns
Seed index	9.16**	21.90**	12.02**	ns
Lint index	ns	9.38**	13.16**	1.56*
Lint %	8.64*	31.06**	16.54**	7.95**

GENERAL DISCUSSION

Much of the literature on homeostasis appeared after 1960. The wide range of plants and animals studied covers wild species, crop plants, obligate outbreeders, and highly inbred strains. One would expect great variation in both the optimum amount of variability or uniformity and the breeding system through which the species reaches its optimum level of homeo-

stasis. It is not surprising that the data reported in the literature are inconsistent, or even contradictory. For evidence that heterozygotes are better buffered than homozygotes one could cite the report by Adams and Shank (1959) that buffering capacity in maize hybrids depends largely on level of heterozygosity, by Hassan and Nordskog (1967) that in chickens cross *line* genotypes were better than pure lines for factors affecting hatchability, by Byth and Weber (1968) that in soybeans F_2-derived lines had greater stability across environments than F_5-derived lines, or by Meredith *et al.* (1970) that F_1 and F_2 hybrids of cotton are more stable than their parents. For evidence that heterozygotes are not as well buffered as homozygotes, one could cite Kohel's (1968) report that cotton seed development was less variable from selfed flowers than from flowers pollinated with F_1 or genetically different pollen, the report by Koehl and White (1963) that for 7 of the 10 characters measured in cotton hybrids homozygous parents were less variable than the F_1's, or Sammeta's (1967) report that barley hybrids gave higher yields than lines or corresponding mixtures of lines but they tended to be less stable. We could cite evidence that homozygotes and heterozygotes do not differ significantly in buffering capacity, some of it by the authors already cited, or even from the same papers: Clay (1969) found that for barley mixtures, varieties, and hybrids comparisons of stability were of a limited nature and did not favor the hybrids; Kohel (1969) found no clear-cut distinction between cotton hybrids and their parents; Williams (1960) found tomato hybrids to be neither more or less stable than their inbred parents over the same range of environments; and Meredith *et al.* (1970) found that doubled haploids do not differ significantly in variability from their parent varieties; (as noted above, however, hybrids were more stable than their parents).

For cotton the information now available suggests that the amount of homeostasis and the basic mechanisms controlling it may vary for different properties and for different varieties. Cotton geneticists and breeders are now looking for greater homeostasis in fiber properties because modern textile machinery requires more uniformity for efficient operation at higher speeds. Biologically cotton as a crop is in the same position as a wild species facing competition for an ecological niche.

The data presented in this paper show that variability in cotton has a wide variety of causes. However, in view of cotton's biology and history, it is astonishing to find as much uniformity as we do. Unlike grain crops, which produce all of their flowers almost simultaneously, cotton opens flowers daily over a long growing season. Cotton breeders have been very successful in developing varieties capable of producing acceptable yield and quality under the climatic conditions usual for each region where cotton is grown. The grower's problems with variation in yield or quality frequently come from unusual weather which would cause a complete crop failure for plants with a shorter growing season. Varieties differ in their ability to withstand extremely hot or extremely cold weather. Richardson and Blanc (Agron. Abs. 1966, p. 23) conclude that "we have unknowingly selected for tolerance to high temperature in warmer areas".

Breeding cotton for more uniform fiber quality does not necessarily require us to assemble genetic buffering systems which can maintain fiber quality in late-maturing bolls. An alternative which we are beginning to consider is early, determinate varieties which cease flower and boll production before weather unfavorable for fiber development sets in. Perhaps such varieties would have lower yield than present long-season varieties, but the decrease might be offset by more uniform fiber quality, less expensive insect control because of a shorter growing season, less or no expense for defoliation, and less cost for harvesting because all of the crop could be picked in one early harvest.

The cotton breeder has at least two routes to more uniform fiber quality. He can select to improve the plant's buffering system so that it is less affected by extreme weather conditions, or he can shorten the period during which the plant matures bolls, so that it will not need to cope with cool weather at the end of the growing season. The data now available indicate that many factors can affect variability, but whether he uses hybrids, pure lines, doubled haploids, or breeders' selections, homozygous genes are of less importance to fiber variability than the physiological balance produced in the plants by the combination of genes that he gets into his final product.

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