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The Genetics of Certain Factors Responsible for Lint Quantity in American Upland Cotton

T. R. RICHMOND

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Preface

The experiments reported in this bulletin demonstrate two genetic systems which control the quantity of lint on seeds of American Upland cotton. The first is a single major gene for presence or absence of lint, which also controls the presence (fuzzy) or absence (glabrous) of seed fuzz. The second system involves lint quantity modifiers, or genes with minor effects, which are able to bring about their reactions in the presence of the major lint quantity gene, and can be detected directly on a homozygous glabrous seed coat background.

This suggests practical methods of breeding for increased lint quantity. They involve the isolation of the lint quantity modifiers of various normal stocks on a glabrous seed cover background; testing of the modifying complexes of the isolated lines; combining of lines with different complexes into new lines with larger and more potent complexes; cyclic crossing and selection of new lines from as many diverse sources of lint quantity modifiers as possible; and the transference of the genes in the various complexes to normal agricultural varieties.

These methods should not only prove to be useful in identifying and accumulating the lint quantity modifiers in American Upland cotton and increasing the yields of present agricultural varieties, but they also will afford a means of isolating and classifying the lint quantity modifying complexes in other taxonomic varieties of Gossypium hirsutum L., and in certain induced allotetraploids.

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T. R. RICHMOND

Professor, Department of Agronomy, Texas Agricultural Experiment Station, and Senior Agronomist, Division of Cotton and Other Fiber Crops and Diseases, Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Department of Agriculture

CULTIVATED AMERICAN UPLAND cottons, *Gossypium hirsutum* L., (n=26), according to the theory advanced by Skovsted (*21*) and confirmed independently by Beasley (*3*) and Harland (*8*), are tetraploids which have arisen by amphidiploidy from hybrids of Asiatic (n=13) and American Wild (n=13) parentage. Seeds of cultivated American Upland cottons bear hairs which are single celled protuberances from the epidermal layer of the seed coat and, chemically, are almost pure alpha-cellulose. These hairs occur in two layers: (1) An outer layer of relatively long fibers commonly called "lint" which is separated from the seed in the ginning process, and (2) a layer of short fibers or "fuzz" which remains attached to the seeds after ginning. Some of the components of yield of lint which are at least partly under genetic control are: number of bolls per plant, size of bolls (usually determined by weight), the number of seeds per boll and the quantity of lint on the seeds. All of these components have received attention by cotton breeders, but the potentialities of the quantity of lint on seeds as a contributor to total yield of lint per unit area of land have not been fully exploited by American workers.

In the early years of upland cotton culture in the United States, seeds which were completely devoid of fuzz (or nearly so) were frequently observed in cultivated varieties. Such types were rigidly selected against as they were commonly believed to be degenerate, cf. Griffee and Ligon (*6*). This glabrous-seeded condition presumably arose through simple gene mutation. By repeated selection it has been possible to extract a true-breeding, glabrous-seeded type which bears no lint, although under certain conditions such types may show a few scattered, loosely attached seed hairs. By similar breeding methods following hybridization, glabrous-seeded lines have been extracted which are so heavily linted as to be difficult to distinguish from fuzzy-seeded, fully-linted types when scored solely on the basis of amount of lint. Selected strains of the glabrous-seeded type, together with certain breeding stocks of normal American Upland cotton, were used in the studies of inheritance of lint production reported in this bulletin.

Previous Work

Hutchinson and Stephens (*14*) recognized two main types of seed hairs: (1) Unconvoluted, simple hairs borne on seeds of wild diploid species and (2) convoluted, flat, spirally twisted hairs of the cultivated Old and New World cottons. Hutchinson, *et al,* (*13*) and Stephens (*23*) hold that only convoluted cotton hairs are capable of being spun and that only such fibers are "true lint." They give evidence to support their belief that convoluted fibers may have arisen through a simple genetic change in some unconvoluted progenitor of the cultivated cottons and they attribute a great part of the evolution and distribution of cotton to man's early recognition and utilization of such convoluted types. All New World cottons, which originated as amphidiploids (n=26), were described as having true lint. Differences in the seed hairs of American Wild (n=13) cottons were studied by Hutchinson, *et al,* (*15*). These writers, using colchicine-induced polyploids of Asiatic and American Wild species, found that the chromosomes of the latter had no influence on the formation of convolutions but had an important influence on the quantity of seed hairs developed.

Glabrous-seeded mutants have been reported in the Asiatic cottons, *Gossypium arboreum* L. and *G. herbaceum* L. Kottur (*17,18*), Afzal and Hutchinson (*1*), Hutchinson (*10*), Hutchinson and Gadkari (*11*) and Silow (*20*) have studied the glabrous-seeded character in crosses with fuzzy-seeded lines. All report dominance for fuzzy (covered) in F_1 and simple Mendelian segregation in F_2. According to Hutchinson and Gadkari (*11*), Punjab Glabrous is the only one of the several glabrous mutants reported in Asiatic cottons entirely devoid of seed fuzz. The other glabrous mutants have a scant covering of very short seed hairs which allow the seed coat to show through quite prominently. The Punjab mutant appears to have the same type of glabrousness as that conditioned by the glabrous seed-cover gene in American Upland, but proof of the genetic relationship has not been given. Types with seed fuzz and no lint were reported in the Asiatic cottons but no such types have been reported in American Upland cotton.

The genetics of lint quantity in Asiatic cottons was investigated by Silow (*20*). He found that glabrousness and lintlessness were pleiotropic effects of the same gene in the study of a cross between a mutant which had glabrous seed coat and no lint and a normal line with fuzzy (covered) seed and fully developed lint. From certain crosses involving the glabrous-lintless type, homozygous glabrous lines were extracted which were linted, "usually to a lesser degree, but occasionally as heavy as, the normal, hairy fully linted plants in the same families." The presence of lint hairs on seeds with a homozygous glabrous genotype was attributed to a complex of modifiers. The modifiers were separated into a hypostatic and an epistatic series with respect to their action in the presence of the glabrous seed coat condition.

According to Harland (*7*), "A true naked (glabrous) seed is found in all three of the main sections of New World cottons, Upland, Peruvian and Bourbon. Upland naked is dominant over all other forms of fuzz distribution while Peruvian naked is recessive to all other forms so far examined." The upland glabrous gene was given the symbol, *N*. Later, in a revision of gene symbols for *Gossypium,* Hutchinson and Silow (*12*) proposed to change Harland's *N* to *Fn*. Practically all workers who have investigated the glabrousness of seeds in American Upland cotton, including Ware (*25,26*), Kearney and Harrison (*16*), Thadani (*24*), Griffee and Ligon (*6*) and Carver (*4*) have found it to be dominant to the covered condition in F_1, giving monohybrid ratios for glabrous and covered seed coat in F_2. Inheritance, with respect to glabrous seed cover, is often complicated in crosses involving *Gossypium barbadense* L., an allotetraploid species whose members, according to Balls (*2*) and Kearney and Harrison (*16*), (Sea Island, Peruvian, Egyptian and others) cross readily with *G. hirsutum* L.

Studies of the inheritance of lint quantity in the New World cottons have been made by Thadani (*24*), Kearney and Harrison (*16*), Ware (*25,26*), Griffee and Ligon (*6*) and Harland (*7*). In American Upland cotton, Thadani (*24*), found full development of lint to be dominant to sparse lint in the F_1 crosses of such types. Monohybrid ratios were obtained in the F_2. He concluded that the genes for smooth seeds and sparse lint are completely linked. Monohybrid inheritance of dense lint and sparse lint also has been reported by Griffee and Ligon (*6*), but these writers attributed glabrous seed coat and sparse lint to a single gene.

As early as 1908, Cook (*5*) pointed out the dangers in judging cotton varieties by their lint percentages and discussed the relationship of seed size and weight to percentage of lint. "To avoid some of the uncertainties of lint percentages," he proposed a *lint index* as a measure of lint quantity. Using lint percentage as a measure of lint quantity, Ware (*25*) found the F_1 of crosses of Pima (American-Egyptian) and lines of American Upland to be less than the mean lint percentage of either parent while the F_1 of Sea Island x Upland and sparse lint Upland x Upland took an intermediate position. In further studies with some of the same material Ware (*26*) showed that the amount of lint from a given number of seeds was a more reliable measure of lint quantity.

Methods

The lint quantity of the individual plants analyzed in this study was determined by the calculation of a *lint index*, which is defined as the weight, in grams, of the lint from 100 seeds and may be calculated by the following formula:

$$\frac{\text{seed index x total weight of lint in sample}}{\text{total weight of seed in sample}}$$

where the seed index is the weight, in grams, of 100 seeds.

In the tables in which lint index distributions are given, 0.0 lint index is represented as one class and the class interval of succeeding classes is one lint index. Each class is represented by its class center, i.e. 0.0, 0.5, 1.5 and so on. The mean and mode of each progeny or each seed cover class within a population also are given in the tables, the latter being in italics.

The F_2 crosses of the glabrous-seeded parents, Lintless and High-Smooth, with covered-seeded parents, Missdel and Half & Half, respectively, were scored by visual methods for seed cover and lint quantity. *Glabrous* and *covered* were the descriptive terms used in scoring for seed cover. Two general, though by no means discrete, classes were recognized when scoring of the F_2 material for lint quantity by visual methods was attempted: (1) A class in which the quantity of lint is so reduced that the black color of the glabrous seed coat shows through a thin to heavy veil of lint (In large populations, a small number of the plants in this class will be devoid of lint.); (2) A class which, if the seeds are not examined, is indistinguishable from the fully linted condition of the covered seeded parent. The first class was designated *sparse* and the second, *dense;* scoring by visual methods was done on this basis. In those crosses where the F_2 lint index distributions were clearly bimodal, separation into two classes, *sparse* and *dense,* was made at, or near, the point of minimum frequency between the modes. In the Half & Half x Lintless crosses, separation was made at the class limits of 3.0 and 3.1. This was not the point of minimum frequency in all cases but it was the lower limit of the lint index distribution of the F_1 of these crosses. Certain progeny tests substantiated the choice of this point but such tests could not be made of each plant to be classified. The point given was used in the sparse vs. dense lint classifications and also in the separation of "homozygous" glabrous and "heterozygous" glabrous seed coat in the presentation of the data for lint index distributions for crosses of Half & Half x Lintless. Separation of the "heterozygous" glabrous and the "homozygous" covered seed coat types was easily accomplished by inspection of the seed coats of the individual segregates.

In such statistical analyses as were made, Mather's (*19*) methods were followed in the analysis of the Chi-square, and formulae given by Hayes and Immer (*9*) and Snedecor (*22*) were used in calculating correlation coefficients and other common statistics. Since many of the distributions were skewed or otherwise distorted and, therefore, not adapted to binomial analysis, tables and figures have been used extensively in the presentation and interpretation of the data.

Materials

The parental lines used in this study were extracted by inbreeding from cultivated varieties of American Upland cotton. The designations of the strains and their seed coat and lint quantity characteristics are given below:

Strain	Seed coat and lint quantity
Lintless (Ls.)	glabrous—no lint
High-Smooth (HS)	glabrous—approx. lint index = 3.5
Missdel (Ms.)	covered—approx. lint index = 5.0
Half & Half (H&H)	covered—approx. lint index = 7.5

A brief history and description of each strain follows:

Lintless: Lintless has been carried as a type line in the genetics nursery of the Texas Agricultural Experiment Station at College Station, Texas, for more than 20 years. The early pedigree of the strain is obscure but it is known to have originated, presumably by a single gene mutation, in a commercial variety. The seeds of Lintless are completely glabrous. Occasionally a plant may bear seeds with a very few, loosely attached, lint fibers but never more than 8 or 10, which are not separated from the seeds in the ginning process. Also, seeds in a single boll, or in a single lock within a boll on plants otherwise completely lintless, occasionally may exhibit this condition. Since many generations of selection have failed to eliminate these few hairs and since the condition occurs as often among bolls within plants as between plants in progeny rows, the presence of a very small number of hairs must be considered a characteristic of the line. The seeds of Lintless would be classified as small for American Upland cotton, the mean seed index under good growing conditions being about 10. In a newly opened boll the seeds in each locule of a boll often stick together forming a "kidney." As the boll opens fully and the seeds dry out, they fall to the ground unless they are bagged.

High-Smooth. This strain originated from a cross, made in 1936, between synthetic Line 2 (a genetic stock with glabrous seeds, brown, sparse lint and three other simply inherited characters) and Half & Half (a selfed line of a commercial variety that had covered seeds and white lint). The strain extracted by selection for high lint quantity from this cross, and designated as High-Smooth in 1942, has glabrous seeds which are approximately the same size as those of Lintless. But unlike Lintless, it bears a considerable quantity of lint, the mean lint index under good growing conditions approximating 3.5.

Missdel. The Missdel strain used in these experiments was selected in 1939 as having the lowest level of lint quantity (lint index 5.0 to 5.5) in a large number of selfed lines from commercial varieties with covered (fuzzy) seeds. The seeds of Missdel are classified as average in size and give a seed index of 12.0 to 12.3 under conditions comparable to those mentioned above.

Half & Half. This strain, selected in 1939 from the same group of selfed lines from commercial varieties with covered seeds which furnished Missdel, was taken to represent the highest available level of lint quantity, the mean lint index being approximately 7.5. The seeds give a seed index of about 10.5 and are classified as small.

Experimental Results

The lint quantity data for the four parental types, Lintless, High-Smooth, Missdel and Half & Half, and the six possible crosses of these types fall conveniently into three main categories: (A) Crosses involving parental types with glabrous and covered seed coats—Cross 1, Half & Half x Lintless; Cross 2, Missdel x Lintless; Cross 3, Half & Half x High-Smooth; Cross 4, Missdel x High-Smooth. (B) Crosses involving parental types with glabrous seed coats—Cross 5, High-Smooth x Lintless. (C) Crosses involving parental types with covered seed coats—Cross 6, Half & Half x Missdel.

Cross 1. Half & Half x Lintless

Lint index distributions for the Lintless and Half & Half parental lines grown during the period 1942-1945, the F_1 hybrids grown during the period 1942-1944, and the F_2 populations grown in 1943 and 1945 are given in Table 1. Diagrams in Figures 1 and 2 show the lint index distributions for the 1943 and 1945 Half & Half x Lintless crosses, respectively, and frequencies are given in terms of the percentage of the total number of plants in each population.

The Lintless parents, in all 4 years, had glabrous seed coats and were devoid of lint. The Half & Half lines all had covered seeds and were quite uniform in lint quantity, the modal class, with the exception of two small progenies, being 7.5. The F_1's had glabrous seed coats and were intermediate in lint index though they approached the Half & Half closer than the Lintless parent and were no more variable than Half & Half.

A small F_2 progeny in 1943 gave similar results to those obtained from larger populations in 1945. The 1945 Group A F_2 progeny of 13 families with a total of 399 plants and Group B of 9 families totaling 290 plants decended from crosses of different original parent plants and, though similar in major respects, their identity has been maintained to bring out certain minor points.

Only the parental seed cover types, glabrous and covered, were recovered in F_2, and as is shown in Table 2, simple

Table 1. Distribution of lint indexes in parental lines of Lintless and Half & Half, and F_1 and F_2 generations of their crosses

Year	Parental or hybrid designation	Gen.	Seed cover	L.I. of parents	Distribution of lint index [1] 0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	Total	Mean
1942	Lintless [2]	P	G		36												36	0
1943	Lintless [3]	P	G		15												15	0
1943	Lintless 326-5	P	G	0	4												4	0
1944	Lintless 326-5-1	P	G	0	4												4	0
1944	Lintless 326-5-3	P	G	0	12												12	0
1945	Lintless 326-5-1-1	P	G	0	7												7	0
1945	Lintless 326-5-3-1	P	G	0	10												10	0
1942	Half & Half [4]	P	C								2	10	*11*	2			25	7.0
1943	Half & Half [5]	P	C									6	7	3			16	7.3
1943	Half & Half 432-4	P	C	6.4								*2*	1	1			4	7.3
1943	Half & Half 432-5	P	C	6.6								*1*	*1*				2	7.0
1944	Half & Half 432-4-4	P	C	6.9								2	*6*	2			10	7.5
1944	Half & Half 432-5-2	P	C	6.6								2	7	6			15	7.8
1945	Half & Half 432-4-4-2	P	C	7.4								2	*11*	7			20	7.8
1945	Half & Half 432-5-2-4	P	C	6.3								1	*12*	3			16	7.6
1942	Half & Half x Lintless [6]	F_1	G							*14*	13	3					30	5.1
1943	Half & Half x Lintless [7]	F_1	G							6	7	3					16	5.3
1944	H&H 432-4-4 x Ls. 326-5-3	F_1	G						2	21	*35*	2					60	5.1
1944	H&H 432-5-2 x Ls. 326-5-4	F_1	G						3	*11*	9						23	4.8
1943	Half & Half x Lintless	F_2	Homo. G*		1	*3*	1	*3*									8	1.3
			Het. G						3	7	*8*						18	4.8
			Homo. C								2	7	3	2			14	6.9

Table 1 (continued)

Year	Parental or hybrid designation	Gen.	Seed cover	L.I. of parents	0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	Total	Mean
					Distribution of lint index [1]													
1945	H&H x Ls. Group A[8]	F_2	Homo. G*		8	*60*	10	8									86	0.8
			Het. G						40	*75*	*75*	17	1				208	4.8
			Homo. C							10	19	31	*33*	11	1		105	6.7
1945	H&H x Ls. Group B[9]	F_2	Homo. G*		11	*50*	4	9									74	0.7
			Het. G						33	*60*	35	7	1				136	4.6
			Homo. C						3	8	*32*	21	7	8	1		80	6.1
1945	H&H x Ls. Groups A & B	F_2	Homo. G*		*19*	*110*	14	17									160	0.7
	combined		Het. G						73	*135*	110	24	2				344	4.8
			Homo. C						3	18	51	*53*	39	19	2		185	6.4
1945	H&H x Ls. Group A	F_2	G		1	*27*	3		1								32	0.7
	F_2's tested in F_3		G						20	20	*32*	5					77	4.8
			C								2	4	*10*	4			20	7.3
1945	H&H x Ls. Group B	F_2	G		4	*11*		1									16	0.5
	F_2's tested in F_3		G						8	*19*	10	4					41	4.7
			C							1	*3*	*3*					7	5.8
1945	H&H x Ls. Groups A & B	F_2	G		5	*38*	3	1	1								48	0.6
	combined		G						28	39	*42*	9					118	4.8
	F_2's tested in F_3		C						1	5	7	10	4				27	5.9

[1] Modal class italicized.
[2] 4 progenies combined.
[3] 5 progenies combined.
[4] 4 progenies combined.
[5] 5 progenies combined.
[6] 4 progenies combined.
[7] 5 progenies combined.
[8] 8 families combined.
[9] 9 families combined.
* Homozygous glabrous and heterozygous glabrous classes separated at the class limits of 3.0-3.1.

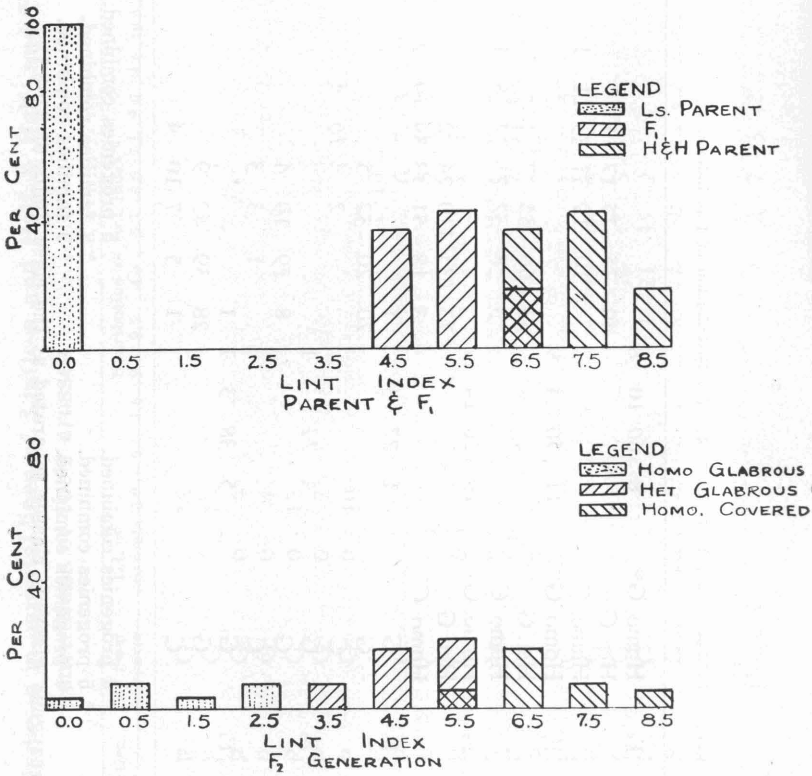

Figure 1. Distribution of lint indexes of Half & Half and Lintless parents and the F_1 and F_2 generations in 1943.

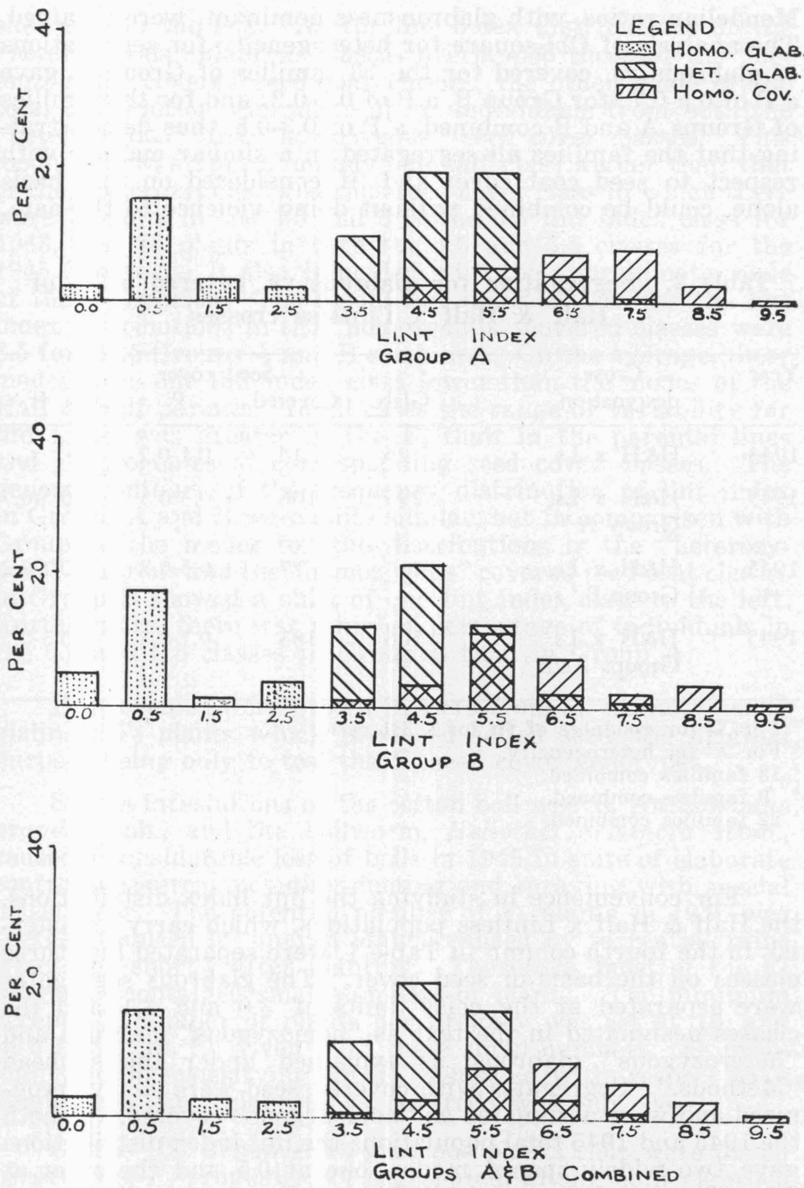

Figure 2. Distribution of lint indexes in the 1945 F_2 generation of crosses between Half & Half and Lintless showing the frequencies of combined families in Group A and in Group B and the total frequencies of Group A and Group B combined.

Mendelian ratios, with glabrousness dominant, were obtained. The analysis of Chi-square for heterogeneity for segregations of glabrous vs. covered for the 13 families of Group A gave a P of 0.5-0.7; for Group B, a P of 0.1-0.2; and for the families of Groups A and B combined, a P of 0.3-0.5, thus demonstrating that the families all segregated in a similar manner with respect to seed coat cover and, if considered on this basis alone, could be combined without doing violence to the data.

Table 2. Segregation for glabrous vs. covered in F_2 of Half & Half x Lintless crosses

Year	Cross designation	Seed cover Glab.	Covered	P[1]	P[2]
1943	H&H x Ls.	26	14	0.1-0.2	
1945	H&H x Ls. Group A [3]	293	106	0.3-0.5	0.5-0.7
1945	H&H x Ls. Group B [4]	213	77	0.5-0.7	0.1-0.2
1945	H&H x Ls. Groups A&B [5]	506	183	0.7-0.8	0.3-0.5

[1] For X^2 for goodness of fit for a 3:1 ratio.
[2] For X^2 for heterogeneity.
[3] 13 families combined.
[4] 9 families combined.
[5] 22 families combined.

For convenience in studying the lint index distributions, the Half & Half x Lintless populations, which carry an asterisk in the fourth column in Table 1, were separated into three classes on the basis of seed cover. The glabrous segregates were separated at the class limits of 3.0 and 3.1 and the classes designated in the text as "homozygous" glabrous and "heterozygous" glabrous, as explained under the subhead "Methods." Segregates with covered seed were easily recognized and were designated as "homozygous" covered. In both the 1943 and 1945 total populations the lint index distributions gave two widely spaced modes, one at 0.5 and the other at 5.5. The modal class at 0.5 fell in the "homozygous" glabrous seed coat class. Small numbers of lintless (0.0 lint index) segregates were obtained and the lint index distributions, particularly in the larger 1945 populations, exhibited definite skewness to the left. As the lint index distributions of the "heterozygous" glabrous classes overlapped those of the "homozygous" covered seed coat classes, the other mode of the total distribution was made up of individuals from both the "heterozygous" and "homozygous" seed cover classes. This mode, 5.5, was approximately one-half class higher than that of the "heterozygous" glabrous seed cover class in which there were 7 plants in the 4.5 and 8 in the 5.5 lint index class for 1943, and 75 plants in both the 4.5 and 5.5 classes for the 1945 Group A. It also coincided with the approximate mode of the F_1 hybrids. The modal lint index classes for the lint index distributions in the "homozygous" covered classes were 6.5 for 1945 Groups A and B combined. On the average, these modes were one lint index class lower than the modes of the Half & Half parents. In all cases the range of variability for lint index was greater in the F_2 than in the parental lines and F_1 progenies of corresponding seed cover classes. The general contours of the frequency distribution of lint index in Groups A and B were quite similar, but in comparison with Group A, the modes for the distributions in the "heterozygous" glabrous and the "homozygous" covered seed coat classes in Group B showed a shift of one lint index class to the left. Furthermore, there was a higher percentage of individuals in the 0.0 and 2.5 classes in Group B than in Group A.

F_3 progenies were grown in 1946 from all phenotypically glabrous F_2 plants which produced selfed seed, the original purpose being only to test the F_2 seed cover genotypes.

Severe infestations of the cotton boll weevil, *Anthonomus grandis* Boh., and the bollworm, *Heliothis armigera* Hbm., caused a considerable loss of bolls in 1945 in spite of elaborate control measures, including dusting and spraying with special insecticides. The potential number of F_3 plants in 1946 was further reduced by uneven stands caused by torrential rains which fell shortly after planting. Therefore, most of the F_3 progenies contained small numbers of plants. The minimum acceptable number of plants per progeny was set at 10, and in 5 instances, 9. Even with these small numbers, the probability of misclassifying an F_2 genotype with respect to a single gene pair (glabrous vs. covered) was only .05.

Of the 109 Group A F_2 glabrous plants that were tested by growing F_3 progenies, 77 segregated, giving both glabrous and covered plants, and 32 bred true. The segregation in Group B was 41:16. In both groups, the ratio of segregating to true breeding F_3 progenies fit the theoretical 2:1 ratio, the probabilities being 0.3-0.5 and 0.5-0.7, respectively. These results show that, in respect to the distribution of the genes for seed cover, the F_3 progenies represent a random sampling of the F_2 glabrous phenotypes. A few F_3 progenies of F_2 plants with covered seeds were grown to confirm the recessive genotype; all bred true for covered seeds. The lint index distributions for the tested F_2 plants were similar to those of the total populations from which they were taken. One Group A F_2 plant with a lint index which fell in the 3.5 class was found to be homozygous glabrous when tested in F_3. This plant represented approximately 5 percent of the tested plants in the 3.5 lint index class and on this basis, 2 such plants in the total Group A population would be expected. One of the 9 individuals in the 2.5 lint index class in the Group B population was tested in F_3 and found to be homozygous. The lowest lint index range in which F_2 plants were proved to be heterozygous glabrous by F_3 test was the 3.5 class. Twenty such plants from Group A and 8 from Group B were tested. Although these findings can not be considered as conclusive evidence, they lend weight to the choice of the point of separation for "homozygous" and "heterozygous" glabrous seed coat used in the total populations.

Most of the previous work on the inheritance of lint quantity in crosses involving glabrous and covered seed types has been done by scoring individual plant samples for "dense" and "sparse" lint in segregating populations, as described under the subhead "Methods." The F_2 material of the 1943 and 1945 Half & Half x Lintless crosses was scored in this manner and the data are given in Table 3 under "Lint (Visual)."

Taking P .05 as the minimum acceptable probability, only one progeny, 1945 Group B, gave a satisfactory fit to a ratio of 3 dense: 1 sparse when classified by the visual method. The same material was classified for lint quantity by separating the individual plant samples into dense and sparse lint groups at the lint index class limits of 3.0 and 3.1, as described and all of the segregations gave a satisfactory fit to a 3:1 ratio. As measured by their probabilities, the heterogeneity Chi-square determinations for the 13 families in 1945 Group A, the 9 families in Group B and 22 families combined were not significant under the visual or the lint index methods of classification. While the heterogeneity tests show that the 1945 F_2 families segregated in a consistent manner and might be combined for purposes of Chi-square analysis of dense vs. sparse lint, it should be pointed out that the sparse lint class was usually deficient in numbers, i.e. contained less than 25 percent of the total.

Table 3. Segregation for sparse vs. dense lint in F_2 of Half & Half x Lintless crosses

Year	Cross designation	Lint (Visual) Dense	Sparse	P[1]	P[2]	Lint (Lint index) Dense	Sparse	P[1]	P[2]
1943	H&H x Ls.	36	4	.02-.05		34	6	0.1-0.2	
1945	H&H x Ls. Group A[3]	323	76	0.01	0.2-0.3	313	86	0.1-0.2	0.3-0.5
1945	H&H x Ls. Group B[4]	227	63	0.1-0.2	0.9-.95	216	74	0.8-0.9	0.9-.95
1945	H&H x Ls. Groups A&B[5]	550	139	0-0.01	0.7-0.8	529	160	0.2-0.3	0.8-0.9

[1] For X^2 for goodness of fit for a 3:1 ratio.
[2] For X^2 for heterogeneity.
[3] 13 families combined.
[4] 9 families combined.
[5] 22 families combined.

F_3 progenies of the 1945 Half & Half x Lintless crosses, grown principally to check the F_2 seed-cover genotype, were also analyzed by individual plant for lint index. Simple covariance analysis of lint index in the homozygous glabrous material showed significant positive correlation between the lint indexes of the F_2 parent plants and the mean lint indexes of corresponding F_3 progenies in both Group A ($r = 0.697 \pm 0.169$, d.f. = 30) and Group B ($r = 0.892 \pm 0.141$, d.f. = 14). In Group A, only one F_2 plant with 0.0 lint index was tested and it bred true in F_3. Three F_2 plants with lint indexes of 0.2 segregated in F_3 but the range was confined to the 0.0 and 0.5 classes, and in 2 of the cases the modal class was 0.0. The lint indexes of the F_3 progeny of the F_2 plant with the highest lint index tested, 3.8, ranged between the limits of the 0.5 and 2.5 classes with only one plant falling in the latter class. Four Group B F_2 plants with 0.0 lint index were tested in F_3 and 2 of these bred true for lintless and 2 segregated, giving plants in the 0.0 and 0.5 lint index classes. The F_2 plant with the highest F_2 lint index in the group, 2.1, gave a lint index distribution in F_3 in which 1 plant fell in the 2.5 class and another in the 3.5 class. The latter was the highest lint index segregate observed in the homozygous glabrous F_3 populations and approximated the lint index of the High-Smooth parental type which was extracted by similar methods several years ago.

In the simple covariance analysis of the lint index of parents with covered seeds and corresponding means of homozygous covered progenies, $r = 0.302 \pm .59$ (d.f. = 18) for Group A and $r = 0.447 \pm .72$ (d.f. = 5) for Group B. In both groups the correlation coefficients, though in a positive direction, were not significant. Considering the progenies in Group A, the range of lint index was 3.1 to 11.0 and the mean lint indexes of F_3 progenies ranged from 4.9 to 7.4, with a general mean of 6.3. In one progeny with an F_2 parental lint index of 6.4, 2 plants fell in the 10.5 lint index class and the segregates covered a range of 7 lint index classes. The distributions in Group B were similar to those of Group A except that the ranges of lint index were generally at a slightly lower level.

Cross. 2. Missdel x Lintless

With respect to seed cover, the Lintless parents were glabrous and the Missdel parents were covered. The F_1 of the crosses was glabrous and the F_2 generation grown in 1943 segregated 36 glabrous: 7 covered giving a satisfactory fit to

Table 4. Distribution of lint indexes in crosses of Missdel x Lintless, Half & Half x High-Smooth and Missdel x High-Smooth and their corresponding parental lines

Year	Parental or hybrid designation	Gen.	Seed cover	Distribution of lint index [1] 0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	Total	Mean
1942	Lintless [2]	P	G	*36*										36	0
1943	Lintless [3]	P	G	*15*										15	0
1942	High Smooth [4]	P	G				5	*20*	1					26	3.3
1943	High Smooth [5]	P	G				9	*25*	8					42	3.5
1942	Missdel [6]	P	C					1	11	*13*	1			26	5.0
1943	Missdel [7]	P	C						6	*21*	8			35	5.6
1942	Half & Half [8]	P	C							2	10	*11*	2	25	7.0
1943	Half & Half [9]	P	C								6	*7*	3	16	7.3
1942	Missdel x Lintless [10]	F_1	G				8	*19*						27	3.2
1943	Missdel x Lintless [11]	F_1	G				4	*12*	3					19	3.4
1942	Half & Half x High Smooth [12]	F_1	G							6	*19*	8		33	6.6
1943	Half & Half x High Smooth [13]	F_1	G						4	*5*	4	1		14	5.7
1942	Missdel x High Smooth [14]	F_1	G					2	10	*15*	1			28	5.0
1943	Missdel x High Smooth [15]	F_1	G						*8*	3				11	4.8
1943	Missdel x Lintless	F_2	Homo. G*	*9*	1									10	0.1
			Het. G			4	*12*	8	2					26	2.8
			Homo. C						2	*4*	1			7	5.4
1943	Half & Half x High Smooth	F_2	Glab.			1	5	4	*12*	10	2			*34*	*4.4*
			Homo. C					2	1	*5*	*5*	4		17	6.0
1943	Missdel x High Smooth	F_2	Homo. G*		9	7	5							21	1.3
			Het. G					14	*18*	11	6	1		50	4.7
			Homo. C					1	3	*8*	6	3	1	22	6.0

[1] Modal class italicized.
[2] 4 progenies combined.
[3] 5 progenies combined.
[4] 4 progenies combined.
[5] 9 progenies combined.
[6] 4 progenies combined.
[7] 5 progenies combined.
[8] 4 progenies combined.
[9] 5 progenies combined.
[10] 4 progenies combined.
[11] 2 progenies combined.
[12] 4 progenies combined.
[13] 5 progenies combined.
[14] 4 progenies combined.
[15] 3 progenies combined.

*Homozygous glabrous and heterozygous glabrous classes separated at the class limits of 1.0—1.1.

a 3:1 ratio since the probability for Chi-square for goodness of fit was 0.2-0.3.

Table 4 shows that the Lintless parents were truly lintless since every plant had 0.0 lint index. The modal lint index class for the Missdel parents was 5.5 in both years. The F_1 progenies of this combination were intermediate in lint quantity and, on the average, showed approximately the same variability as the Missdel parents. The modal F_1 class in each case was 3.5, but the mode as well as the general mean fell 1 lint index class to the right of the median position between the 2 parents. In F_2 the modal lint index class of the "homozygous" glabrous seed cover class was 0.0. Nine plants, or 21 percent of the total population, fell within this class and the 1 remaining plant in the seed cover class fell in the

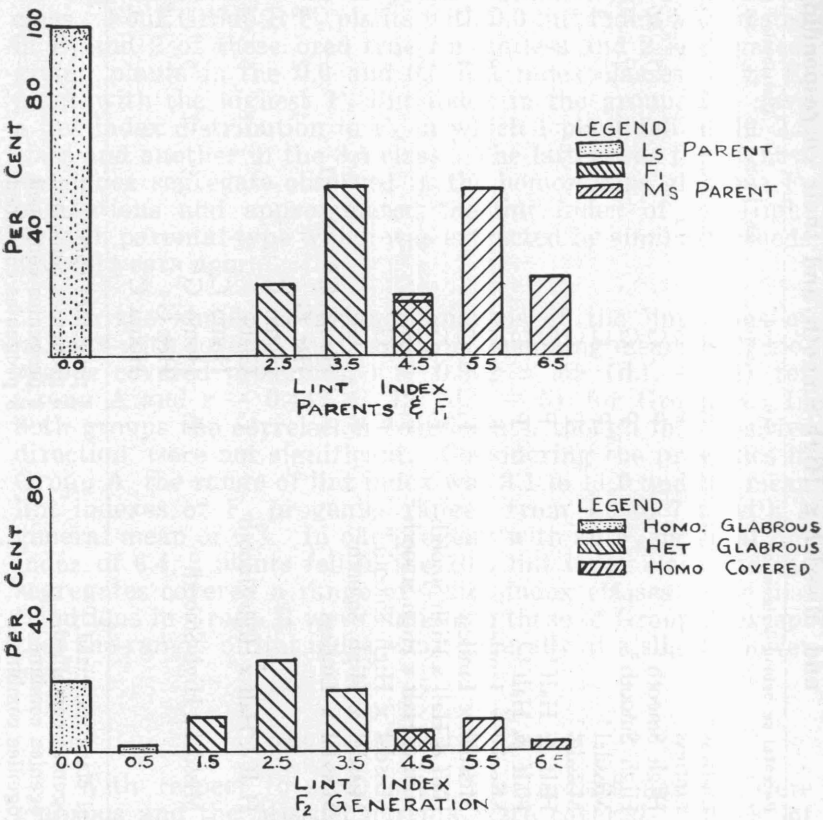

Figure 3. Distribution of lint indexes of Missdel and Lintless parents and the F_1 and F_2 generations in 1943.

next higher lint index class. The lint index mode of the "heterozygous" glabrous seed cover class was 2.5 while that of the F_1 was 3.5 and appears to be only slightly more variable than the F_1. The modal lint index class of the covered seed coat class was the same as that of the Missdel parents.

The segregation for lint quantity in the F_2 was 33 dense: 10 sparse, when classifications were made by both the visual and the lint index methods. In the latter case, separation of dense and sparse was made at the 1.0 point, which was the upper limit of the lint index class of minimum frequency between the extremes of distribution. The probability for Chi-square for goodness of fit of the above ratio to a theoretical ratio of 3 dense: 1 sparse was 0.7-0.8.

Figure 3 gives a graphic presentation of the lint index distributions of the parents, F_1 and F_2, of the Missdel x Lintless cross for 1943.

Cross 3. Half & Half x High-Smooth

The lint index distribution data for the High-Smooth and Half & Half parental lines and their hybrids are given in Table 4 and diagrams of these distributions are given in Figure 4. The Half & Half parental lines for 1942 and 1943 were the same as those given for Cross 1 in these years. The 1942 and 1943 High-Smooth lines had glabrous seed coats and a considerable quantity of lint, the modal lint index class being 3.5. The F_1 lint index distributions, with modes at 6.5 in 1942 and 5.5 in 1943, were intermediate, though they approached the Half & Half parent. The F_1's were no more variable than either parent.

The seed cover segregations in F_2 were 34 glabrous: 17 covered which gives a probability of 0.1-0.2 for Chi-square for goodness of fit for a 3:1 ratio.

When seed cover classes are not taken into consideration, the distinctly bimodal distribution of lint indexes observed in the F_2 generation of other crosses involving glabrous and covered seed coat types is not in evidence in this cross, although a slight depression in the contour of the class points in Figure 4 is noted and classification on the basis of dense and sparse lint was not attempted. In the total F_2 population of only 51 plants, the maximum lint index range of the Half & Half parent was not attained in the F_2, although it is probable that this point would have been reached in a larger F_2 population. On the covered seed coat background the lint

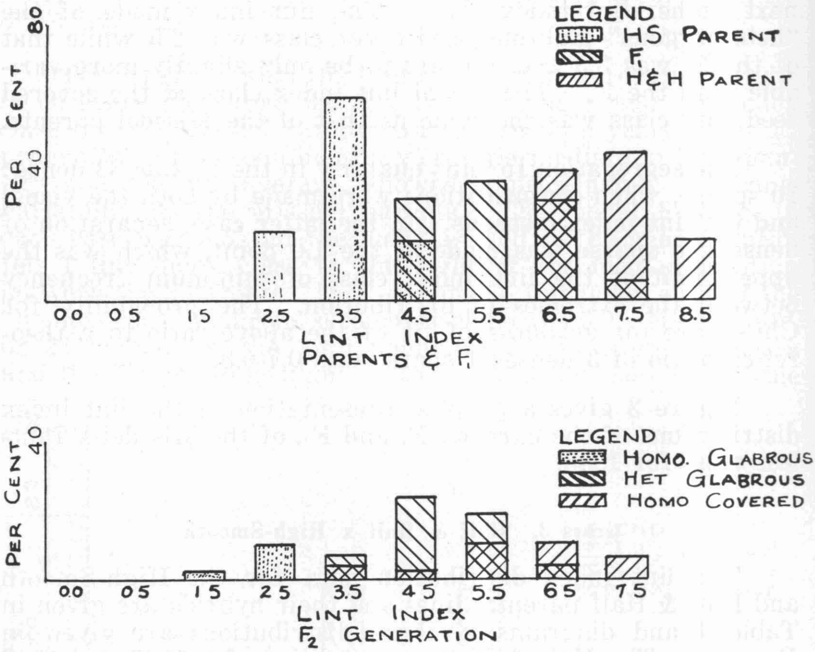

Figure 4. Distribution of lint indexes of Half & Half and High-Smooth parents and F_1 and F_2 generations in 1943.

index range was from 3.5 to 8.0 with the mode divided between classes 5.5 and 6.5. No segregates occurred in the 0.0 and 0.05 classes.

Cross 4. Missdel x High-Smooth

The seed coat cover characteristics and lint quantity behavior of the 1942 and 1943 Missdel and High-Smooth lines have been described previously in connection with Crosses 2 and 3, respectively. The lint index modes of the F_1 and the Missdel parent were in the 5.5 class in 1942, however, the F_1 mode in 1943 was 4.5. There was partial to complete phenotypic dominance of the Missdel parent.

As in other crosses involving glabrous and covered seed coat, the Missdel x High-Smooth F_1 was glabrous. The F_2 segregated 72 glabrous: 21 covered. The probability for a Chi-square for goodness of fit on a 3:1 basis was 0.5-0.7.

Lint index distributions for the F_2 and backcrosses of this cross are presented in Table 4 and Figure 5. The total range of lint indexes in the F_2 population exceeds the ranges of the parents in both directions, clearly indicating transgressive segregation. The modal lint index class of the covered seed class was 5.5 which was also the modal class of the Missdel parent, but the range of distribution was much greater than that of Missdel. On the "heterozygous" glabrous background in F_2 the mode approximated the general mode of the F_1 progenies and in this case also, the range of lint indexes was considerably greater than that of the F_1. The F_2 lint indexes in the "homozygous" glabrous seed coat class were largely outside of and lower than the range of the High-Smooth parents.

When classified by the visual method, the segregation for

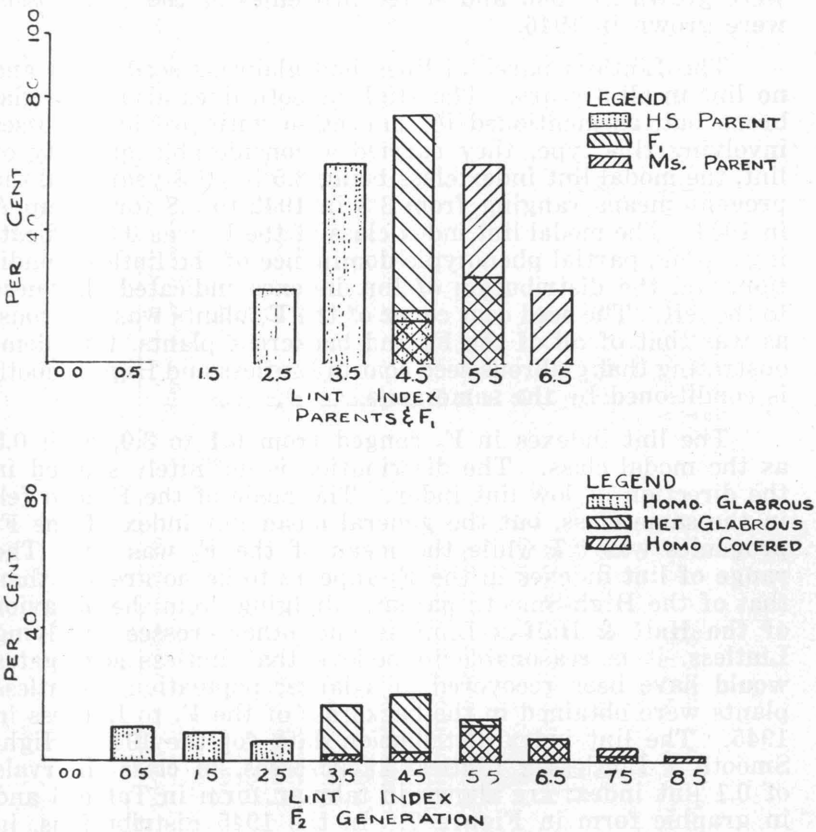

Figure 5. Distribution of lint indexes of Missdel and High-Smooth parents and F_1 and F_2 generations in 1943.

dense vs. sparse lint was 84:9 which gave a probability of less than 0.01 for goodness of fit to a 3:1 ratio, but when classified on the basis of lint index, using 3.0 as the point of minimum lint index frequency, the segregation was 72 dense: 21 sparse and as measured by its probability, 0.5-0.7, the Chi-square for goodness of fit to a 3:1 ratio was satisfactory.

Cross 5. High-Smooth x Lintless

Lint index distributions for the Lintless and High-Smooth parental lines, the F_1 hybrids and F_2 and backcross generations are presented in Table 5 and Figure 6. The parental lines and F_1 progenies were grown during the 3-year period, 1942-44. Backcross populations, designated as Groups A and B, were grown in 1945 and selfed progenies of the backcrosses were grown in 1946.

The Lintless parental lines had glabrous seed coats and no lint in all 3 years. The High-Smooth lines also were glabrous but, as mentioned in connection with previous crosses involving this type, they carried a considerable quantity of lint, the modal lint index class being 3.5 in all 3 years and the progeny means ranging from 3.3 in 1942 to 3.8 for Group A in 1944. The modal lint index class of the F_1 was 0.5, indicating strong, partial phenotypic dominance of the lintless condition, and the distribution of lint indexes indicated skewness to the left. The seed coat cover of the F_1 plants was glabrous, as was that of all of the F_2 and backcross plants, thus demonstrating that glabrous seed coat in Lintless and High-Smooth is conditioned by the same gene.

The lint indexes in F_2 ranged from 0.1 to 3.0, with 0.5 as the modal class. The distribution is definitely skewed in the direction of low lint index. The mode of the F_1 also fell in the same class, but the general mean lint index of the F_1 progenies was 0.7 while the mean of the F_2 was 1.0. The range of lint indexes in the F_2 appears to be no greater than that of the High-Smooth parent. Judging from the behavior of the Half & Half x Lintless and other crosses involving Lintless, it is reasonable to believe that lintless segregates would have been recovered in a larger population. Lintless plants were obtained in the backcross of the F_1 to Lintless in 1945. The lint index distribution data for the 1945 (High-Smooth x Lintless x Lintless backcrosses, in class intervals of 0.1 lint index, are shown in tabular form in Table 6 and in graphic form in Figure 7. In the 1945 distributions, in which the class interval was 1.0 (Table 5), 12 plants of a total of 39 Group A and 21 out of a total of 87 Group B plants

Table 5. Distribution of lint indexes in parental lines of Lintless and High-Smooth, and the F_1, F_2 and backcross generations

Year	Parental or hybrid designation	Gen.	Seed cover	L.I. of parents	Distribution of lint index [1] 0.0	0.5	1.5	2.5	3.5	4.5	5.5	Total	Mean
1942	Lintless [2]	P	G		*36*							36	0
1943	Lintless [3]	P	G	0	*15*							15	0
1944	Lintless 326-5-1	P	G	0	*4*							4	0
1944	Lintless 325-5-2	P	G	0	*3*							3	0
1942	High-Smooth [4]	P	G					5	*20*	1		26	3.3
1943	High-Smooth [5]	P	G					9	*25*	8		42	3.5
1944	High-Smooth 121-8-1	P	G						*8*	3		11	3.8
1944	High-Smooth 429-1-1	P	G					3	*12*	2		17	3.4
1942	High-Smooth x Lintless [6]	F_1				*24*	3					27	0.6
1943	High-Smooth x Lintless [7]	F_1				*15*	4					19	0.7
1944	HS 121-8-1 x Ls. 326-5-1	F_1				*32*	13					45	0.8
1944	HS 429-1-1 x Ls. 326-5-2	F_1				*29*	3	1				33	0.7
1943	High-Smooth x Lintless	F_2	G			*44*	27	7				78	1.0
1945	(HS x Ls) x Ls Group A	B/C_1	G		12	*27*						39	0.3
1945	(HS x Ls) x Ls Groug B	B/C_1	G		21	*65*	1					87	0.5

[1] Modal class italicized.
[2] 4 progenies combined.
[3] 5 progenies combined.
[4] 4 progenies combined.
[5] 9 progenies combined.
[6] 4 progenies combined.
[7] 3 progenies combined.

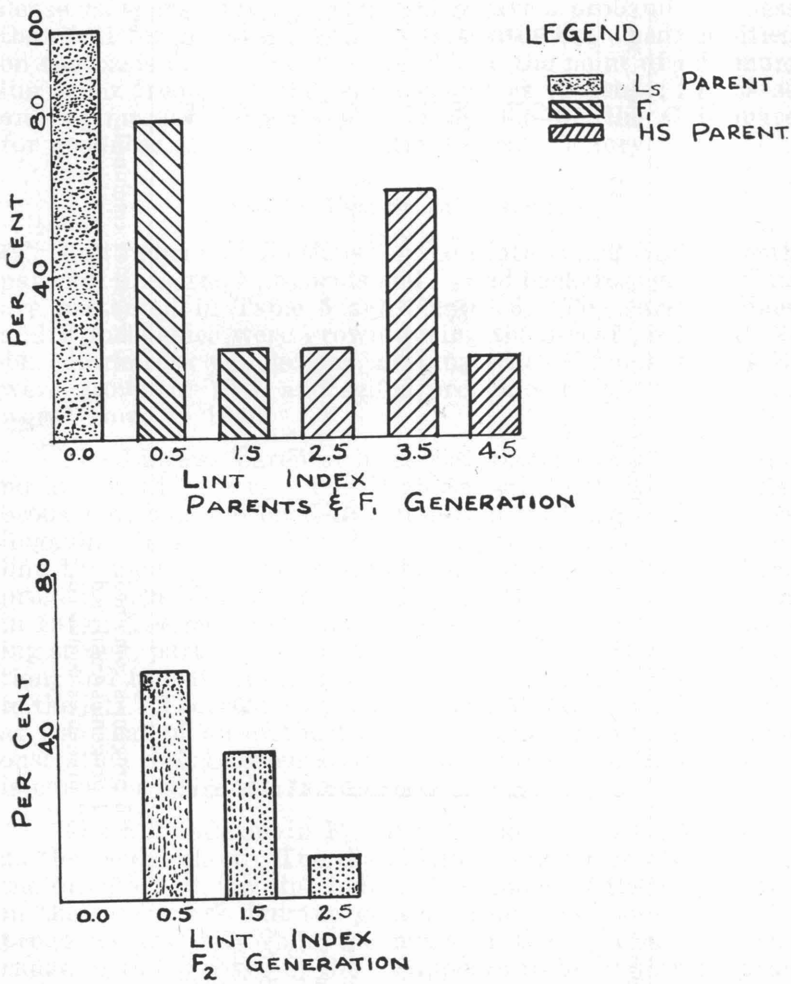

Figure 6. Distribution of lint indexes of High-Smooth and Lintless parents and the F_1 and F_2 generations in 1943.

had 0.0 lint index and the modal class in both groups was 0.5. In the distributions on the basis of a class interval of 0.1 (Table 6), the range of lint index in Group A was 0.0 to 0.8, and was 0.0 to 1.2 in Group B. In the distributions in which the 0.1 class interval was employed, the 0.0 class becomes the mode of the entire distribution but, considering the classes in which lint was produced, the 0.2 class was the mode in both

Table 6. Distribution of lint indexes in (High Smooth x Lintless) x Lintless backcrosses

Year	Strain or hybrid designation	Seed cover	Mean L.I. of F_1 parent	Distribution of lint index 0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	Total	Mean
1945	(HS x Ls) x Ls, Group A	G	0.8	12	5	9	3	5	2	2		1					39	0.2
1945	(HS x Ls) x Ls, Group B	G	0.7	21	9	11	10	7	9	8	7	1	1	2		1	87	0.3
1945	Groups A and B	G		33	14	20	13	12	11	10	7	2	1	2		1	126	0.3

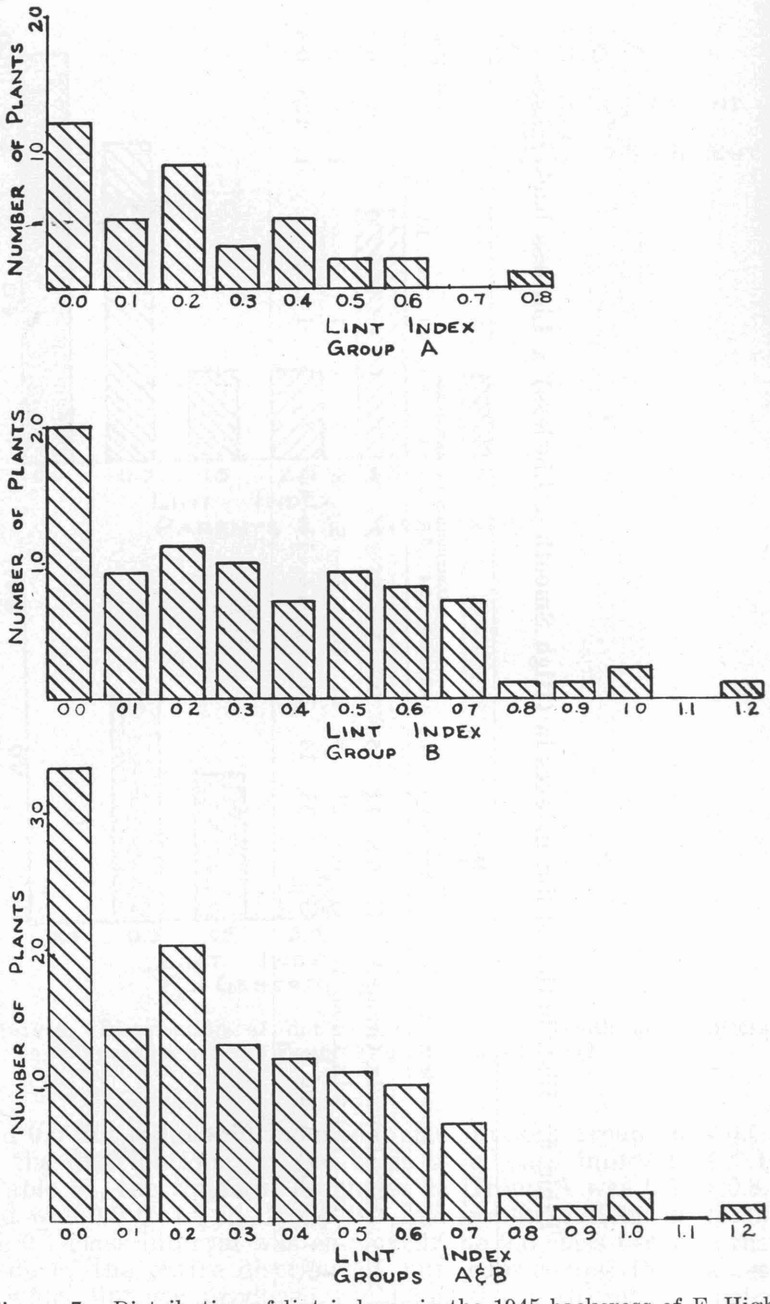

Figure 7. Distribution of lint indexes in the 1945 backcross of F_1 High-Smooth x Lintless to Lintless.

Table 7. Distribution of lint indexes in parental lines of Missdel and Half & Half, and F_1 and F_2 generations

Year	Parental or hybrid designation	Gen.	Seed cover	Distribution of lint index[1] 0.0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	Total	Mean
1942	Missdel[2]	P	C					1	11	*13*	1			26	5.0
1943	Missdel[3]	P	C						6	*21*	8			35	5.6
1944	Missdel 112-1-10	P	C						1	7	*10*			18	6.0
1944	Missdel 112-5-1	P	C					1		*6*				7	5.2
1942	Half & Half[4]	P	C							2	10	*11*	2	25	7.0
1943	Half & Half[5]	P	C								6	*7*	3	16	7.3
1944	H&H 211-5-6	P	C							1	2	*9*	1	13	7.3
1944	H&H 329-1-3	P	C								*3*	*3*	1	7	7.2
1942	H&H x Missdel[6]	F_1	C						5	*15*	8			28	5.6
1943	H&H x Missdel[7]	F_1	C					1	1	*2*	*2*			6	5.3
1944	H&H 211-5-6 x Ms 112-1-10	F_1	C						1	3	7	*12*	1	24	7.0
1944	H&H 329-1-3 x Ms 112-5-1	F_1	C								*3*	*3*	1	7	7.2
1943	H&H x Missdel	F_2	C					3	3	8	*10*	2	1	27	5.8

[1] Modal class italicized.
[2] 4 progenies combined.
[3] 5 progenies combined.
[4] 4 progenies combined.
[5] 5 progenies combined.
[6] 4 progenies combined.
[7] 2 progenies combined.

Group A and Group B and the mean lint index was 0.2 and 0.3, respectively. The difference in means within each group shown in Tables 5 and 6 is due simply to the fact that calculations were based on different distribution scales.

Table 5 also gives the lint indexes of 24 Group A and 57 Group B plants of the 1945 (High-Smooth x Lintless) x Lintless backcrosses. There was a significant positive correlation between the lint indexes of the parent plants and the mean lint indexes of their corresponding progenies. In Group A, r = 0.472 ± 0.147 (22 d.f.) and in Group B, r = 0.637 ± 0.187 (56 d.f.). In Group A, 9 backcross plants with 0.0 lint index were tested; 3 bred true for lintless and the others segregated for lint quantity. Five progenies had a lint index range of 0.0 to 2.0 and the progeny of 1 backcross plant whose lint index was 0.4 ranged in lint index from 0.0 to 3.0. The range of lint indexes of the tested Group B parents was 0.0. to 1.2. Of 12 backcross plants with 0.0 lint index tested, 5 bred true while 8 segregated for lint quantity, the distribution of the segregate being confined to the 0.0 and 0.5 lint index

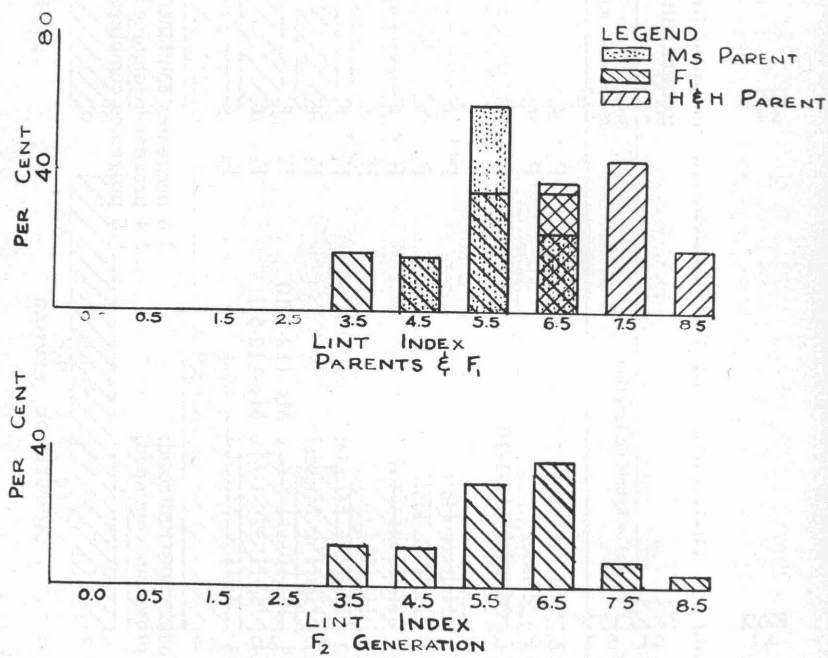

Figure 8. Distribution of lint indexes of Half & Half and Missdel parents and the F_1 and F_2 generations in 1943.

classes. In one case, a backcross plant with 0.6 lint index produced a progeny in which 1 segregate fell in the 2.5 index class.

Cross 6. Half & Half x Missdel

The F_2 and backcross generations of this cross, shown in Table 7 and Figure 8, are represented by such small populations that most generalizations would be subject to question. All of the plants in both the parental lines and the hybrids had covered seed coats. The lowest lint index range in the F_2 was 3.5 while the upper range was 8.5, which corresponds to the upper and lower ranges, respectively, of the Half & Half and Missdel parents.

The F_2 lint index mode was in the 6.5 lint index class. So far as can be concluded from the data, there seems little probability of recovering genotypes from this cross that are greatly higher or lower in lint index than that of the parents.

Discussion and Conclusions

General

Interpretation of the experimental results obtained in this study leads to the following generalizations:

(1) The quantity of lint on seeds of cultivated varieties of American Upland cotton is controlled by at least two genetic systems.

(2) In one system, a single pair of alleles, *Fn fn,* has a major effect on lint quantity. The homozygous phase of this gene, *fn fn,* produces covered (fuzzy) seed coat and also conditions the production of lint, while in the homozygous condition, *Fn Fn,* no seed fuzz is produced. The amount of lint is greatly reduced, the lint, if any, produced being due to the action of modifiers as given under (3) below. In the heterozygous state, *Fn fn,* the seed coat is glabrous and an intermediate quantity of lint is produced.

(3) The other system is composed of a complex of modifiers or genes which independently have minor effects in the production of lint but which may have a considerable effect as a group. These modifiers act to produce varying quantities of lint even in the presence of *Fn* in the homozygous condition and are, therefore, epistatic to it. When modifiers are absent, the *Fn Fn* phenotype is glabrous and completely lintless. Apparently these epistatic modifiers also

have a positive effect when acting in the presence of the linting phase of the major gene.

The interpretation just given differs radically from that of Thadani (*24*) who concluded that the so called "sparse lint" gene was completely linked with another gene which was responsible for glabrous seed coat. In all of the F_2 material involving glabrous and covered seed coat hybrids classified by other workers and in more than 5,000 F_2 plants examined by the writer in addition to the 916 plants of the breeding used in this study, there has not been a single authentic case of a plant with covered (fuzzy) seeds and no lint. Therefore, rather than postulate two completely linked genes, the most logical genetic interpretation is the one given here, i.e., that glabrousness and lintlessness, and covered seed coat and lint production are pleiotropic effects of a single pair of alleles. It should be emphasized that the interpretation just given hypothesizes a pleiotropic effect of a single gene in the homozygous state which conditions glabrousness and lintlessness, not glabrousness and sparse lint as reported by Griffee and Ligon (*6*).

Major Gene and Modifiers

The data obtained from the four crosses, Half & Half x Lintless, Missdel x Lintless, Half & Half x High-Smooth and Missdel x High-Smooth, involving glabrous and covered seed coats in these experiments prove conclusively that these manifestations for seed coat cover are controlled by a single pair of alleles and that the glabrous condition apparently is completely dominant. These results confirm the findings of numerous other workers and, though of some general genetic interest, would be of doubtful practical value were it not for the fact that this single pair of alleles also controls the presence or absence of the major quantity of lint produced on cotton seeds. Glabrousness and lintlessness being pleiotropic effects of the same gene pair, seeds of all homozygous glabrous plants would be devoid of lint were it not for the action of lint quantity modifiers which are epistatic to glabrous seed coat and which give complex segregations on the glabrous seed coat background such as would be expected from the action of multiple factors. Stripped of modifiers, this major lint quantity gene has three rather distinct phases, which correspond to its three possible genotypes: (1) a *lintless phase* in which no lint is produced when the gene is homozygous for glabrous seed coat, (2) a *linting phase* in which a normal quantity of lint is produced when the gene is homozygous for covered seed coat and (3) an *intermediate phase* in which the gene, in the heterozygous condition, conditions the production of glabrous seed coat and partial dominance for lint. The major gene pair has a pronounced effect on the general lint quantity pattern and this pattern is in evidence in all of the hybrid populations in which it is segregating. That the general patterns of lint index distribution of the four crosses under discussion do not all have the same modes, ranges and other characteristics is apparently due to the modifying or buffering action of genes with minor effects, the degree of alteration presumably depending on the number and potency of the genes in the modifying complex.

In view of the breeding behavior of the four parental types employed in this study, the following conclusions may be drawn with respect to their general genetic make-up: The major lint quantity gene is in the "lintless" phase in the Lintless parental types and no modifying genes which are epistatic to glabrous seed coat, are present. In the High-Smooth lines, the major gene also is in the "lintless" phase but a complex of lint quantity modifiers is present which conditions the production of a considerable amount of lint. In Missdel the major gene is in the "linting" phase but its low mean lint index in comparison with most other upland lines with covered seeds suggests that few or no epistatic lint quantity modifiers are present. The Half & Half lines carry the major gene in the "linting" phase and a complex of epistatic modifiers of considerable potency.

The pattern of the major lint quantity gene is evident in the Half & Half x Lintless crosses, though in these crosses the effects of the lint quantity modifiers brought in from Half & Half are apparent in shifts of means and modes and in greater ranges in the lint indexes on the three seed cover backgrounds in F_2 as compared with the parents and the F_1. Skewness of lint index frequency distribution similar to that observed in the High-Smooth x Lintless crosses was observed in the approximate one-fourth of the Half & Half x Lintless F_2 on the "homozygous" glabrous background. It seems evident that Half & Half must carry a complex of modifiers similar to that of High-Smooth and the skewness may be attributed to similar factors. Theories as to the causes of this skewness will be presented later in the discussion.

The Missdel x Lintless cross affords an example of the action of the major lint quantity gene when few, if any, modifiers are present. In F_2, 21 percent of the total plants were lintless while only 2 percent of the total fell in the 0.5 lint index class, thus confirming the assumption that Missdel carries very few lint quantity modifiers. Adding the frequencies in the low lint index range gives 23 percent, which does not differ significantly from the 25 percent of the total expected in the lintless phase of the major gene.

The F_2 generation of the Half & Half x High-Smooth cross shows a considerable alteration of the general lint quantity pattern of the major gene. Both of the parents carry a complex of epistatic modifiers while in Half & Half, the major gene is in the linting phase and in High-Smooth it is in the lintless phase. The F_2 lint index distribution is practically continuous though a slight depression is observed in the 3.5 class. Even in this distribution the action of the major gene in its three phases may be detected when the lint indexes on the corresponding seed cover backgrounds are studied separately, though the combined action of the two modifying complexes tend to obscure the major effects in the total population.

The effect of the major lint quantity gene in setting the distribution pattern is strikingly illustrated by the Missdel x High-Smooth cross. Though the parents are relatively close together in average lint index because of the concentration of lint quantity modifiers in the lintless phase in one, and low concentration of modifiers in the linting phase of the other parent, the F_2 gave a distribution quite similar to that of the Half & Half x Lintless cross, though, in this case the lint quantity modifiers enter the cross from the High-Smooth line. Though the parents do not differ greatly in lint index, the F_2 distribution exceeds the range of the parents in both directions. This is clear evidence of transgressive segregation which shows that other genes are involved in addition to the major factor pair which conditions lint production. While no lintless segregates were observed in the 0.0 lint index class, it is probable that such types would have been obtained in larger populations. The frequency distribution of lint index in the homozygous glabrous seed coat class was skewed in similar manner to that of the High-Smooth x Lintless and the Half & Half x Lintless crosses.

Since glabrousness and lintlessness are conditioned by the same gene, *Fn* in the homozygous condition, and any lint produced on homozygous glabrous seed is due to the action of modifiers, the classification of segregates for lint quantity as "sparse" and "dense," on a simple Mendelian basis in studies of lint quantity in crosses of glabrous and covered seed coat types, is technically spurious. If the seed-cover genotype for the major gene is known, the segregation for lint quantity follows directly and the proper two-class designation for the action of the major gene pair in this connection would be lintless vs. dense lint. The so-called "sparse" class which also includes any lintless segregates present in the population is simply a convenient method of identifying the glabrous-lintless phase of the major gene in the absence of F_3 test data; the accuracy with which this genotype can be identified depends on the number and potency of the lint quantity modifiers present. In spite of its erroneous employment in the past in connection with factorial studies on the inheritance of lint quantity, classification in this manner is of some practical value in relation to a method of breeding proposed in the preface. Moreover, segregations obtained by these methods make it possible to illustrate certain points with reference to lint quantity modifiers.

Additional Evidence and Theories

In crosses of High-Smooth and Lintless, the frequency distributions in the F_1 and F_2 generations and in the backcross of the F_1 to the lintless parent give curves which are skewed to the left. This skewness is strikingly illustrated in Table 6 and Figure 7 where the lint index class interval was 0.1 rather than 1.0, as was used in the preparation of the other diagrams and the tables in this paper. When the original data, from which the lint index distribution of the (HS x Ls) x Ls backcrosses were transformed in terms of logarithms and plotted, the 0.0 lint index class, of course, was not altered, but the frequency distribution of the linted classes showed skewness, this time in the direction of the higher lint indexes. Transformation of the original data by the square root of the original values gave a slightly more normal appearing curve. The higher range of lint indexes in the Group B of the (HS x Ls) x Ls backcross in 1945 suggests the presence of higher potency genes in this modifying complex than were present in Group A, or perhaps a slightly different interacting complex. Groups A and B in these backcrosses should not be confused with Groups A and B of the Half & Half x Lintless crosses.

Skewness of lint index frequency distributions similar to that observed in the High-Smooth x Lintless crosses was observed in the approximate one-fourth of the individuals of the Half & Half x Lintless and the Missdel x High-Smooth crosses on the homozygous glabrous seed cover background. The skewness observed in these crosses may be explained simply by assuming dominance within the lint quantity gene pairs in the modifying complexes of the Half & Half and High-

Smooth parental lines. This assumption would explain the skewness in the High-Smooth x Lintless F_1 as well as that observed in the F_2 and the backcross of the F_1 to Lintless. Certain systems of gene interaction also would give skewed curves in F_1 and segregating generations, as would also linkage. There is no reason to believe that the skewness could not have been the result of more than one of these genetic actions and interactions.

The results of progeny tests of F_2 and backcross plants with 0.0 lint index indicate that not more than half of the plants classified as lintless in segregating populations are actually genotypically lintless. In those cases where a plant, whose progeny segregated for lint quantity, was classified as lintless, the segregation was always within the range of 0.0 to 1.0. Presumably, some low potency modifiers may be suppressed or inactivated by certain conditions of environment or peculiar physiological conditions.

It has been pointed out that Group A and Group B of the Half & Half X Lintless cross differ slightly but consistently in their expression and, therefore, the difference is unlikely to be wholly due to environmental effects. The general observation is that, on the same seed cover genotypes, the lint quantity of Group B is at a slightly lower level than that of Group A. The lint indexes of the original 1943 Half & Half parent plants of these two groups were approximately the same. Assuming that the contribution to lint quantity in these two plants by the major lint quantity gene was equal, the total effect of the lint modifiers also must have been equal. However, the modifiers in Group A could have been higher in individual potency though fewer in aggregate numbers than those in the modifying complex of Group B. This theory would serve not only to explain the difference in lint index frequency distributions in Groups A and B but also the observed difference in their two-class segregations when lint quantity was classified by visual methods. In the latter case, a greater number of the homozygous glabrous plants in Group A may have carried high potency modifiers, thus causing them to be placed in the dense lint class, while in Group B the larger number of lower potency modifiers segregated in the lower lint index range in a majority of cases and were thus classified as sparse lint types.

Throughout these experiments it has been observed that the effects of epistatic lint quantity modifiers are much less striking in the presence of the linting phase of the major gene than in the lintless phase. The parent-progeny correlations in the Half & Half x Lintless crosses were significant in the lintless phase of the main gene but were not significant in the linting phase of the same gene. It is reasonable to assume that the total effect of an epistatic complex of modifying genes observed in the lintless phase of the major gene may not be realized in the linting phase. Even if the effect were strictly additive, the gross effect of the major gene together with its non-genetic variation is no doubt sufficient to obscure the effects of the modifiers.

Further evidence of the heritability of the genes that make up the lint modifier complex of High-Smooth and Half & Half may be found in (HS x Ls) x Ls material and in the homozygous glabrous genotypes of the Half & Half x Lintless crosses.

Summary

1. Seed hairs of cultivated American Upland cotton occur in two layers, fuzz and lint. A mutant seed cover type occasionally arises which has no seed fuzz but which may either produce measurable quantities of lint or be devoid of lint. The fuzzy and fuzzless seed coat conditions have been designated as "covered" and "glabrous," respectively. Studies reported here give the interactions of lint with glabrous and covered seed coat.

2. Data were obtained on the quantity of lint of four strains of American Upland cotton, *Gossypium hirsutum* L., Lintless (glabrous seed coat—no lint), High-Smooth (glabrous seed coat—linted), Missdel (covered seed coat—low lint quantity), Half & Half (covered seed coat—high lint quantity), and their hybrids.

3. Two genetic systems, which control lint quantity in American Upland cottons, were identified. (1) A single gene with major, pleiotropic effects whose action is manifested in three phases corresponding to its three possible genotypes: (a) a *lintless phase* in which no lint is produced when the gene is homozygous for glabrous seed coat; (b) a *linting phase* in which the quantity of lint found in the range of normal cultivated American Upland cotton is produced when the gene is homozygous for covered seed coat, and (c) an *intermediate phase* in which the gene in the heterozygous condition leads to the production of an intermediate amount of lint and a glabrous seed coat. (2) A complex of modifiers, or genes each with a minor effect, but which together may greatly modify lint production, which are epistatic for lint

production to the major gene in its glabrous-lintless phase, and which also have a very important positive effect on lint production when acting in the presence of the linting phase of the major gene.

4. In the crosses studied, the major gene has a pronounced effect on the lint quantity distribution pattern while the epistatic modifiers may alter or buffer this pattern. The spurious nature of the so-called sparse lint category usually employed in the analysis of two-class segregations was demonstrated and significant Chi-square values obtained in such analyses, when the populations are large, may be attributed to misclassification of a small number of individuals which are genotypically lintless as regards the major gene, but phenotypically linted due to the action of epistatic modifiers.

5. The effects of the epistatic lint quantity modifiers are easily recognized on the glabrous seed coat background when the major gene is in its lintless phase. On such a background the lint index distribution curves are strongly skewed in the direction of low lint index, which condition may be explained on the assumption of unequal potencies for the genes in the modifying complex. Dominance, interaction and linkage, or combinations of these genetic actions and interactions, also offer an interpretation. Significant correlations were obtained when the lint indexes of individual plants, homozygous for glabrous seed coat, were compared with the mean lint indexes of their selfed progenies.

6. The effects of the epistatic lint quantity modifiers were much less striking in the presence of the major gene in its linting phase, though their presence was evidenced particularly by transgressive inheritance in the F_2 of the High-Smooth x Missdel cross and by the breeding behavior of the Half & Half parental lines in crosses with Lintless and High-Smooth. Apparently, the gross effect of the major lint quantity gene in its linting phase is such that the separate effects of the modifying complex can not be clearly distinguished.

7. Increased production of lint (the most valuable product of the cotton plant) is the principal objective of most cotton breeders. The amount or quantity of lint produced on seeds is an important component of lint yield. Breeding methods were suggested in the preface which utilize the homozygous glabrous seed coat background for the isolation and combination of lint quantity modifiers, both from agricultural stocks and taxonomic varieties, of *Gossypium hirsutum* L.

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