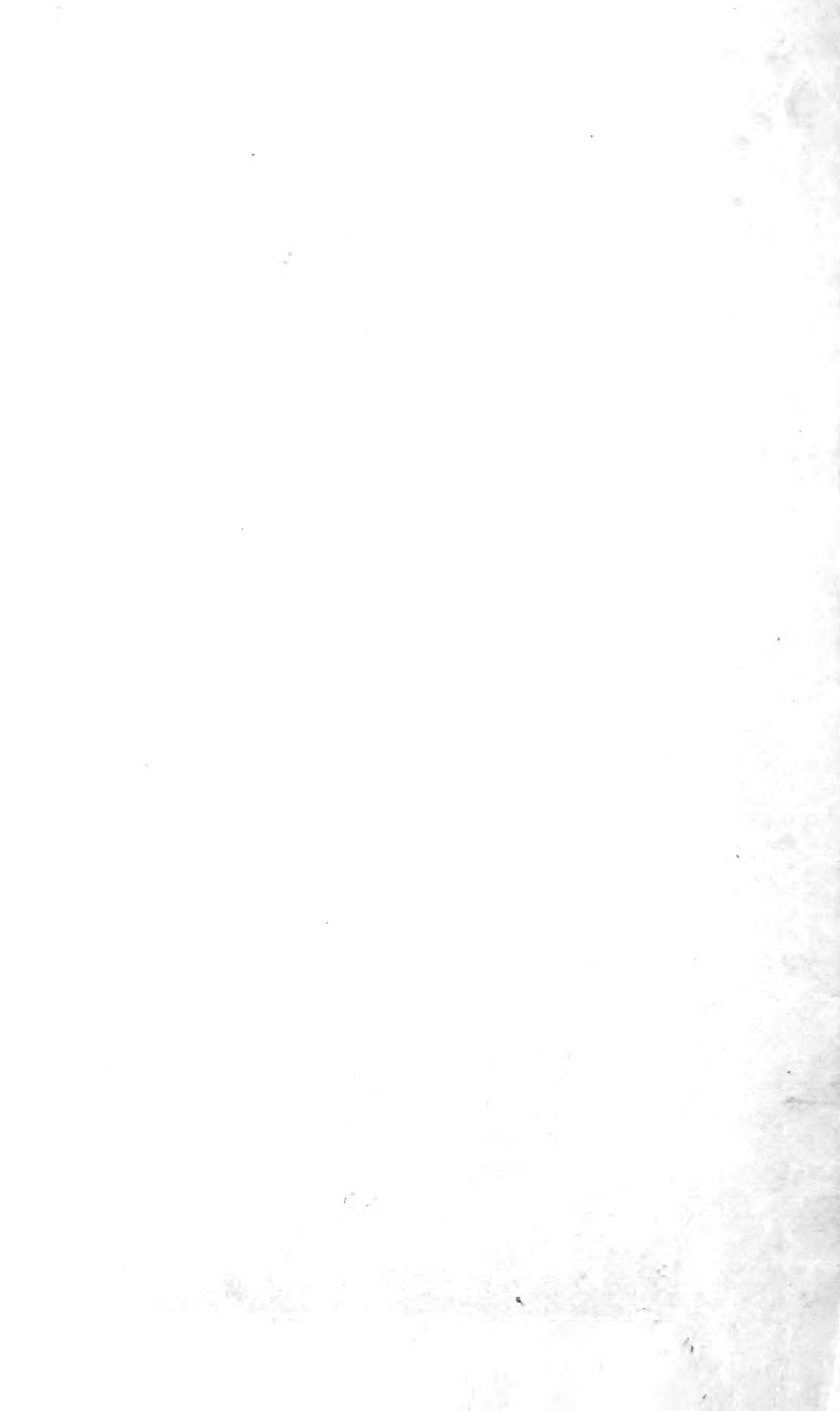


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UNITED STATES DEPARTMENT OF AGRICULTURE



DEPARTMENT BULLETIN No. 1164



Washington, D. C.

August 10, 1923

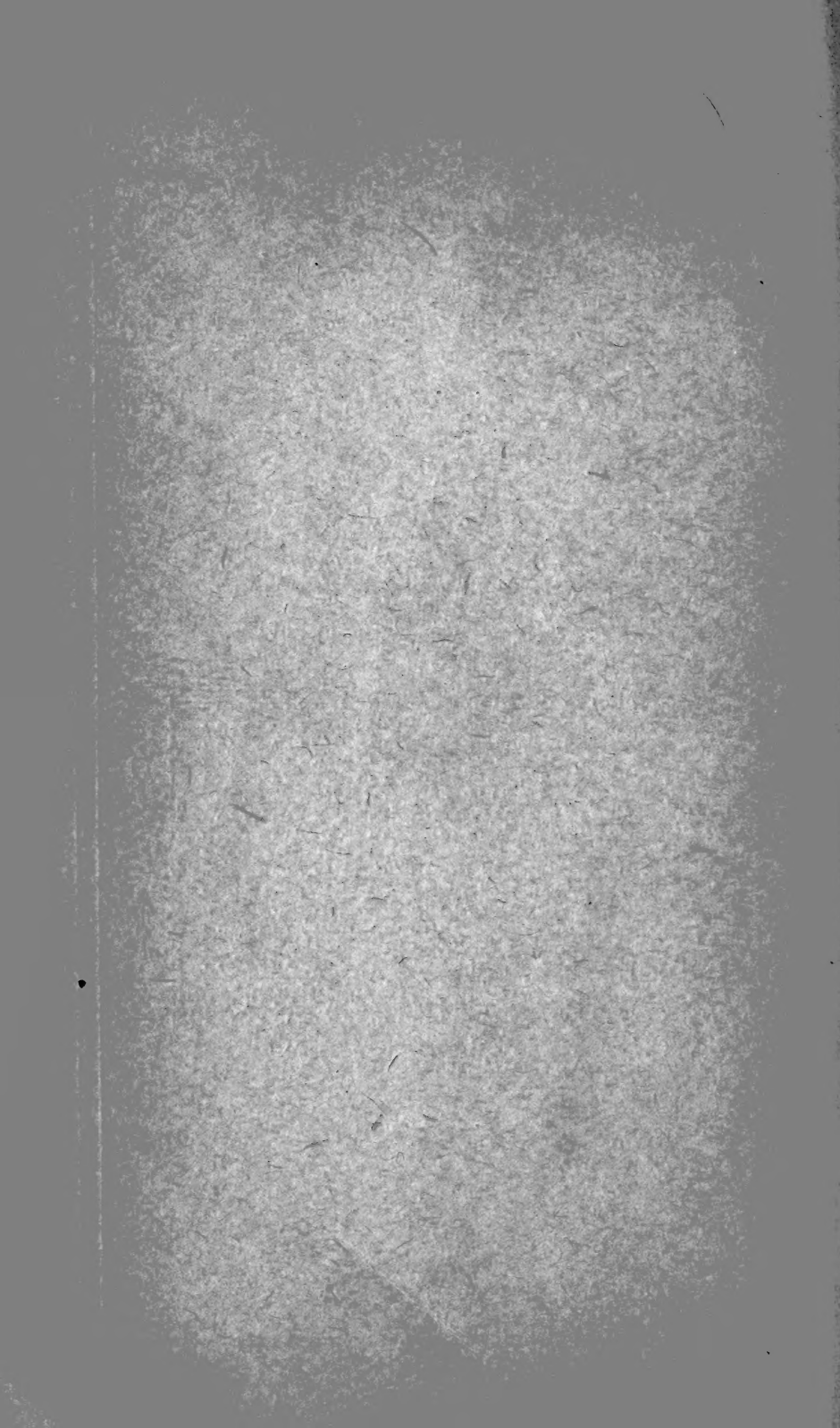
SEGREGATION AND CORRELATION OF CHARACTERS IN AN UPLAND-EGYPTIAN COTTON HYBRID

By

THOMAS H. KEARNEY, Physiologist in Charge, Office of Alkali and Drought
Resistant Plant Investigations, Bureau of Plant Industry

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INTRODUCTION.

The inheritance of characters in hybrids between different varieties of the Egyptian type of cotton was discussed in an earlier paper (28)¹. The parent varieties, Pima and Gila, differed significantly in respect to 24 size and shape characters. The hybrid modes and means for most of these characters were approximately intermediate in F_1 and F_2 and no extraparental characters appeared in F_2 . The inheritance was of the "blend" type, the frequency distributions of F_2 having been unimodal. The second generation was more variable than the first in some but not all of the characters, but the differences in variability between the two generations were relatively slight. These facts indicate, according to the current interpretation, that the characters in question involve several factors. Comparison of the coefficients of correlation of 40 character pairs in the first and second generations of the hybrid gave no evidence of the existence of genetic correlation or coherence (8).

Subsequent study of the data indicated that, although the distributions were unimodal, segregation had in fact occurred in the second

¹ The serial numbers (*italic*) in parentheses refer to "Literature cited," at the end of this bulletin.

generation. The means for leaf index and boll index of the F_3 progenies which gave, respectively, the highest and the lowest mean for the character in question, differed by amounts equal to about 10 times the probable error of the difference. There was a high parent-offspring correlation, for the character boll index, between the means of 11 F_3 progenies and the values for the corresponding F_2 parents, the coefficient having been 0.81 ± 0.07 . The coefficients of variation of the several F_3 progenies for the characters leaf index and boll index ranged from not greater than that of the less variable parental population to fully as great as that of F_2 .

It is well known that segregation is much more pronounced in hybrids between different types of cotton, such as upland and Egyptian and upland and sea island, in which cases the magnitude of the parental difference is fully as great as ordinarily exists between very distinct botanical species. cursory inspection of a second-generation population of such a hybrid shows the occurrence of characters not expressed by either parental type and the presence of individuals which bear little resemblance to any of the cultivated varieties of cotton.

Systematic study of a hybrid between upland and Egyptian cottons was undertaken in order to obtain statistical evidence of the kind and degree of segregation occurring. It was sought also to determine, by study of the correlations of characters, whether coherence occurs; in other words, whether there is a tendency for the characters to be associated in the hybrid as they are received from the parents. The results of this investigation have a practical bearing in throwing light upon the nature of the variants to be looked for in a field of Egyptian or of upland cotton which has been exposed to accidental cross-pollination by the other type. This knowledge should be useful both in determining the fact of whether such cross-pollination has occurred and in guiding the work of roguing to maintain supplies of pure planting seed.

The cotton plant has both advantages and disadvantages as a subject of genetic study. Certain advantages are the large size of the flowers (which facilitates cross-pollination), the readiness with which controlled self-fertilization may be effected, the large size of the seeds (which makes it easy to handle and count them), and the high visibility of many of the characters. On the other hand, the relatively small number of seeds produced by each flower is a serious disadvantage, especially as the ordinary method of field sowing requires the planting of not less than four seeds to the hill, all but one of the resulting plants being finally removed. A good stand is not likely to be obtained when fewer seeds are planted unless a nurse crop is used or the seeds are covered with sand instead of with ordinary soil. Transplanting has not been uniformly successful with cotton, although this method deserves further trial. This waste of seed in field planting is a serious disadvantage from any point of view, but especially so when the computation of Mendelian ratios is to be undertaken.

Another drawback is the long growth period of the plant, which results in the leaves, bolls, and fiber borne at different nodes being developed under different weather conditions, thus unduly augmenting the variability of the characters. To obviate, as far as possible, the effects of this factor it was sought to measure on different individuals

leaves and other organs in as nearly as possible the same stage of development. But with two such different types of cotton as upland and Egyptian, and with the very great diversity which characterizes the hybrid between them, it is difficult to select for measurement organs which are contemporaneous.

The investigation was carried on at the Cooperative Testing Station at Sacaton, Ariz. Valuable service was rendered by Walton G. Wells, who had supervision of the field plantings and did much of the work of hybridization, measurement, and computation in 1917, 1918, and 1919, and by Walter F. Gilpin, who assisted in the work during 1919 and took the place of Mr. Wells in 1920. Others who assisted in the investigation were F. Ben Clark, George J. Harrison, R. H. Manthey, and Max Willett. To G. N. Collins and J. H. Kempton the writer is indebted for much aid in the computation of the coefficients of correlation and for valuable suggestions throughout the course of the investigation.²

ANCESTRY OF THE HYBRID.

The cross determined upon was between the Holdon variety of upland cotton and the Pima variety of American Egyptian cotton. The Pima variety was described and illustrated in an earlier publication (25, pp. 292-294, pls. 18, 23, and 24). The Holdon variety, which is an extreme representative of the Texas big-bolled type of upland cotton, was developed by D. A. Saunders from a plant selected in 1905 in a field of the Jackson variety near Smithville, Tex.³

Plants of the Holdon variety were grown at Sacaton, Ariz., in 1916 and flowers were cross-pollinated with Pima pollen, giving rise to an F_1 grown in 1917 and the latter to an F_2 grown in 1918. Owing to war conditions, however, an intensive study of these populations was not practicable. A population of Holdon was grown in 1917 from seed produced by self-pollinated flowers on the 1916 plants, and on a half dozen plants in this population flowers were cross-pollinated with pollen from two plants of family P1A40 of the Pima variety. The latter, as indicated by the pedigree given in another publication (26, fig. 1, p. 229), was in the third strictly self-fertilized generation and was doubtless much more nearly homozygous than the Holdon family to which the female parent of the hybrid belonged. It would have been desirable, of course, to have started with a strain of upland cotton which had been as closely inbred as the Egyptian parental strain, but in view of the specific magnitude of the difference between the two varieties and considering the fact that none of the Holdon plants showed the slightest evidence of other than upland characters, it is not believed that the results of the investigation are seriously prejudiced by this possible difference in the genetic purity of the parents.⁴

Very few bolls matured from the cross-pollinated flowers on each of the Holdon parent plants in 1917, and for this reason the cross-pollinated seed from all except one of the mother plants was mixed together and was planted as a single F_1 population in 1918. Progenies

²The illustrations were prepared from photographs by Walter F. Gilpin, with the exception of Plates X and XI, which were prepared from photographs by Robert L. Taylor.

³A description of the Holdon variety is given in "Distribution of Cotton Seed in 1915," U. S. Dept. Agr., Bureau of Plant Industry Doc. 1163, p. 12-13. 1915.

⁴The preponderance of self-fertilization in cotton, even when the flowers are naturally open pollinated, makes the chances good that most of the progeny of any individual in a well-bred stock will be approximately homozygous (27, p. 11).

of Holdon and of Pima were also grown in 1918 from self-fertilized seed of plants in the corresponding progenies of 1917.

In 1919 F_2 progenies were grown from each of 3 F_1 individuals of 1918, the three progenies having comprised, respectively, 69, 95, and 51 individuals. An F_1 progeny, the parents of which were a single individual in the selfed Holdon and a single individual in the selfed Pima progeny of 1917, was also planted, but great difficulty was experienced in obtaining a stand and only 5 individuals survived. Like difficulty occurred with the parental progenies grown in 1919, only 15 plants of Holdon and 13 plants of Pima having survived. Fortunately, the magnitude of the difference between these varieties in respect to most of the characters made the small size of the parental progenies a less serious disadvantage than would otherwise have been the case for the purpose of comparison with the hybrid.

The Holdon progeny was from self-fertilized seed produced by a plant in the population of 1917. The Pima progeny was from self-fertilized seed produced by a plant in the progeny of 1918. The Holdon parental progeny of 1919 was in the second generation of strict self-fertilization, and the Pima parental progeny of 1919 was in the fifth self-fertilized generation. For the sake of brevity these Holdon and Pima populations will be referred to hereafter as the "parental populations" regardless of what generation of the hybrid is being compared with them.

In 1920 F_3 progenies of 48 individuals in the F_2 of 1919 were grown. Of the F_3 progenies 13 were from self-fertilized seed only, 21 comprised plants from both self-fertilized and open-pollinated seed, and 14 (the F_2 parents of which had matured no bolls from strictly self-fertilized flowers) were grown from open-pollinated seed only.⁵

An F_1 of 24 individuals, obtained by cross-pollinating, in 1919, flowers on a plant in the Holdon parental progeny with pollen from a plant in the Pima parental progeny, was grown in 1920. The Holdon and Pima populations grown in 1920 were unfortunately situated in strong alkali soil, and the plants were so stunted that they could not be used for comparison with the hybrids.

CHARACTERS DISTINGUISHING THE HOLDON AND PIMA VARIETIES.

Some of the more important characters distinguishing the Holdon variety from the Pima are summarized in the following paragraphs. Many of these characters are also diagnostic as between the upland and Egyptian types of cotton in general. Differences which lend themselves to direct measurement or grading are indicated by comparison of the means in Table 1.

Stem and branch characters (Pl. I).—Pima, as compared with Holdon, has a much taller axis with longer and more numerous internodes. The fruiting branches of Pima are very much longer and have very much longer internodes than those of Holdon. In the first generation of the hybrid (Pl. II) the type of plant is intermediate but shows a marked degree of heterosis or hybrid vigor.

⁵No measurements of characters were made on progenies grown from open-pollinated seed only with the exception of No. 161, in which about one-third of the plants were so similar in all their characters and corresponded so closely to the description of the F_2 parent as to leave no reasonable doubt of their derivation from self-fertilized ovules. In four of the progenies, which comprised both selfed and open-pollinated plants, the number of the former having been too small to furnish satisfactory statistical constants, measurements were also made upon such of the individuals from open-pollinated seed as showed, by comparison with the individuals resulting from controlled self-fertilization, that they, too, were presumably the product of self-fertilized ovules.

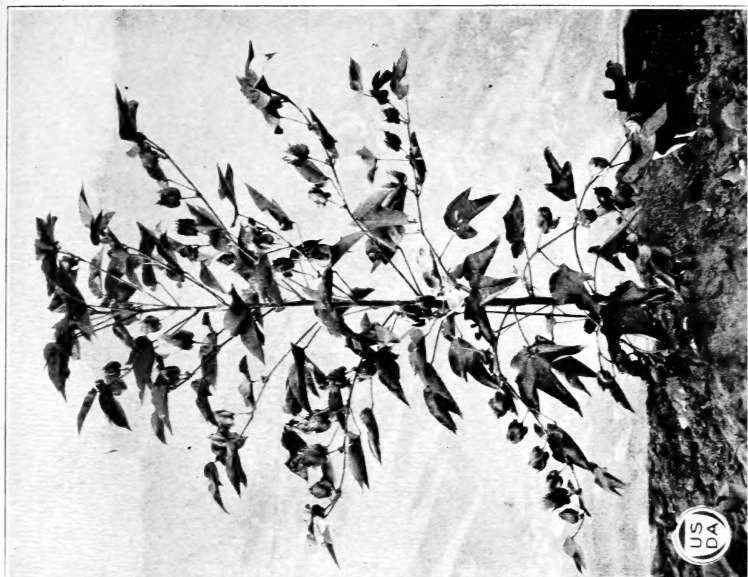


FIG. 2.—A PLANT OF THE PIMA (EGYPTIAN) PARENT OF THE COTTON HYBRID, DESCRIBED ON PAGE 4.

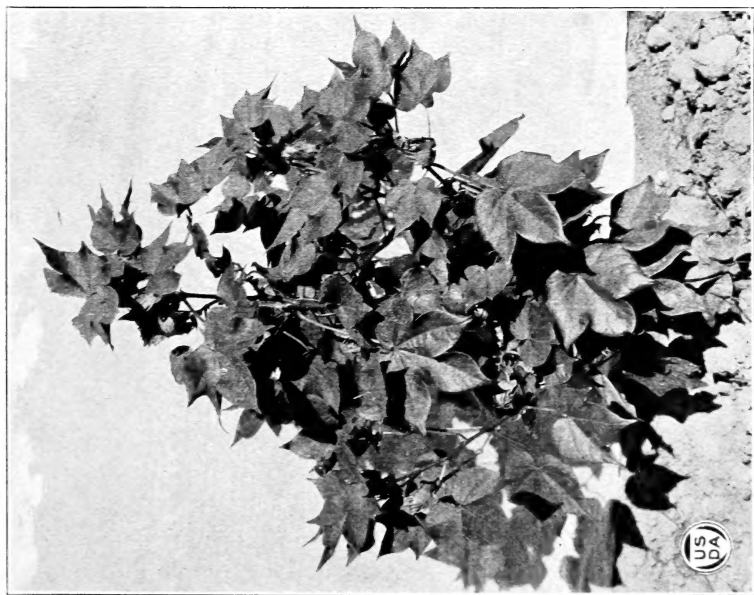


FIG. 1.—A PLANT OF THE HOLDON (UPLAND) PARENT OF THE COTTON HYBRID, DESCRIBED ON PAGE 4.



A PLANT OF THE FIRST GENERATION OF THE HOLDON-PIMA COTTON HYBRID,
DESCRIBED ON PAGE 4, SHOWING HETEROSIS OR HYBRID VIGOR.

Leaf characters (Pl. III).—The Pima leaf is much longer and broader and has a somewhat greater relative width than that of Holdon. The Pima leaf is more deeply lobed, its veins are somewhat more divergent, and the basal prolongations of the blade which form the sinus around the insertion of the petiole are relatively shorter than in the case of Holdon. The Pima leaf is comparatively thick and leathery, nearly glabrous (as is also the petiole), somewhat shiny of surface, dark olive green in color, and the callus, or pulvinus, at the base of the blade is greenish or dull brown, not contrasting strongly with the general color of the leaf. In Holdon the leaf is comparatively thin and soft, hairy, especially along the veins on the lower surface and on the petiole, dull of surface, bright green in color, and the color of the callus is red, between maroon and carmine, contrasting sharply with that of the rest of the blade. The nectary on the under side of the midvein is elongated and of rather indefinite outline in Pima, round, almost heart-shaped, and sharply defined in Holdon. The leaf of the first generation hybrid (Pl. IV) is intermediate in form but is larger than that of either parent, showing pronounced heterosis.

Involucre characters (Pl. V, figs. 1 and 3).—The bracts in Pima are of crisper texture and more connate near the base than in Holdon. The Holdon bracts are more deeply cleft than in Pima, and the teeth are relatively broad, leaflike, and nearly erect, while in Pima they are slender, bristlelike, and widely spreading.

Calyx characters (Pl. VI).—The Pima calyx is characterized by an entire margin, numerous and crowded oil glands, and uniform color, while in Holdon the calyx has five large teeth of somewhat unequal size, the oil glands are relatively few and scattered, and the margin and teeth are of a bright leaf-green color strongly contrasting with the pale yellowish green of the rest of the calyx.

Corolla characters.—The Pima corolla (Pl. VI, fig. 2) is much longer and is relatively much narrower than that of Holdon (Pl. VI, fig. 1), being narrowly funnel shaped when fully expanded, while the widely flaring corolla of Holdon is broadly funnel shaped. The petals of Pima (Pl. VII, fig. 3) are pale greenish yellow (35, pl. 5) in general color and have a large and very conspicuous Bordeaux red (35, pl. 12) spot near the base, while in Holdon (Pl. VII, fig. 1) the petal color is nearest sea-foam green (35, pl. 31) and the spot is absent, as is the case in nearly all varieties of upland cotton.

Stamen characters.—Pima (Pl. VIII, fig. 3) has much shorter filaments and somewhat larger anthers than Holdon (Pl. VIII, fig. 1). The color of the anthers, or rather of the pollen, is near-empire yellow (35, pl. 4) in Pima, and pale chalcedony yellow (35, pl. 17) in Holdon.

Pistil characters.—The total length of the pistil and the relative length of the stigmas, or portion of the pistil projecting above the staminal column, are much greater in Pima (Pl. VIII, fig. 3) than in Holdon (Pl. VIII, fig. 1). The prevailing number of stigmas and of locules of the ovary is three in Pima and four or five in Holdon.

Boll characters.—The usually three-locked boll of Pima (Pl. IX, fig. 3) is approximately conical with a rather narrow base and decreases in diameter somewhat rapidly from below the middle toward the apex, ending in a conspicuous but not sharp point. The four or five locked Holdon boll (Pl. IX, fig. 1) is almost globular, with a

very broad base and a very short, abrupt, blunt "nose" at the apex (which is sometimes almost entirely lacking). The average length is nearly the same in the two varieties, but the Holdon boll has a much greater diameter. The Holdon boll is characterized by a short but conspicuous "midlock furrow" extending two to five millimeters down from the apex, which is entirely lacking in Pima. The surface of the unripe boll in Pima is somewhat shiny, light elm green in color (35, pl. 17) and somewhat roughened by the pits at the bottom of which lie the rather conspicuous oil glands. In Holdon the boll surface is paler colored or asphodel green (35, pl. 41), is very smooth and not pitted, and the oil glands are very inconspicuous.⁶

Fiber characters.—The fiber of Pima (Pl. X, B) averages about 41 millimeters ($1\frac{5}{8}$ inches) in length, that of Holdon (Pl. X, A) about 29 millimeters ($1\frac{1}{4}$ inches). In color the Pima fiber is a pale buff (nearest the tilleul buff of Ridgway (35, pl. 40), while that of Holdon is nearly white. The weight of fiber per seed (lint index) is considerably greater in Holdon than in Pima.

Seed characters.—In Pima (Pl. XI, B) much of the seed coat is naked, the fuzz, which varies in color from dull green to brownish white, being largely confined to the two ends. The Holdon (Pl. XI, A) seed is entirely covered with bright white fuzz.

CHARACTERS OF THE FIRST-GENERATION HYBRID.

In a field of either type of cotton, first-generation upland-Egyptian hybrids are always conspicuous because of the vigor and fertility of the plants (Pl. II). The conjugate generation (F_1) of Holdon \times Pima exhibited heterosis or intensification in most of the size characters. It was intermediate or nearly so in color and texture of the leaves (Pl. IV), divergence of the teeth of the involucre bracts (Pl. V, fig. 2), dentation of the calyx and abundance of oil glands in the calyx (Pl. VIII, fig. 2), color of the petals, average number of boll locks, color and surface of the boll (Pl. IX, fig. 2), and color of the fiber. It approached the Holdon parent in the red color of the leaf callus, in the length of the filaments of the stamens (Pl. VIII, fig. 2), and in having the seeds completely covered with fuzz (Pl. XI, E). Characters in respect to which the conjugate generation approached the Pima parent were: Deeply lobed leaves (Pl. IV), relative freedom from hairs of the petiole and under surface of the leaf, connate and not very deeply toothed involucre bracts (Pl. V, fig. 2), presence of a petal spot (Pl. VII, fig. 2), although the spot was much smaller, streakier, and less deeply colored than in Pima, bright-yellow color of the anthers, long pistil, relatively long stigmas (Pl. VIII, fig. 2), pointed bolls (Pl. IX, fig. 2), absence of a midlock furrow, and relatively long fiber (Pl. X, E).⁷

Two characters were noted in the first generation of this hybrid which may be regarded as extraparental, although not belonging to

⁶ In the bolls of upland cottons, as was pointed out by Balls (4, p. 59) the glands lie beneath several layers of subepidermal parenchyma.

⁷ It was noted by Balls in Egypt (1, p. 73) and by Cook in Arizona (11, pp. 14, 15) that first-generation Egyptian-upland hybrids frequently surpass in length of fiber the longer fibered (Egyptian) parent. An interesting example of absence of intensification of this character in a first-generation hybrid of Kekchi, a Central American variety of the upland type, with American upland cotton is reported by Cook (ibid., p. 14).

the category of intensified size characters. These were a slight crinkliness of the leaf margins (Pl. IV), a character much more fully developed in many of the F_2 plants, and bright-green color of the fuzz on most of the seeds. The prevailing color of the fuzz in the Pima parent is also green, but of a duller shade than in F_1 . This peculiarity of first-generation hybrids between upland and Egyptian or sea-island cottons has been noticed by Cook (10).⁸

DEFINITION OF THE CHARACTERS MEASURED OR GRADED.

The descriptive list which follows comprises the characters which were determined, by measurement or grading, on the parental and the hybrid F_2 progenies grown in 1919 and on the hybrid F_1 progeny grown in 1920. Some of these characters were determined also on the parental and hybrid F_1 progenies grown in 1917 and 1918 and on the F_3 progenies in 1920. Holdon and Pima are distinguished by numerous other characters, some of them indicated in the foregoing botanical descriptions, which could not be measured or graded with accuracy in F_2 . Examples of such characters are color of the leaf, smoothness of the boll surface, and color of the fuzz on the seed.

All measurements were made in the field except that certain boll characters were measured on natural-size photographs. The measurements were made on one fruiting branch, one leaf, one flower, and one boll on each plant. Of the graded characters, those of the leaf were determined in the field and those of the bracts and flowers in the laboratory on freshly gathered material. All fiber and seed characters were measured or graded in the laboratory.

Axis length was measured in centimeters on the main stem from the surface of the ground (approximate level of the cotyledon node) to the terminal bud. Of the parental populations, Pima gave the higher mean for axis length.

Axis internode length is the average length, in millimeters, as determined by dividing the axis length by the number of internodes. The mean internode length was higher in Pima than in Holdon.

Axis internode number includes all internodes above the cotyledon node up to and including the highest one which had reached a length of about 15 millimeters. The mean internode number was higher in Pima than in Holdon.

Fruiting branch length, in centimeters. The longest fruiting branch on each plant was measured. The determination of this character on some half dozen of the F_2 hybrid plants was rendered difficult by the absence of a sharp distinction at relatively high nodes between vegetative branches and fruiting branches, all possible intergradations having existed. In such cases measurement was made of the longest branch above the zone of typical vegetative branches which had an approximately horizontal position. The fruiting branches of Pima averaged longer than those of Holdon.

Fruiting branch first internode length, in centimeters, was measured on the same branch of which the total length was determined. Pima exceeded Holdon in the mean for this character.

Leaf length (fig. 1, *a b*), in millimeters, was measured from the base of the blade to the apex of the terminal lobe. Pima gave a higher mean for leaf length than Holdon.

Leaf width (fig. 1, *c d*), in millimeters, was measured from tip to tip of the principal lateral lobes. Pima gave a higher mean than Holdon for this character.

Leaf index, leaf width as a percentage of the length. A relatively broad leaf has a high leaf index and vice versa. The mean leaf index was higher in Pima than in Holdon.

Leaf lobe index, the distance from the base of the blade to the bottom of the sinus between the terminal lobe and the upper right-hand lateral lobe (fig. 1, *a e*), expressed

⁸ Extraparental characters appearing in the first generation of a hybrid between sea island and a cotton native to St. Croix, the latter belonging apparently to the upland series, are mentioned by Harland (21, p. 54).

as a percentage of the length of the leaf. A high lobe index indicates a shallow-lobed leaf and vice versa.⁹ Holdon gave a higher mean lobe index than Pima.

Leaf vein angle (fig. 1, *f a g*) is the width, in degrees, of the angle subtended by the principal lateral veins. Of the parental populations, Pima gave the higher mean for this character.

Leaf extension index is the length of the basal prolongation of the blade, below a line bisecting the base of the midvein at a right angle to the latter (fig. 1, *h k*), expressed as a percentage of the length of the leaf. A high extension index indicates a relatively great prolongation of the base. The mean leaf extension index was higher in Holdon than in Pima.

Leaf callus color was graded in the field with the aid of types consisting of a set of leaf bases representing the range from grade 1 (callus pale brownish green) to grade 9 (callus liver colored). The grading was done on newly unfolded leaves in which the color was freshest. Variations in the size of the colored area, in hairiness, and in the general color of the leaf blade made it difficult to determine the true grade of some of the F_2 plants. Of the parental populations, Holdon gave the higher mean grade for callus color.

Petiole hairiness was graded with the aid of types consisting of a set of petioles representing the range from grade 1 (glabrous or very nearly so) to grade 8 (extremely hairy). The petiole was found to be the most convenient organ for accurate grading of the character of hairiness. In general, the hairiness of the petiole appeared to be closely correlated with that of the lower surface of the leaf blade, although in some of the F_2 plants the leaf surface was decidedly hairier than the petiole and in one plant the converse was true. The degree of hairiness is modified by the age of the leaf, young leaves being usually much hairier than mature ones. The grading was done on the petioles of approximately half-grown leaves. A further complication was the diversity in F_2 in respect to the nature of the hairiness, which varied from short and felt-like to long and almost bristly; but as the number

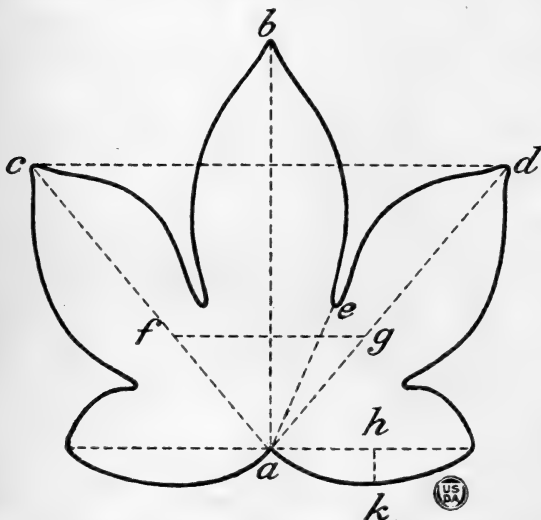


FIG. 1.—Diagram of a cotton leaf, showing the location of the measurements: Length (*a-b*), width (*c-d*), sinus distance (*a-c*), vein angle (*f-a-g*), basal extension (*h-k*).

rather than the length or character of the hairs was taken as the criterion, little difficulty was experienced in fixing the grade number of most of the plants. Holdon gave a higher mean grade for petiole hairiness than Pima.

Pedicle length, in millimeters, was that of the flower on which the other measured characters were determined. Pima normally has a pedicle much longer than Holdon.

Bract length, in millimeters, was that of the longest of the three bracts in the involucre of the flower on which the other measured characters were determined. Pima gave a higher mean for bract length than Holdon.

Bract connation index, determined on the same involucre, is the distance from the base of the involucre to the base of the sinus formed by the two most connate bract margins, measured in millimeters and expressed as a percentage of the length of the longest bract in the involucre. A high connation index indicates that the bracts are strongly connate. The mean index of bract connation was higher in Pima than in Holdon.

⁹ Balls (6, p. 158) used the same expression of depth of lobation. The writer in a recent publication (26, p. 230, footnote 6 to Table 1) used the converse (leaf length as a percentage of sinus distance) as the lobe index. This expression has the advantage that a high lobe index indicates a deeply lobed leaf and vice versa. But as the correlations in the Holdon \times Pima hybrids had been previously calculated on the other basis, it seemed advisable to retain the above expression in this bulletin.

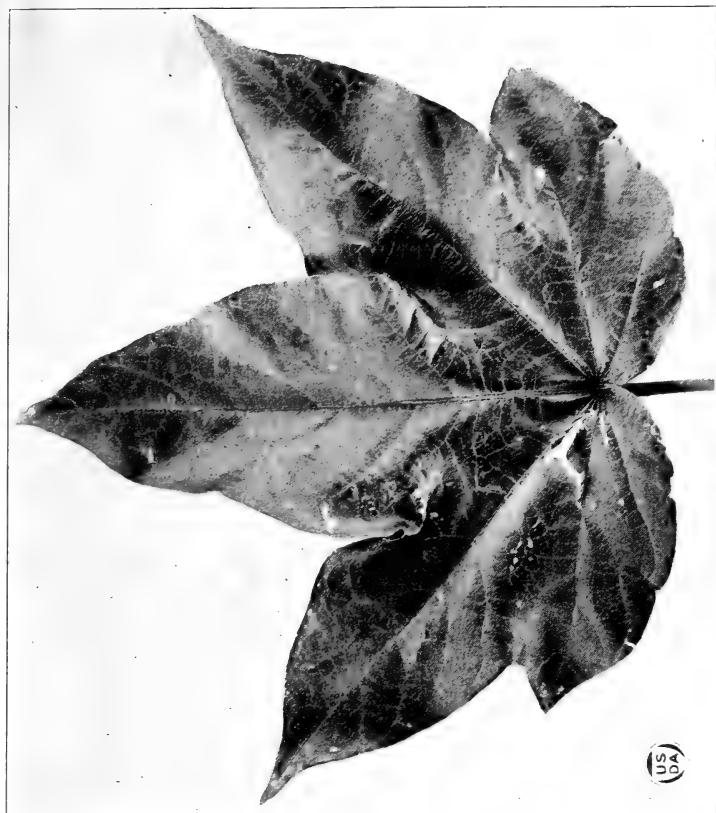


FIG. 2.—A TYPICAL LEAF OF THE PIMA VARIETY OF EGYPTIAN COTTON.

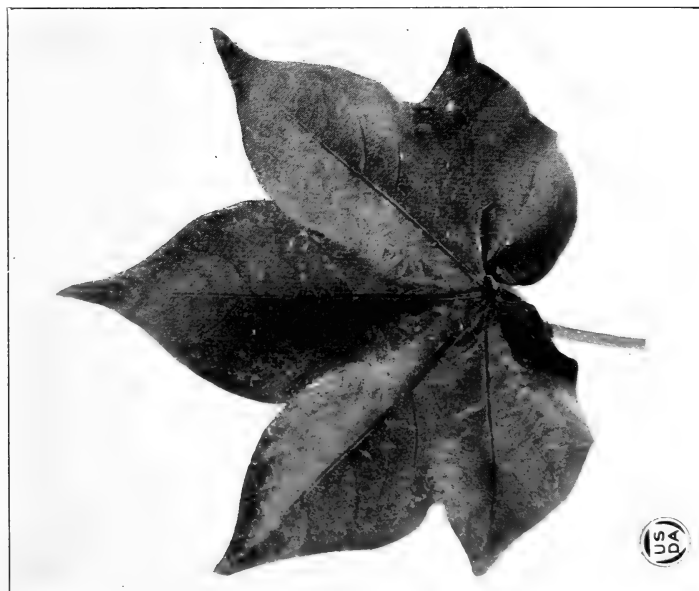
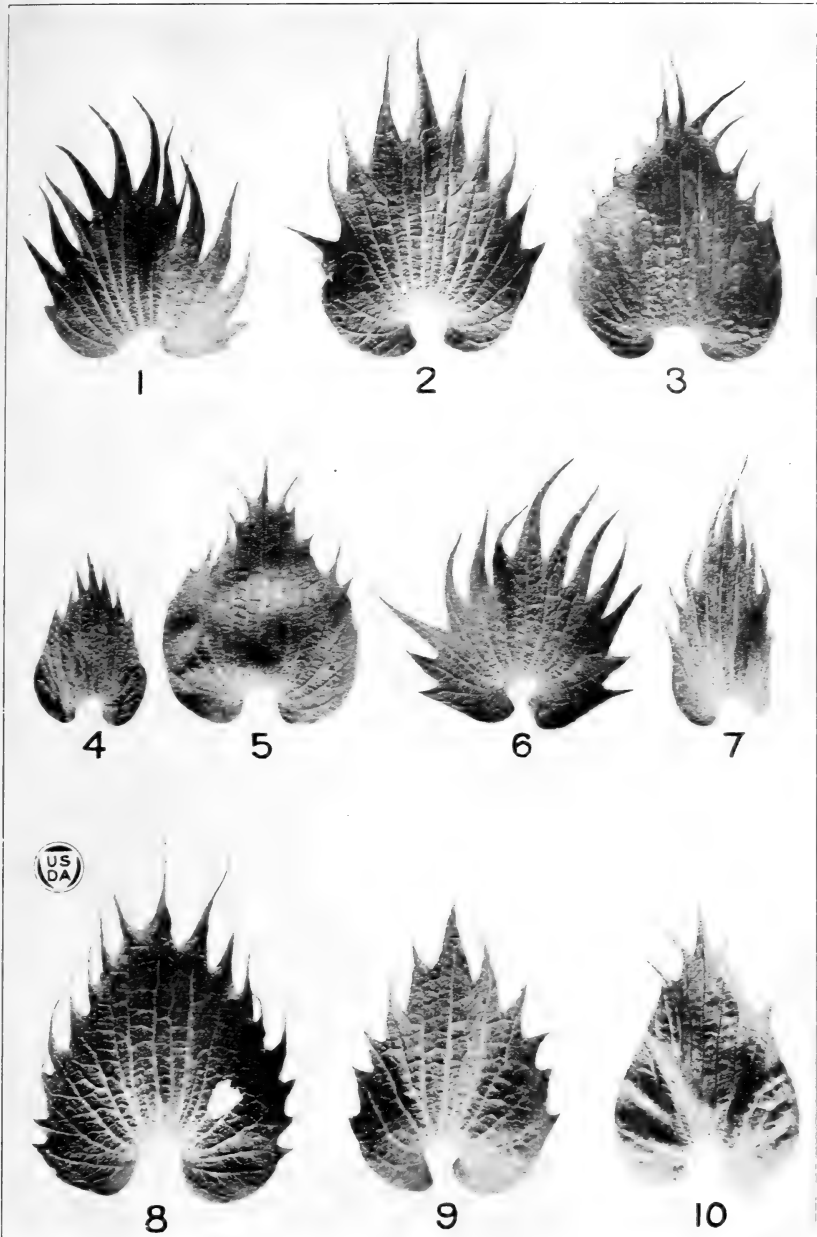


FIG. 1.—A TYPICAL LEAF OF THE HOLDON VARIETY OF UPLAND COTTON.



LEAF OF HOLDON X PIMA F₁ COTTON.

The large size, relatively deep lobation, and slightly sinuate or crinkled margin are characteristic.



INVOLUCRAL BRACTS OF THE PARENTAL AND HYBRID COTTON PLANTS.

Two-thirds natural size.

FIG. 1.—The Holdon parent, showing the very deeply toothed bract, with the teeth broad, leaflike in texture, and nearly erect. FIG. 2.—The first-generation hybrid, showing the intermediate expression of the characters. FIG. 3.—The Pima parent, showing the much less deeply toothed bract with bristlelike spreading teeth. FIGS. 4 TO 10.—Second-generation hybrid individuals, showing range of variation as follows: 4 and 8, Range in size of bract and number of teeth; 6 and 7, range in width of bract; 5 and 6, range in relative length of teeth (bract dentation index); 6 and 10, range in width of teeth; 5 and 7, range in spread of teeth.

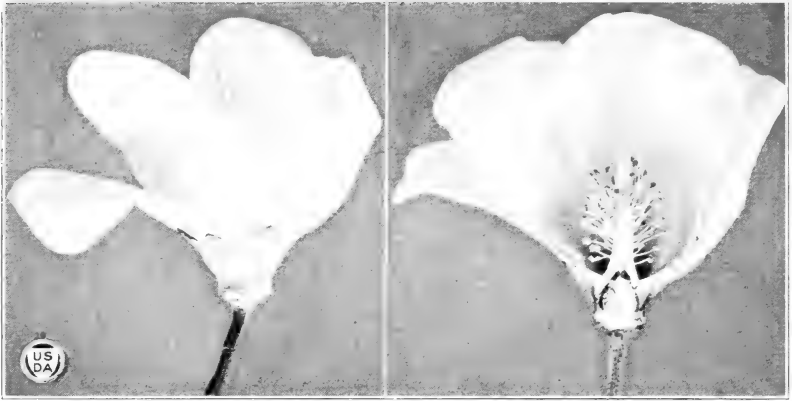


FIG. 1.—FLOWERS OF HOLDON COTTON.

This type is characterized by a dentate calyx with few oil glands, a small corolla, long filaments, and short stigmas.

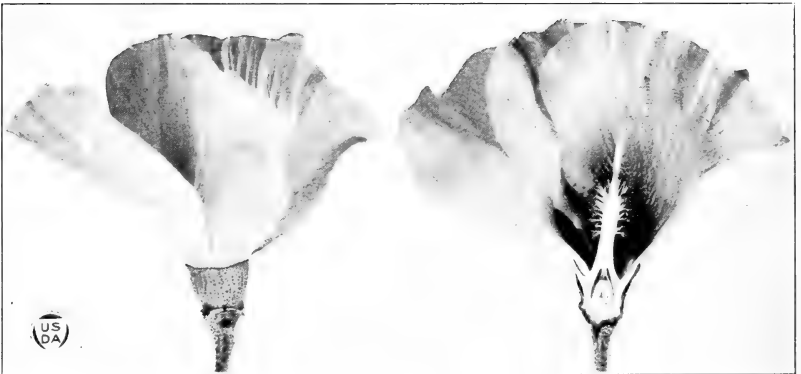
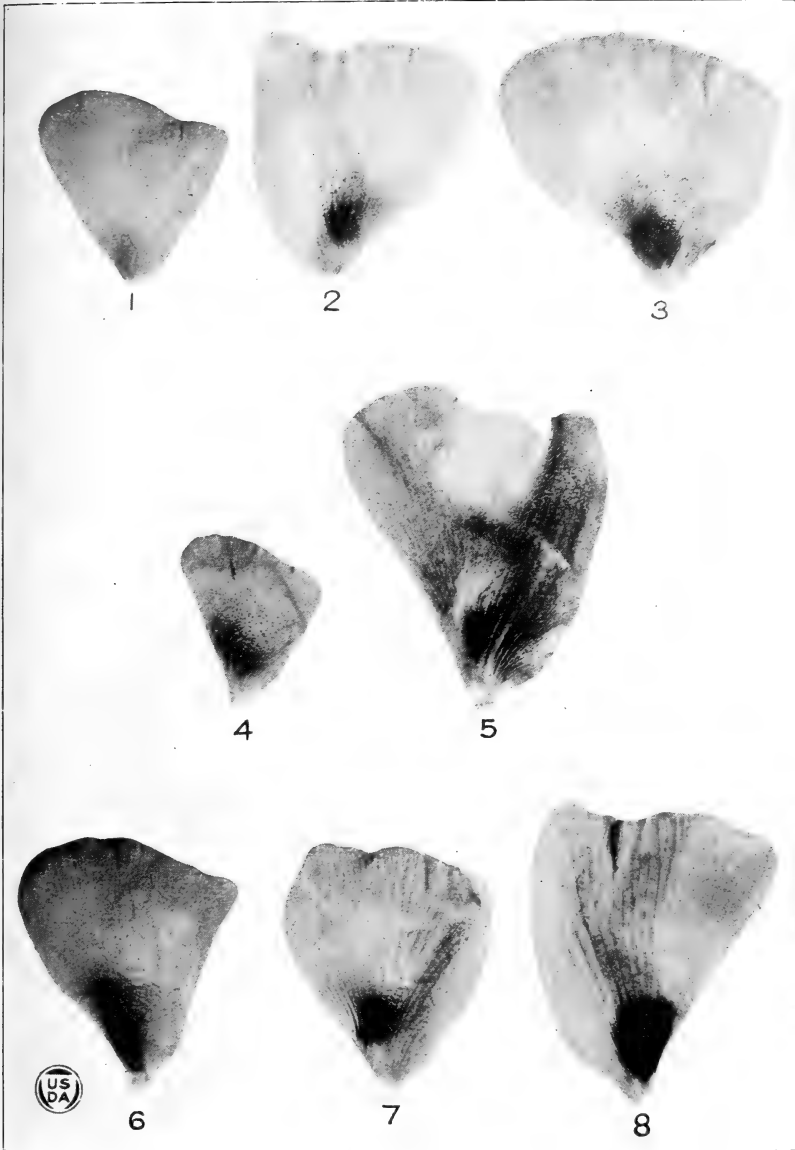


FIG. 2.—FLOWERS OF PIMA COTTON.

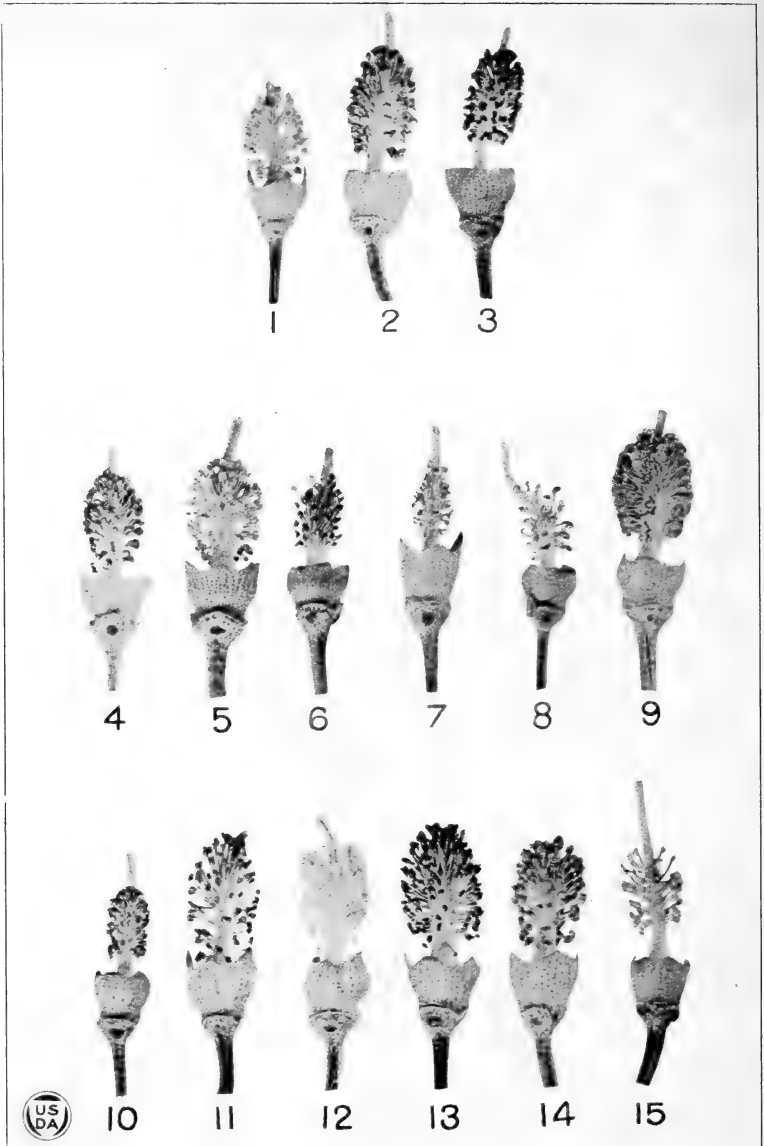
This type is characterized by an entire calyx with numerous oil glands, large corolla, short filaments, and long stigmas.



PETALS OF THE PARENTAL AND HYBRID COTTON PLANTS.

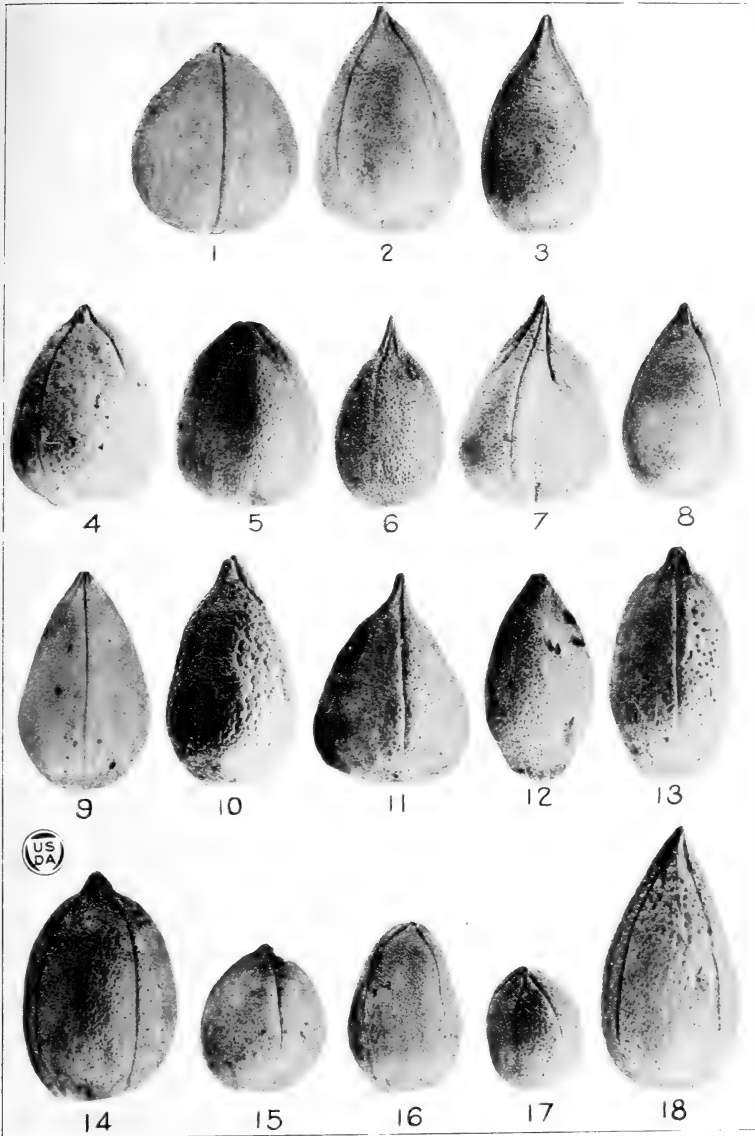
Two-thirds natural size.

FIG. 1.—The Holdon parent, showing the small petal without spot. FIG. 2.—The first-generation hybrid, showing the large petal intermediate in development of the spot. FIG. 3.—The Pima parent, showing the large petal and large spot. FIGS. 4 TO 8.—Second-generation hybrid individuals, showing range of variation in size (4 and 5) and in development of the spot (4, 6, 7, and 8).



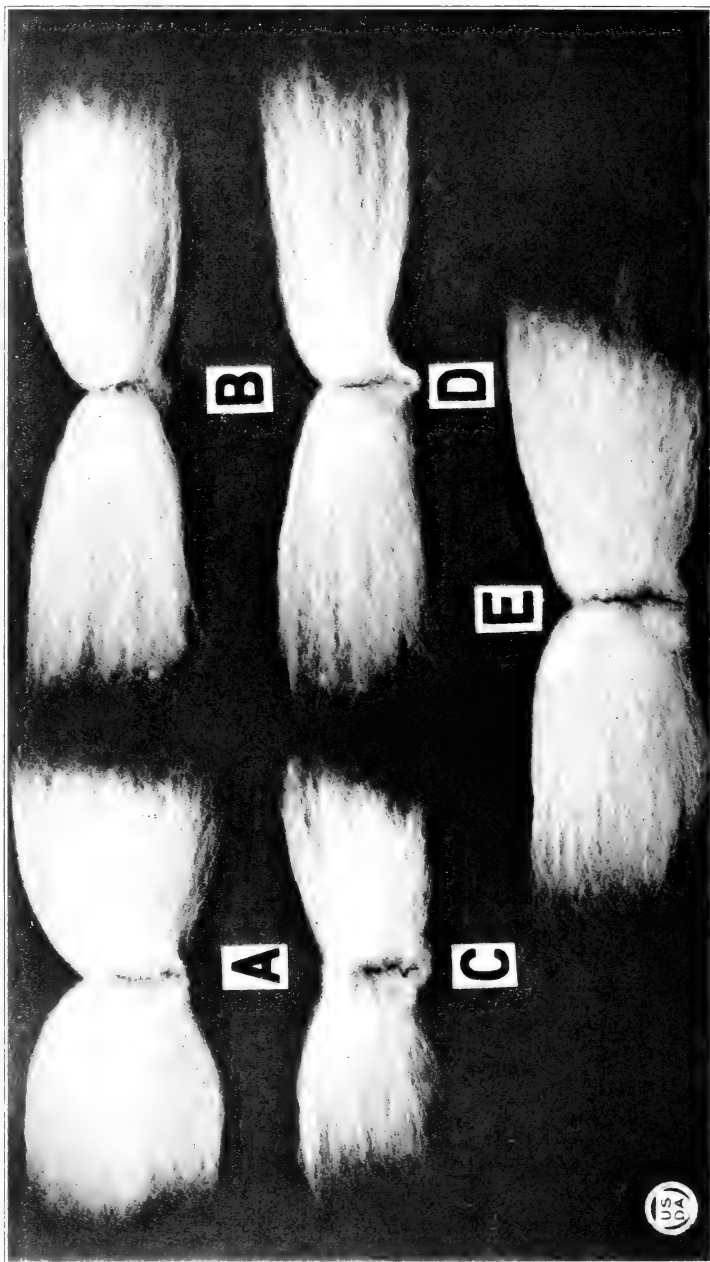
CALYX, STAMINAL COLUMN, AND STIGMAS OF THE PARENTAL AND HYBRID COTTON PLANTS.

FIG. 1.—The Holdon parent, showing the dentate calyx with few and scattered oil glands, the long filaments and pale-colored anthers, and the short stigmas. FIG. 2.—The first-generation hybrid, showing an intermediate condition in the dentation and abundance of oil glands of the calyx and in the color of the anthers, but resembling Holdon in the length of the filaments and Pima in the length of the stigmas. FIG. 3.—The Pima parent, showing the entire-margined calyx with numerous oil glands, short filaments, deeply colored anthers, and long stigmas. FIGS. 4 TO 15.—Second-generation hybrid individuals, showing range of variation as follows: 4 and 5, Calyx glands few and many; 6 and 7, calyx margin entire and deeply toothed; 8 and 9, stamens few and many (fig. 8 shows also malformation of the staminal column, abortion of most of the anthers, and a bent pistil); 10 and 11, filaments short and long; 12 and 13, anthers light and dark (deep yellow); 14 and 15, stigmas short (not exceeding the stamens) and long. Two-thirds natural size.



BOLLS OF THE PARENTAL AND HYBRID COTTON PLANTS.

FIG. 1.—The Holdon parent, showing the relatively large maximum and apical diameters (boll index and boll apex index high), almost complete absence of a beak, short midlock furrows, light color, and smooth surface, the oil glands being very inconspicuous. FIG. 2.—The first-generation hybrid, intermediate in shape, relative diameter (boll index), and character of the surface, but resembling the Pima parent in having a well-developed beak and no midlock furrow. FIG. 3.—The Pima parent, showing the relatively small maximum and apical diameters, conspicuous beak, absence of a midlock furrow, dark color, and pitted surface. FIGS. 4 TO 18.—Second-generation hybrid individuals, showing variations as follows: 4, The most Uplandlike; 8, the most Pima-like; 4 and 5, very light and very dark colored; 5 and 6, beakless and strongly beaked; 9 and 10, very smooth and very rough surface; 11 to 16, extreme variations in shape; 17 and 18, very small and very large; 7 and 9, presence of midlock furrow in different degrees; 16 and 18, termination of the lock furrows at considerable distances from the base of the boll.



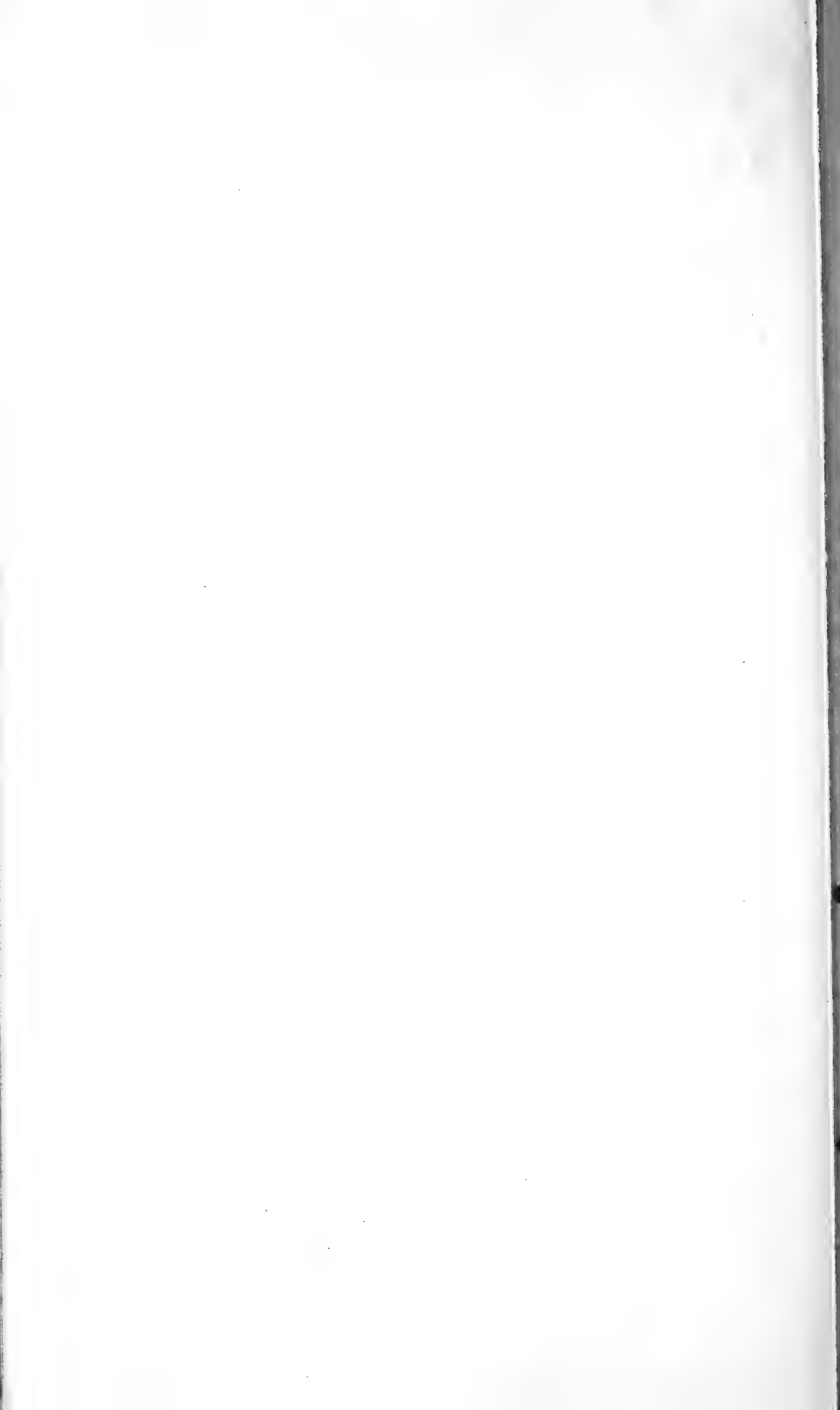
COMBED-OUT FIBER ON THE SEED OF THE PARENTAL AND HYBRID COTTON PLANTS.

A, The Holdon or short-fibered parent; B, the Pima or long-fibered parent; C and D, the shortest fibered and the longest fibered second-generation hybrid plants; E, the first-generation hybrid, showing approximation in fiber length to the long-fibered (Pima) parent.



SEEDS, AFTER REMOVAL OF THE FIBER, OF THE PARENTAL AND HYBRID COTTON PLANTS.

1. The Haldon parent, having the seed completely covered with long white fuzz; 2, the Pima parent, having the seeds partly covered with short greenish or brown fuzz; 3 and 4, the fuzziest seeded and the smoothest seeded second-generation hybrid plants; 5, the first-generation hybrid, having the seed completely covered with long green or white fuzz.



Bract, number of teeth was determined on the longest bract of the involucre. Pima (in 1917 and 1918) gave a higher mean for this character than Holdon.

Bract dentation index is the length of the terminal tooth of the longest bract, expressed as a percentage of the bract length. A high dentation index indicates that the bract is deeply toothed or rather cleft. Holdon exceeds Pima in the mean index of bract dentation.

Bract tooth spread, graded. The size of the grade number indicates the degree of divergence of the teeth of the bract, grade 1 indicating an erect position. Pima gave a higher mean grade for this character than Holdon.

Calyx dentation, graded, indicates the degree of indentation of the calyx, ranging from a slightly undulate but entire margin (grade 1) to a deeply toothed condition (grade 6). Holdon gave a higher mean grade for calyx dentation than Pima.

Calyx gland abundance, graded. The size of the grade number indicates the relative abundance of oil glands per unit of surface. The number of the oil glands rather than their conspicuousness and regularity of distribution was the criterion in grading. The mean grade for calyx gland abundance was higher in Pima than in Holdon.

Corolla length, measured in millimeters. Pima gave a higher mean than Holdon for this character.

Corolla index, width of the corolla at the summit¹⁰ as a percentage of the length. A high index indicates that the corolla is relatively broad and flaring when fully expanded. Holdon gave a higher mean for corolla index than Pima.

Petal color, graded, the palest color (Holdon) being indicated by grade 1 and the deepest yellow (Pima) by grade 5.

Petal spot, graded, the lowest grade number (0) indicating complete absence of the spot, as in the Holdon parent, and the highest grade number indicating the greatest intensity of the spot in the Pima parent. The variation in F_2 appeared to be in the density rather than in the kind of pigment present. The red pigment of the spot was never mixed with the yellow ground color of the petal. There was also great variation in the size of the red area, but in grading the endeavor was to consider the intensity rather than the size of the spot. Individual flowers on many of the F_2 plants differed greatly in respect to this character, the range in some plants having amounted to four grades. In such cases that flower open at the time of grading which showed the highest degree of red pigmentation in this area was selected, although, if the time available had permitted, it would have been preferable to determine the average grade of numerous flowers on each plant.

Stamen length, measured in millimeters on five stamens from a single flower on each plant, the average of the five measurements being taken as the value for the plant in question. Holdon gave a higher mean for stamen length than Pima.

Anther color, or, more precisely, color of the pollen, was determined by grading, grade 1, that of the Holdon parent, representing the palest and grade 6, that of the Pima parent, the deepest yellow color.

Pistil length, in millimeters, measured from the base of the staminal column to the summit of the stigmas. Pima gave a higher mean than Holdon for this character.

Stigma index is the length of the stigmas or free (extracolumnar) portion of the pistil, measured in millimeters and expressed as a percentage of the total length of the pistil. A high stigma index indicates that the stigmas are relatively long. The Pima mean was higher than that of Holdon.

Boll lock number. The numbers of bolls of different lock numbers on each plant were determined, and from these data the mean lock number for all bolls on the plant was computed. All bolls were included which were large enough early in October to permit the determination of the number of locks without sectioning. Holdon gave the higher parental mean.

Boll length, measured in millimeters. Pima gave the higher parental mean.

Boll diameter, in millimeters, measured at the height on the boll where the diameter is greatest. Holdon gave the higher parental mean.

Boll index. Boll diameter expressed as a percentage of the length of the boll.¹¹ A high boll index indicates a relatively broad boll. Holdon gave the higher parental mean.

Boll apex index is the diameter of the boll 5 millimeters below the apex expressed as a percentage of the maximum boll diameter. A high boll apex index indicates that the boll is relatively broad near the apex. Holdon gave the higher parental mean.

¹⁰ The endeavor was to measure the width as soon as possible after the expansion of the corolla had been completed. In the case of the F_1 grown in 1920 the measurements were made probably too early in the morning, and the constants for corolla index in this population are therefore omitted in Table 1. The parental populations of 1919 did not differ significantly in mean corolla width.

¹¹ The same expression of boll shape was used by Balls (4, p. 60).

Midlock furrow index is the length of the groove or furrow extending down from the apex of the boll in the center of the external wall of the lock, expressed as a percentage of the length of the boll. The midlock furrow is present in Holdon, absent in Pima.

Fiber length, graded. Owing to the great amount of labor which would have been involved in determining by measurement the actual average length of the fiber on so large a number of plants, a method of grading was employed which gave satisfactory comparative results. A perpendicular line was ruled off on a sheet of cardboard and parallel to this, on each side, a series of lines were drawn at intervals of about 3 millimeters (one-eighth inch), the first line being three-fourths of an inch from the central line. These lines were numbered from 1 to 9 on each side of the central line. The arrangement is shown in Figure 2. The seeds, with fiber adhering, were exposed for 30 minutes to a moist atmosphere, and the lint was then carefully parted on each side of the seed and was straightened out by combing.

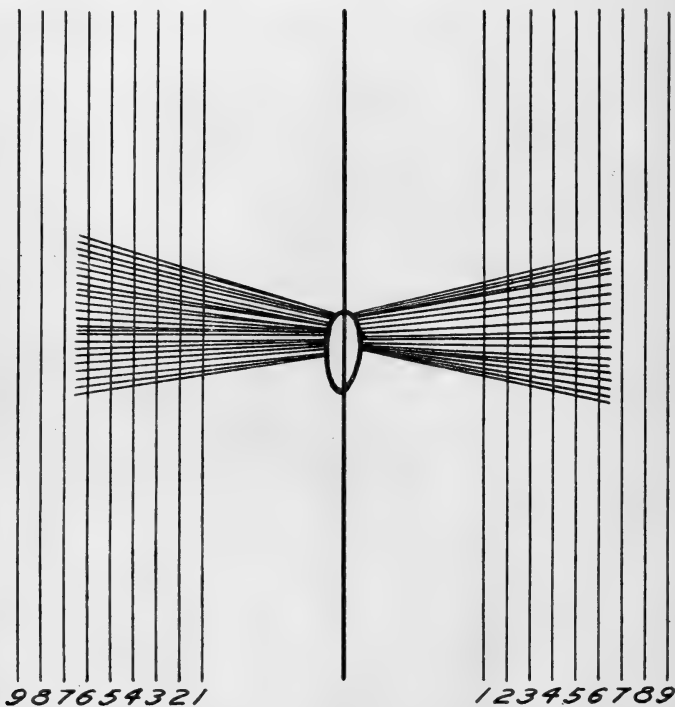


FIG. 2.—Diagram showing the method used in grading the length of cotton fiber, the grade here indicated being 6½.

The seed was placed with its longer axis over the central line and the number of the line on each side to which the bulk of the combed-out fibers extended was noted. If the right-hand fibers extended to line No. 7 and the left-hand fibers to No. 6, 6.5 was taken as the value for that seed. The fiber on five seeds from each plant, each seed from a different boll, was measured in this manner and the average of the resulting values taken as representing the mean fiber length of the plant in question. The means as thus determined were then distributed in a series of grades of equal magnitude, numbered 1 to 9, and these grades were used in computing the statistical constants and coefficients of correlation of this character. The average grade for fiber length was high in Pima, low in Holdon.

Fiber color, graded. Types were selected representing the range of variation in fiber color of the parental and F_2 populations, eight grades having been distinguished. The color grade for each plant was determined by comparing a sample of its ginned fiber with the types until the nearest equivalent was found. Of the parental populations, Pima gave the higher grade for fiber color.

Lint index. Seed cotton from five bolls of each plant was weighed and ginned, the total weight of the seeds was determined and the weight of fiber was ascertained by subtracting the weight of the seeds from the original weight of the seed cotton. The total number of seeds was then determined and the lint index was computed as weight of fiber \div number of seeds \times 100. A high lint index indicates that the fiber is abundant. Holdon gave a higher mean for lint index than Pima.

Seed fuzziness, graded. Types were selected representing the range of variation in this character of the parental and F_2 populations, nine grades having been distinguished. The sample of seeds of each plant obtained by ginning the five-boll sample of seed cotton was compared with the types and the nearest equivalent was taken as the grade of seed fuzziness for the plant in question. The grading was based upon the relative area of the seed coat covered with short hairs or fuzz, although variation in the length and color of the fuzz made the matching somewhat difficult. Of the parental populations, Holdon gave the higher mean grade for seed fuzziness.

STATISTICAL CONSTANTS OF THE PARENTAL AND OF THE F_1 AND F_2 HYBRID POPULATIONS.

Table 1 gives the means, standard deviations, and (for the measured characters) the coefficients of variation of 39 characters which were determined on the parental and F_2 hybrid progenies in 1919 and on the F_1 hybrid progeny in 1920. As was stated on a preceding page, three F_2 Holdon \times Pima populations were grown in 1919, each having been the progeny of a single F_1 plant of 1918. The F_1 parents were not selected as representing the extremes of variation in the F_1 population of 1918 but may be regarded as constituting a random sample. Comparison of the frequency distributions and means of the separate F_2 progenies for 11 characters in respect to which the parent varieties differed very significantly showed no important differences and indicated that there had been no pronounced segregation in the F_1 . For 7 of the 11 characters the means of the three F_2 progenies showed no significant differences, while for 4 characters the highest and the lowest mean differed by from three to five times the probable error of the difference. The modes of the three progenies for none of the characters differed by more than one grade in a total of seven to nine grades. It was decided therefore to treat the F_2 as one array. The total number of plants in this F_2 population was 215, but all of the characters were measured or graded on only 180 individuals. As only the plants on which all characters had been determined were used in computing the coefficients of correlation it was thought best to compute the means and other statistical constants from the same 180 plants.¹²

It is regrettable that the F_1 progeny of the hybrid grown in 1919 was not of adequate size for comparison with the F_2 population of that year. The F_1 grown in 1920 was perforce used for this purpose, but the validity of the comparison is lessened not only because of the probable effect of different weather in the two seasons but also because the F_1 progeny of 1920 was situated on better soil than that upon which the Pima and Holdon parental progenies and the greater part of the F_2 population in 1919 were grown. This makes the comparison unsatisfactory, especially in regard to size characters.

¹²In order to ascertain whether the 180 plants on which all characters were measured or graded constituted a fair sample of the whole population, the frequency distributions and means for 13 characters, which had been determined on all or nearly all F_2 individuals (n-213 to 215), were compared for the two populations. The differences in the frequency distributions were negligible, and in no case did the means of the 180 individuals differ from the means of the larger number by an amount greater than the probable error of the difference.

TABLE 1.—Means, standard deviations (σ), and coefficients of variation (C), of the *Holdon-Pima* parental and hybrid populations.¹

Character.	Holdon.			Pima.			Parental, 1919.			Signifi- cance of the parental differ- ence. ²	Hybrid.					
	Mean.	σ	C	Mean.	σ	C	Mean.	σ	C		F ₁ (1920).			F ₂ (1919).		
											Mean.	σ	C	Mean.	σ	C
Length	92.0±2.20	12.2	13.2	184.0±4.30	20.5	11.1	203.0±2.30	16.4	8.1	167.0±2.20	38.0	22.7				
Axis	35.6±.85	4.7	13.2	47.1±.70	3.4	7.2	50.0±.50	3.6	7.2	42.6±.36	29.0	14.8				
Internode length	26.2±.71	3.9	14.9	39.0±.68	3.3	8.5	40.6±.25	1.8	4.4	39.2±.29	5.0	12.8				
Fruiting branch	21.3±1.06	5.8	27.2	72.2±1.56	8.9	12.3	65.2±1.28	9.2	10.2	54.6±.93	16.3	29.6				
	Length	2.1±.14	7.3	33.3	19.0±.60	3.1	16.3	18.7±.27	1.9	14.2	13.2±.27	4.6	33.6			
Length	127.0±1.70	9.3	7.3	182.0±1.90	9.4	5.2	215.5	189.0±1.40	9.7	5.1	142.0±1.30	37.1	16.2			
	Index	143.0±4.10	22.7	15.9	236.0±4.90	24.0	10.2	271.0±2.60	18.6	6.9	178.0±2.20	23.7	21.1			
Leaf	113.0±2.80	15.7	13.9	130.0±2.30	11.5	8.8	143.0±1.00	7.0	4.9	125.0±1.90	15.9	12.8				
	Lobe index	45.9±.75	4.2	9.1	36.1±.61	3.0	8.3	37.2±.32	2.3	6.2	41.9±.52	9.1	21.7			
Vein angle	94.5±1.10	6.1	6.4	103.4±2.14	10.5	10.2	97.7±.76	5.3	5.4	98.9±.72	12.6	12.7				
	Extension index	23.9±.75	4.2	17.6	16.7±.50	2.9	17.4	17.0±.24	1.8	10.6	19.3±.30	16.8	33.2			
Callus color	6.7±.06	.3		1.0±.02	0.1		5.2±.07	0.5		6.1±.07	1.8					
Petiole hairiness	5.2±.08	.4		1.0±.02	0		2.7±.04	.3		5.0±.10	1.3					
Petiole length	21.4±1.57	8.7	40.2	25.5±1.80	9.3	36.4	41.6	54.2±1.24	9.1	16.8	27.5±.51	8.8	31.6			
	Length	51.3±1.01	5.8	11.3	56.7±1.75	3.9	6.9	4.2	62.7±.47	3.3	35.3	54.3±.39	6.7	32.2		
Constitution index	2.3±.68	3.8	135.7	7.5±.75	3.9	52.0	6.2±.36	2.6	42.0	7.3±.40	7.0	89.7				
	Number of teeth	12.3±.24	1.3	19.6	11.8±.17	.9	6.6	12.9±.33	.9	7.0	11.2±.13	2.3	20.5			
Bract	46.3±.62	3.4	7.3	35.3±.58	3.0	8.5	37.3±.38	2.7	7.2	40.5±.34	5.9	14.6				
	Tooth spread	1.6±.13	.7		4.7±.08	.4		2.9±.01	.1		3.3±.07	1.3				
Calyx	Dentation	5.0±0	0	1.0±0	0		2.8±.05	.4		3.0±.06	1.1					
	Gland abundance	1.0±0	0	4.0±0	0		2.6±.08	.6		2.9±.04	.8					
Corolla	Length	35.1±1.10	6.1	17.4	56.8±.70	3.6	6.3	16.6	61.0±.34	2.5	4.1	52.5±.37	6.5	12.4		
	Index	119.3±5.78	21.0	17.6	70.6±1.41	7.2	10.2	12.1	61.0±.34	2.5	4.1	65.7±1.12	19.5	29.6		
Petal	Spot	0±0	0	5.0±0	0		3.0±0	0		2.7±.05	.9					
	Color	0±0	0	6.5±.14	.7		4.2±.17	1.3		2.6±.13	2.2					
Stamen length	Length	6.3±.17	.9	4.4±.09	.5	11.4	6.0±.03	.2	3.3	5.8±.06	1.0	17.3				
	Index	21.9±.57	3.2	5.9±.02	1.1	5.2	39.5±.23	1.6	4.0	29.4±.24	4.2	14.3				
Anther color	Length	14.3±1.09	6.0	31.8±.36	1.8	9.9	35.5±.75	5.4	15.2	23.0±.65	11.3	49.2				
	Index	4.4±.01	.08	3.0±.01	.04	1.3	3.7±.01	.06	1.6	3.5±.02	.3	8.6				
Lock number	Length	45.1±.42	2.3	47.5±.41	2.0	4.2	44.3±.34	2.5	5.6	44.7±.30	5.2	11.6				
	Index	38.2±.23	1.3	3.4	27.6±.13	.7	2.5	40.0	31.7±.25	1.8	5.7	29.3±.15	2.7	9.2		
Boll	Diameter	84.7±.70	3.8	4.5	58.2±.49	2.5	4.3	71.7±.57	4.1	5.7	65.5±.45	7.9	12.1			
	Index	43.5±.92	5.2	11.9	24.2±.41	2.1	8.7	20.5±.39	2.8	13.7	31.8±.56	9.8	30.8			
Apex index	Length	7.8±.38	2.1	26.9	0±0	0	0±0	0	0	5.3±.41	7.1	134.0				
	Midlock furrow index	2.1±.09	.5		7.4±.12	.6		6.6±.09	.7		5.0±.09	1.5				
Fiber	Length	2.0±0	0	5.3±.08	.4		3.4±.07	.5		4.3±.10	1.8					
	Color	5.8±.14	.8	13.8	4.7±.06	.3	6.4	4.8±.03	.3	4.2	4.8±.06	1.1	22.9			
Lint index	Length	7.1±.09	.5		1.5±.12	.6		6.0±0	0		6.1±.07	1.3				
	Fuzziness															

¹The numbers of the populations were: Pima, 12 or 13 for the several characters; Holdon 13 to 15 for the several characters. H × P, F₁, 24 for all characters; H × P, F₂, 180 for all characters.

²The significance of the parental differences is shown by the difference between the means of Pima and Holdon divided by its probable error.

MEANS OF THE PARENTAL AND HYBRID POPULATIONS.

Comparing the means of the progenies representing the Holdon and Pima parents of the hybrid as to the significance of the difference, (Table 1) it is seen that in respect to all but 2 of the 39 characters, pedicel length and bract number of teeth,¹³ the difference amounted to three and one-half or more times its probable error. The parental means of 1919 for 28 characters differed by 10 or more times the probable error. Pima gave a higher mean than Holdon for all size characters excepting stamen length, boll diameter, and boll lock number.

It is of interest to compare the means of the F_1 population grown in 1920 with those of the parental and F_2 populations grown in 1919, although such comparison, as previously noted, is not free from objection. Of the characters which showed differences between the parental means amounting to three and one-half or more times the probable error of the difference, 38 of which were determined in F_{17} , 17 are size characters, and in respect to 14 of these the F_1 mean approached or exceeded that of the parent which gave the higher mean. For 9 of the remaining characters the F_1 mean was approximately intermediate, these characters having been: Leaf vein angle, leaf callus color, petiole hairiness, bract tooth spread, calyx dentation, calyx gland abundance, petal color, boll index, and fiber color. Dominance in greater or less degree was indicated by the F_1 means for the following 12 characters: Leaf index, leaf lobe index, leaf extension index, bract connation index, bract dentation index, petal spot, anther color, stigma index, boll apex index, midlock furrow index, lint index, and seed fuzziness. Of the characters showing a marked tendency to dominance, seed fuzziness is the only one for which the F_1 mean approximated that of Holdon. In all the others F_1 resembled or exceeded Pima. The greater seed fuzziness of Holdon appears to be almost completely dominant while the midlock furrow, a character appearing in the Holdon but not in the Pima parent, was completely absent in F_1 .

The F_2 mean for all characters fell between the parental means or did not differ significantly from the mean of one or the other parent.

STANDARD DEVIATIONS AND COEFFICIENTS OF VARIATION.

In comparing variation in the different populations with respect to measured characters, including indices derived from measurements, the coefficient of variation affords the most satisfactory criterion. The use of the coefficient does not seem to be permissible in the case of characters which were determined by grading; for, with standard deviations of equal size, a population having a high mean grade would give a disproportionately low coefficient of variation in comparison with a population having a low mean grade.¹⁴ The standard deviation, therefore, has been used as the criterion of the variability of the graded characters. The standard deviations for all characters

¹³ These characters are included because the means of the parental progenies in 1917 and 1918 differed significantly, the Pima mean having been the higher for both characters in both years. For pedicel length the difference was 13.4 times E (probable error) in 1917 and 18.6 times E in 1918. For bract number of teeth, the difference was 3.9 times E in 1917 and 5.8 times E in 1918. The Pima population of 1919 gave an abnormally low mean for pedicel length.

¹⁴ For example, the mean grade of seed fuzziness was 1.5 in Pima and 7.1 in Holdon, σ having been respectively, 0.6 and 0.5. The coefficients of variation in this case would have been 40 and 7, yet assuredly the Pima progeny was not six times more variable than the Holdon progeny in respect to this character.

and the coefficients of variation for characters determined by measurement are given in Table 1.

Comparisons of the several populations in respect to the coefficients of variation for 28 characters determined by measurement and the standard deviations for 11 characters determined by grading are summarized in Table 2, which gives the data (1) for all characters and (2) for characters in respect to which the coefficients of variation or the standard deviations differed by an amount equal to three and one-half or more times the probable error of the difference. In comparisons involving the parental populations the small size of the latter and the resulting large probable errors of their constants doubtless explain the relatively small number of cases in which significant differences are shown.

TABLE 2.—*Relative variability of the parental and hybrid populations of Holdon and Pima cotton as expressed by the numbers of characters in respect to which one or the other population gave the higher coefficient of variation of a measured character or standard deviation of a graded character.*

Number of characters showing difference between the coefficients of variation or the standard deviations.	Parental comparison.			Comparison of the hybrid with the more variable parent, whether Holdon or Pima.						Comparison of F ₂ with F ₁ .		
	Holdon with Pima.			F ₁			F ₂					
	Holdon more variable.	Holdon less variable.	No difference.	F ₁ more variable.	F ₁ less variable.	No difference.	F ₂ more variable.	F ₂ less variable.	No difference.	F ₂ more variable.	F ₂ less variable.	No difference.
Showing any difference	29	7	3	10	27	1	33	6	0	38	0	0
Showing a significant difference ¹ .	8	3	3	15	25	0	37	0

¹ Difference amounting to three and one-half or more times its probable error.

Holdon was clearly much the more variable of the parental populations, having given a coefficient of variation or a standard deviation higher than that of Pima for 29 of the 39 characters. Considering only characters in respect to which the constants differed significantly, Holdon was the more variable in 8 and Pima the more variable in 3 characters.

Comparing the hybrid F₁ with the parental population which was the more variable for the character in question, the coefficient of variation or standard deviation for 10 characters was higher and for 27 characters it was lower in F₁ than in the more variable parental population. F₁ gave a significantly higher constant than the more variable parental population for only 3 characters, while for 15 characters it gave a significantly lower constant.

F₂ gave a higher coefficient of variation or standard deviation than the respective more variable parental population for 33 characters and a lower constant for 6 characters, but while F₂ was significantly more variable in 25 characters, it was significantly less variable in none.

F₂ was significantly more variable than F₁ in all but 1 of the 38 characters determined on both populations.

Another expression of the comparative variability of the parental and hybrid progenies was obtained by averaging, for each population, the coefficients of variation of the measured characters and the standard deviations of the graded characters, the averages being given in Table 3.

TABLE 3.—Averages of the coefficients of variation and of the standard deviations of the parental and hybrid populations of Holdon and Pima cotton.

Average of the —	Parental.		Hybrid.	
	Holdon.	Pima.	F ₁ .	F ₂ .
Coefficients of variation of the 28 measured characters.....	19.66±2.17	10.62±0.96	8.31±0.78	26.92±2.54
Standard deviations of the 11 graded characters.....	.22±.05	.29±.07	.38±.08	1.37±.08

Comparing the averages of the coefficients of variation for the measured characters, Holdon is found to be considerably the more variable of the parental populations, and the difference between the average variabilities of the Holdon and Pima populations amounts to nearly four times the probable error of the difference. F₁ is much less variable than the Holdon parental population, and the difference amounts to about five times its probable error. The average variabilities of F₁ and the Pima parental population do not differ significantly. The average variability of F₂ is very significantly greater than that of F₁ and of the less variable parental population (Pima), but F₂ was not significantly more variable than the Holdon parental population, the difference in average variability amounting, in this case, to only about twice the probable error of the difference.

Comparison of the averages of the standard deviations for the graded characters shows no significant differences in variability among the two parental and the F₁ populations, while F₂ is greatly and significantly more variable than the other three populations.

Comparison of the average of the coefficients of variation for measured characters of F₁ with that of F₂ shows F₂ to be more than three times as variable as F₁. A similar comparison on the basis of the standard deviation for the graded characters shows F₂ to be three and one-half times as variable as F₁.

These data, however, give a very inadequate expression of the relative variability of the second generation of this hybrid, for, in addition to the characters here considered, many appeared in F₂ which were not expressed or but slightly expressed in either parental population. (See pages 39 to 41.) If these extraparental characters are taken into account, it must be concluded that the diversity in F₂ was vastly greater than in either parental population or in the first generation of the hybrid.

FREQUENCY DISTRIBUTIONS OF THE SECOND GENERATION OF THE HYBRID.

The frequency distributions for the 39 characters of the hybrid F₂ population grown in 1919 are shown in Figures 3 to 41. The numbers on the axis of ordinates represent percentages of the total

number of individual plants (180) which the population comprised. The numbers on the axis of abscissas are those of the several grades. For characters determined by grading the numbers indicate the original grades under which the population was classed, except that in the case of fiber length, as explained on a preceding page, the plant averages of the original grades were reclassified in nine final grades. For

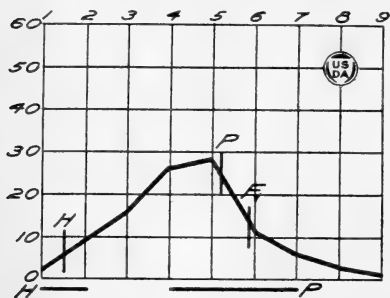


FIG. 3.—Axis length: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

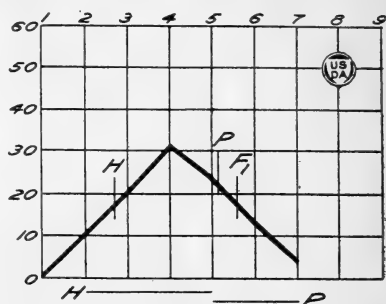


FIG. 4.—Axis internode length: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

measured characters and indices based upon measurement the total range of the actual values was subdivided into a number of grades of equal range. This was done to facilitate calculation of the coefficients of correlation on the tabulating machine, but it was found convenient to plot the frequency distributions on the same basis.

In addition to the F_2 frequency distributions, the diagrams show by means of short vertical lines the positions on the curve of the

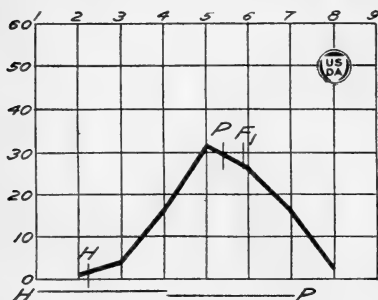


FIG. 5.—Axis internode number: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

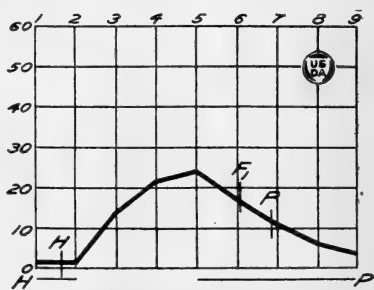


FIG. 6.—Fruiting branch length: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

means of the parental populations (H and P) grown in the same year and of the hybrid F_1 grown in 1920. The ranges of the parental progenies are indicated by horizontal lines at the bottom of the figure.

The wide variation occurring in the second generation of this hybrid, in regard to most of the characters determined by measurement or grading, is clearly shown by the frequency distribution curves. The

F₂ distributions for 37 of the 39 characters comprise the means of both parental populations and for 33 characters they extend to or beyond the extremes of both parental populations. For 10 characters the F₂ range extends in both directions beyond the combined range of the Holdon and Pima populations. For the characters bract connation index, bract number of teeth, and midlock furrow

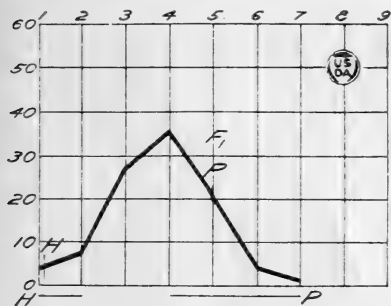


FIG. 7.—Fruiting branch, first internode length: Frequency distribution of Holdon × Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

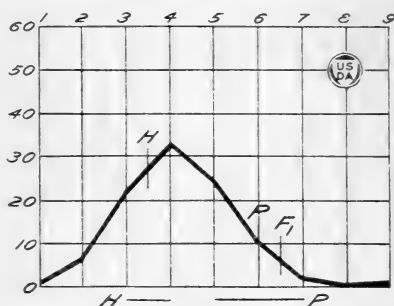


FIG. 8.—Leaf length: Frequency distribution of Holdon × Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

index half or more of the F₂ range lies outside the combined parental range.

On the other hand, the extreme range for six characters of one of the parental populations—in every case the Holdon population—was not fully recovered in F₂. These characters are axis internode number, corolla length, corolla index, anther color, boll diameter,¹⁵ and boll lock number.¹⁶

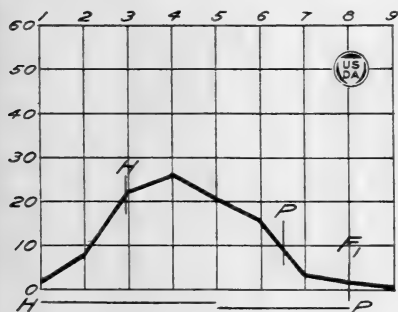


FIG. 9.—Leaf width: Frequency distribution of Holdon × Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

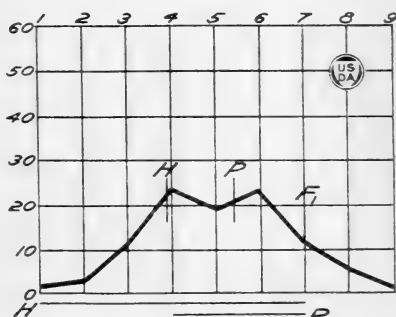


FIG. 10.—Leaf index: Frequency distribution of Holdon × Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

The frequency distributions in two cases show an extreme expression in F₂ of characters which are but slightly expressed in either parent variety. These are pronounced connation of the

¹⁵ Balls (5, p. 262) states that in a cross of the Russell variety of upland cotton with an Egyptian variety "the characteristically fat Russell boll did not reappear exactly among 60 F₂ plants."

¹⁶ An Egyptian-upland cotton hybrid is described by Balls (5, pp. 163, 164) in which the mean lock number of the upland parent was considerably exceeded in F₂.

margins of the bracts (fig. 18) and extension of the furrow in the middle of the lock far below the apex of the boll, this being indicated by a high midlock furrow index (fig. 37). The occurrence in F_2 of numerous additional extraparental characters will be discussed later.

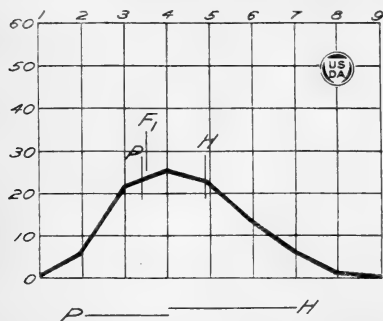


FIG. 11.—Leaf lobe index: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

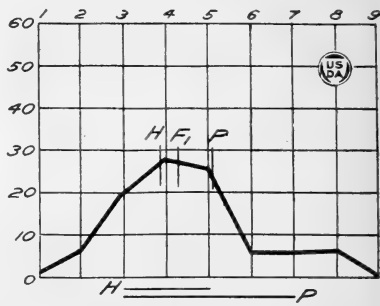


FIG. 12.—Leaf vein angle: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

The frequency distributions of F_2 are in the main such as would be expected for characters in which several factors are involved. The resemblance to a normal frequency curve is usually evident, although pronounced skewness is shown by the distributions for several characters, especially petiole hairiness, bract connation index, calyx dentation, midlock furrow index, and seed fuzziness.

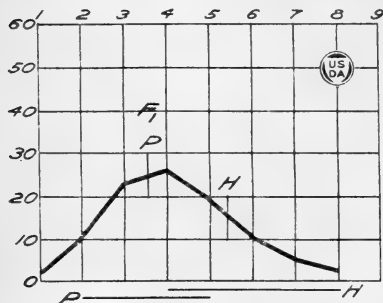


FIG. 13.—Leaf extension index: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

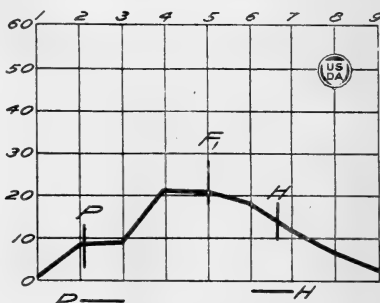


FIG. 14.—Leaf callus color: Frequency distribution of Holden \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

The F_2 mode is much nearer the mean of one than of the other parental population in respect to the following characters, the letter H or P indicating the parent approached by the mode of F_2 and the asterisks indicating pronounced examples of displacement of the F_2 mode in the direction of one or the other parental mean, in other than simple size characters:

- Axis length (P).
- Axis internode number (P).
- Fruiting branch length (P).
- Fruiting branch first internode (P).
- Leaf length (H).
- Leaf width (H).
- *Petiole hairiness (P).
- Bract tooth spread (P).
- *Calyx dentation (P).
- Calyx gland abundance (P).

- Corolla length (P).
- *Corolla index (P).
- Petal spot (P).
- *Anther color (P).
- Stamen length (H).
- Pistil length (P).
- Boll diameter (P).
- Boll lock number (P).
- Fiber color (P).
- *Seed fuzziness (H).

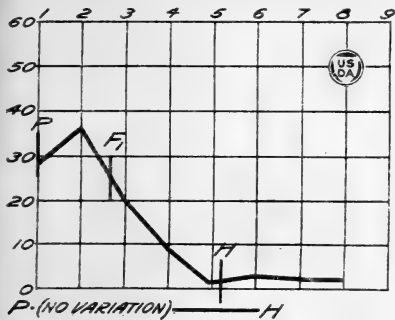


FIG. 15.—Petiole hairiness: Frequency distribution of Holdon × Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

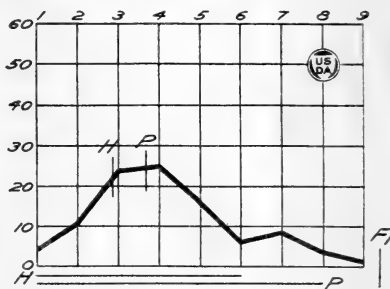


FIG. 16.—Pedicel length: Frequency distribution of Holdon × Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

For several of the size characters the position of the F_2 mode may be attributed to heterosis, exceptions being leaf length, leaf width, boll diameter, and boll lock number, in respect to which the F_2 mode was nearer the parent having the lower mean. For petiole

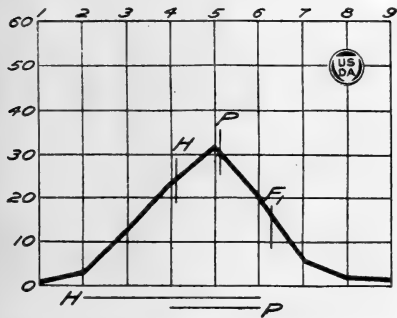


FIG. 17.—Bract length: Frequency distribution of Holdon × Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

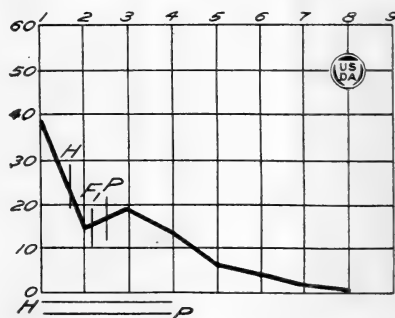


FIG. 18.—Bract connation index: Frequency distribution of Holdon × Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

hairiness and calyx dentation the F_1 mean was approximately intermediate, but for corolla index,¹⁷ anther color, and seed fuzziness the mean of F_1 showed a wide departure from the midpoint in the same direction as the mode of F_2 . Partial dominance of one or the other parent would seem, therefore, to be indicated in these cases.

¹⁷ This was shown for corolla index not only by the doubtful F_1 mean of 1920 but by the more reliable F_1 means of 1917 and 1918.

The range of variation of many of the characters in the second generation of this hybrid is shown in the illustrations as follows:

Habit of growth and general character of the foliage, Plates XII to XV, which show typical plants in F₂ progenies of some of the more remarkable F₂ individuals.

Leaf characters, size, shape, number of lobes, depth of lobation, width of the vein angle, etc., Plates XVI to XXI.

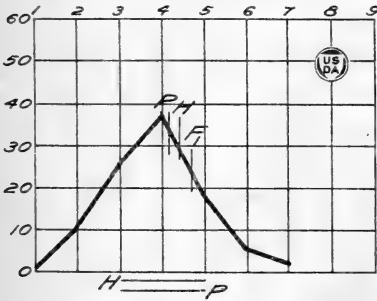


FIG. 19.—Bract, number of teeth: Frequency distribution of Holdon x Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

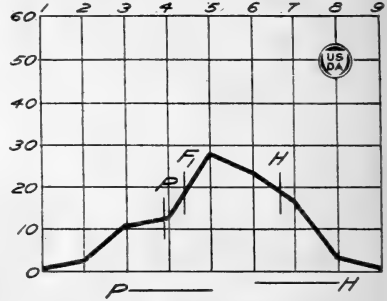


FIG. 20.—Bract dentation index: Frequency distribution of Holdon x Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

Bract characters, size and shape of the bract, and number, length, width, and position of the teeth, Plate V, Figures 4 to 10.

Calyx characters, abundance of the oil glands and degree of dentation, Plate VIII, Figures 4 to 7.

Petal characters, size of the petal and degree of development of the spot, Plate VII, Figures 4 to 8.

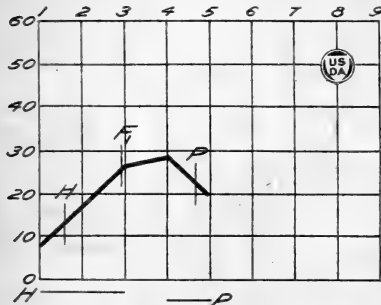


FIG. 21.—Bract tooth spread: Frequency distribution of Holdon x Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

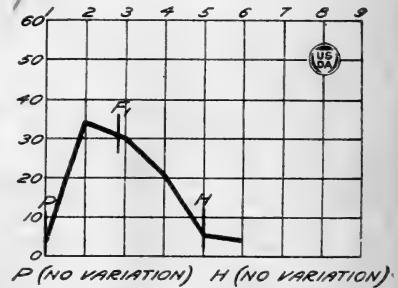


FIG. 22.—Calyx dentation: Frequency distribution of Holdon x Pima F₂ cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

Stamen characters, number of stamens, length of filaments, intensity of color of anthers, Plate VIII, Figures 8 to 13.

Pistil characters, length of pistil and of stigmas, Plate VIII, Figures 14, 15.

Boll characters, size, shape, intensity of color, character of surface, degree of pointedness, presence or absence of a midlock furrow, Plate IX, Figures 4 to 18.



FIG. 2.—A COTTON PLANT OF F₃ PROGENY NO. 40.

This progeny averaged the tallest of all the F₃ progenies and comprised many sterile or nearly sterile plants. The slender habit and erect, vegetative branches are characteristic.



FIG. 1. A PLANT OF F₃ PROGENY NO. 171.

This progeny was uplandlike in many of its characters. It had the very short, fruiting branches of a cluster cotton and large, coarse, dark-green leaves which show a tendency to crumpling or buckling.



FIG. 1.—A COTTON PLANT OF F₃ PROGENY NO. 61.

This progeny was remarkable for the glaucous or bluish color of its foliage and for its open habit, numerous long vegetative branches, large, very open corolla, and pale-colored petals with a conspicuous spot.



FIG. 2.—A COTTON PLANT OF F₃ PROGENY NO. 16.

This progeny was Hindilike in appearance, short and compact, having bright green, tender, crinkly margined, mostly 1 to 3 lobed leaves and very connate bracts.



FIG. 3.—A COTTON PLANT OF F₃ PROGENY NO. 156.

This progeny was characterized by its very dense habit of growth, numerous vegetative branches nearly equaling the axis, small Uplandlike mostly 3-lobed leaves, and bolls of Egyptian color and shape.



FIG. 1.—A COTTON PLANT OF F₃ PROGENY No. 178.

This progeny was slender and rigid in habit, having erect vegetative branches and remarkable for the nearly erect position of the leaf blades of which the ventral surface faces outward instead of downward.



FIG. 2.—A PLANT OF F₃ PROGENY No. 194.

This progeny was characterized by the extreme cluster habit (very short fruiting branches), complete or nearly complete absence of vegetative branches, and deeply and narrowly lobed leaves.



FIG. 2.—A PLANT OF F₃ PROGENY NO. 102.

The leaves of this progeny were very deeply and narrowly five-lobed, the lobes coarsely toothed or cleft, and the margins conspicuously undulate or wavy.



FIG. 1.—A PLANT OF F₃ PROGENY NO. 84.

This progeny was characterized by the very dark color and crispate or fluted margins of its leaves.



FIG. 1.—LEAF FROM ONE OF THE SMALLEST LEAFED PLANTS.



FIG. 2.—LEAF FROM ONE OF THE LARGEST LEAFED PLANTS.

The resemblance to the leaf of the first-generation hybrid is shown by comparison with Plate IV.

LEAVES OF HOLDON \times PIMA COTTON, F₂.



FIG. 1.—A TYPE OF UPLAND TEXTURE.

Note the very shallowly 3-lobed character.



FIG. 2.—A TYPE OF EGYPTIAN TEXTURE.

Note the very deeply 5-lobed character, the pronounced "cupping" of the blade, and the wavy margins.

LEAVES OF HOLDON × PIMA COTTON, F₂.

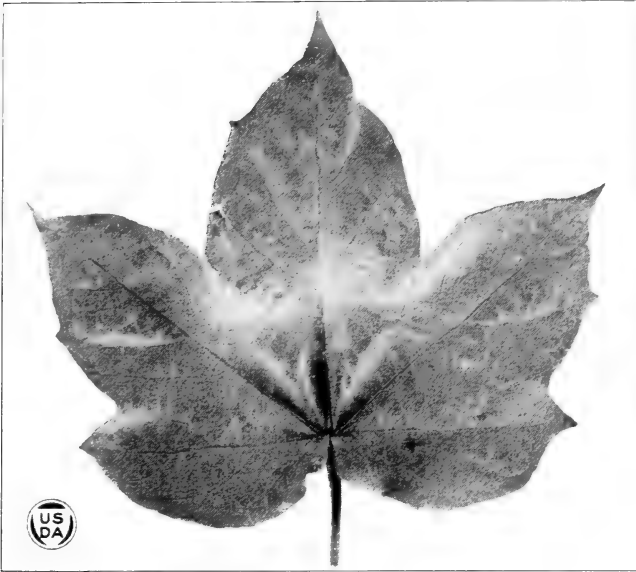


FIG. 1.—LEAF UPLANDLIKE BUT SHOWING COARSE AND IRREGULAR DENTATION, AN EXTRAPARENTAL CHARACTER.

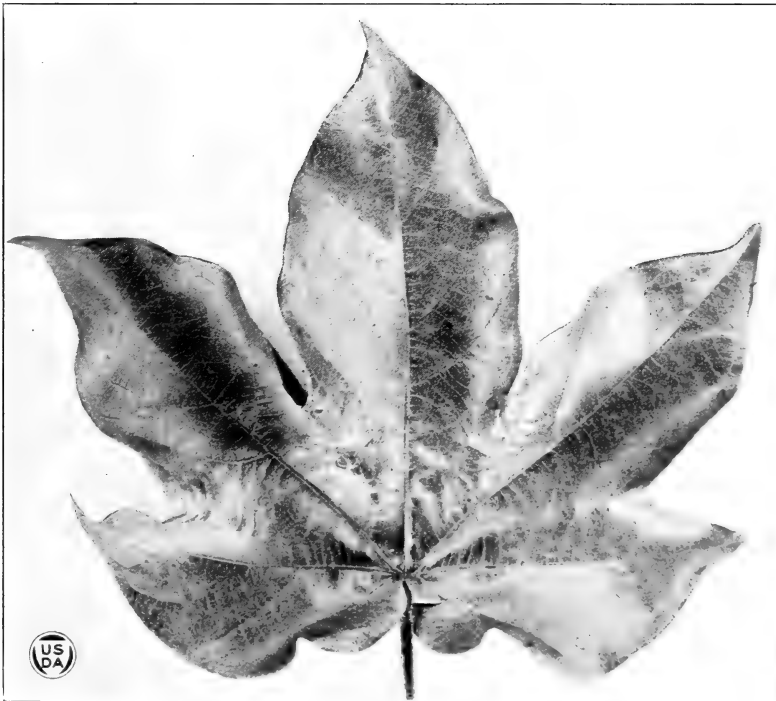


FIG. 2.—A LEAF THAT IS EGYPTIANLIKE IN SHAPE AND TEXTURE.
LEAVES OF HOLDON \times PIMA COTTON, F.

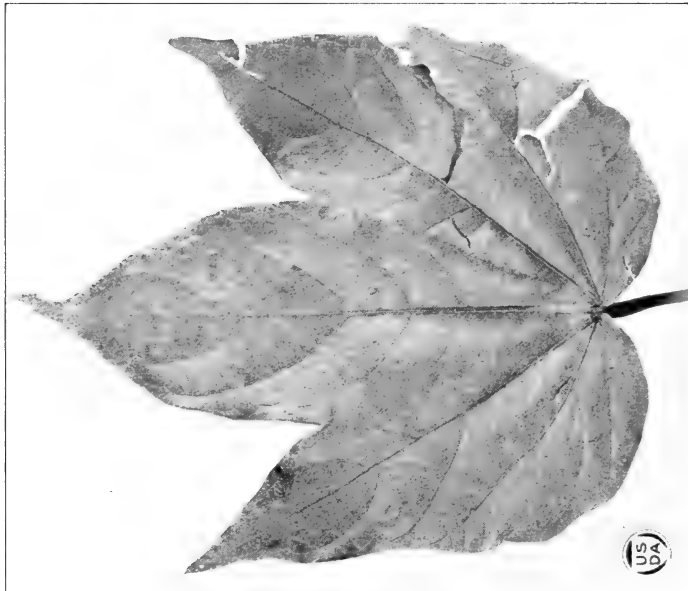


FIG. 1.—A NARROW TYPE OF LEAF.

This has a low leaf index and small vein angle, the lobes being only three and nearly erect.



FIG. 2.—A BROAD TYPE OF LEAF.

This has a high leaf index and large vein angle, and is deeply five lobed, the lobes being very divergent and overlapping at the base.

LEAVES OF HOLDON × PIMA COTTON, F₂.



FIG. 1. A TYPE REMARKABLE FOR THE NARROWING OF THE BASES OF THE LOBES, WAVY MARGINS, AND PROMINENT VEINS. ALL OF THESE BEING EXTRAPARENTAL CHARACTERS.

LEAVES OF HOLDON × PIMA COTTON, F₂.



FIG. 2.—A VERY DEEPLY 5-LOBED LEAF, CHARACTERIZED BY THE THREADLIKE TIPS OF THE LOBES, AN EXTRAPARENTAL CHARACTER.



Fiber character, range of length, Plate X, *C* and *D*.

Seed character, range of fuzziness, Plate XI, *C* and *D*.

MENDELIAN SEGREGATION IN THE HOLDON-PIMA HYBRID.

The only characters which showed a markedly bimodal distribution in F_2 are petal spot (fig. 27), anther color (fig. 29), and midlock

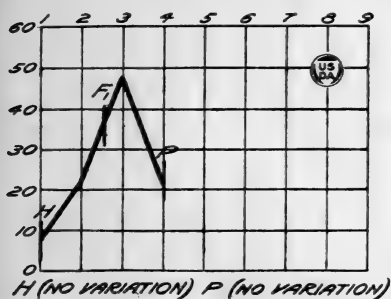


FIG. 23.—Calyx gland abundance: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

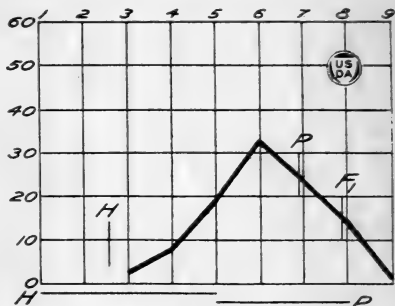


FIG. 24.—Corolla length: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

furrow index (fig. 37). Faint indications of bimodality are also to be noted in the curves for leaf index (fig. 10) and bract connation index (fig. 18), but these are almost certainly not significant. Evidence of Mendelian segregation in petal spot was afforded by data from both F_2 and F_3 . Anther color and midlock furrow index, unfortunately, were not determined on the F_3 populations, but a

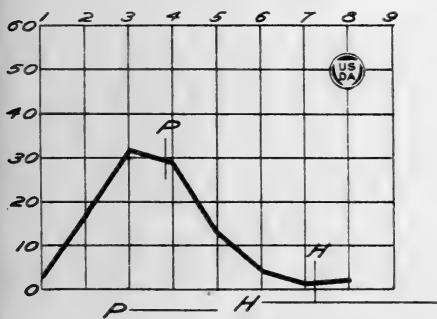


FIG. 25.—Corolla index: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

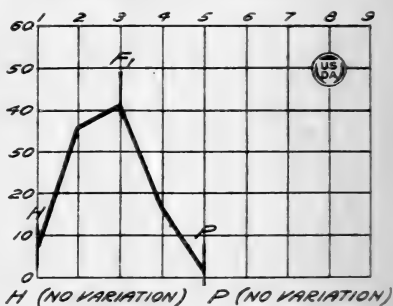


FIG. 26.—Petal color: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

strong presumption of Mendelian segregation is afforded by the frequency distributions in F_2 .

PETAL SPOT.

On the basis of the entire F_2 population (215 individuals) the actual distribution for this character and the distribution to be

expected if total absence of petal spot is a simple, recessive Mendelian character, as given in Table 4, show that the difference between the actual and the expected percentage of plants having no petal spot was only twice its probable error.

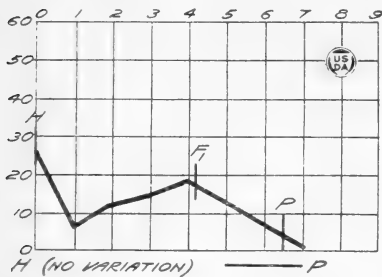


FIG. 27.—Petal spot: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

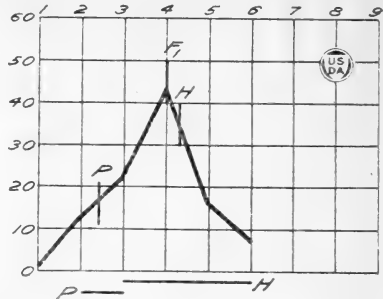


FIG. 28.—Stamen length: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

TABLE 4.—Numbers and percentages of the F_2 population of 215 individuals of Holdon-Pima cotton hybrids, showing the presence, in varying degrees, and the absence of petal spot and the numbers and percentages to be expected on the basis of a monohybrid ratio.

State of petal spot.	Number.		Percentage.	
	Actual.	Expected.	Actual.	Expected.
Petal spot present.....	152	161	70.7	75.0
Petal spot absent.....	63	54	29.3 \pm 2.09	25.0

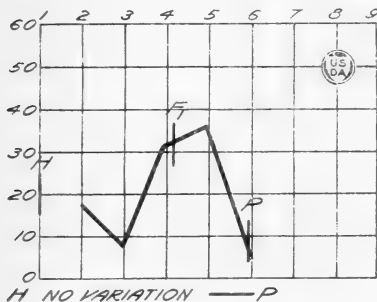


FIG. 29.—Anther color: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

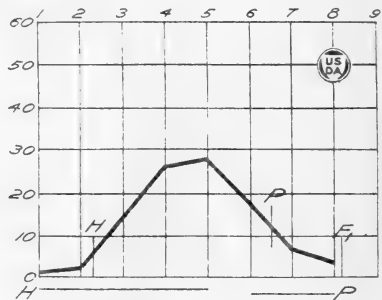


FIG. 30.—Pistil length: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

The mean grade for petal spot of the F_1 progeny of 24 plants grown in 1920 was 4.2, as compared with mean parental grades of 0 in Holdon and 6.5 in Pima and a mean grade of 3.6 for the 152 F_2 individuals in which the spot was present. This character showed considerable variation in F_1 , as is indicated by the frequency distribution in Table 5.

TABLE 5.— F_1 frequency distribution for the character petal spot in Holdon-Pima cotton hybrids.

	Grade numbers.				
	2	3	4	5	6
Number of plants.....	2	6	5	8	3

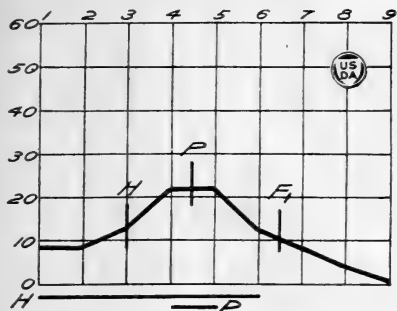


FIG. 31.—Stigma index: Frequency distribution of Holdon x Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

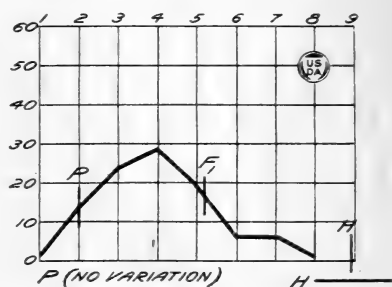


FIG. 32.—Boll lock number: Frequency distribution of Holdon x Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

It would seem that while the presence of the spot is dominant over complete absence, the magnitude of its development when present is conditioned by modifying factors. Further data on the segregation in respect to this character were obtained in F_3 .

Progenies were grown in 1920 from 22 F_2 individuals selected in 1919, of which 4 had been graded as lacking the petal spot while the others showed its presence in varying degree, from grade 1 to grade 7.

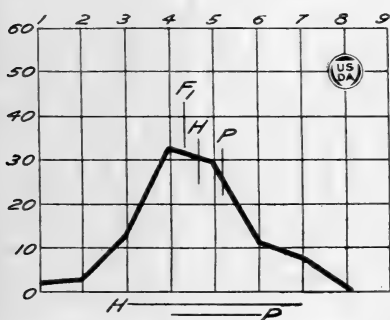


FIG. 33.—Boll length: Frequency distribution of Holdon x Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

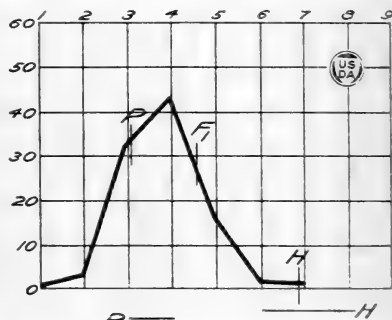


FIG. 34.—Boll diameter: Frequency distribution of Holdon x Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

All points on the F_2 frequency distribution for this character (fig. 27) were represented by one or more of the parents of F_3 progenies. Table 6 gives the frequency distributions for petal spot of the parental and F_2 populations of 1919 and of the F_3 progenies of 1920, the latter being arranged in the order of the grade value for this character of the respective F_2 parent, as shown in column 4.

TABLE 6.—Frequency distributions for petal spot of the F_3 progenies of 1920 and of the parental and F_2 populations of 1919 of the Holdon-Pima cotton hybrids.

[The nature of the seed from which each F_3 progeny was grown, the grade values of the F_2 parents, and the mean grades of the several populations are stated in columns 3, 4, and 5, respectively. In column 3 the symbols S and Op indicate, respectively, seed from selfed or open pollinated flowers.]

Designation of the F_2 parent and the F_3 progeny.	Number of individuals.	Nature of the seed planted.	Grade value of the F_3 parent.	Mean grade of F_2 progeny or other population.	Frequency distributions (grades).															
					0	1	2	3	4	5	6	7	8							
1	2	3	4	5																
No. 82	9	S + Op.	0	0	9															
No. 172	12	S	0	0	12															
No. 161	10	Op.	0	.2	9		1													
No. 123	13	S + Op.	0	.4	12						1									
No. 19	9	S + Op.	1	0	9															
No. 61	22	S	1	3.1	3	3	4	2	2	5	2	1								
No. 102	10	S	2	1.0	7			2	1											
No. 13	32	S	2	1.6	16	4	3	3	1	2	3									
No. 178	16	S	2	2.0	5	4		3	2	1	1									
No. 171	10	S	3	0	10															
No. 156	37	S	3	2.2	19	2	2	2		4	8									
No. 40	31	S	3	2.5	7	3	7	4	3	7										
No. 20	23	S	3	3.5	1	7	1	2	1	6	4	1								
No. 9	11	S	4	1.9	4	2	2			1	1									
No. 140	13	S	4	1.9	7		1	1	2		2									
No. 16	8	S	4	3.1	2	1	1			2	2									
No. 142	21	S + Op.	4	3.4	8	1		1	2		6	1	2							
No. 45	14	S	5	2.8	4	3		1	2	2		1	1							
No. 70	14	S	5	4.0	4		1			3	3	3								
No. 134	16	S	5	4.9	1			1	1	7	5	1								
No. 44	18	S	6	6.3							4	5	8	1						
No. 29	28	S	7	6.6						3	2	6	10	7						
Holdon	13	S		0	13															
Pima	13	S		6.5							2	3	8							
F_2	215	S		2.5	63	15	25	30	38	28	15	1								

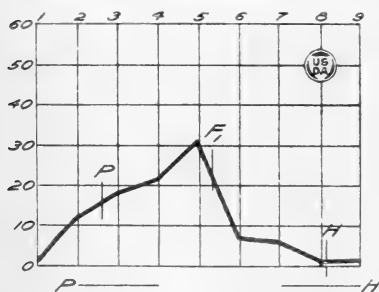


FIG. 35.—Boll index: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

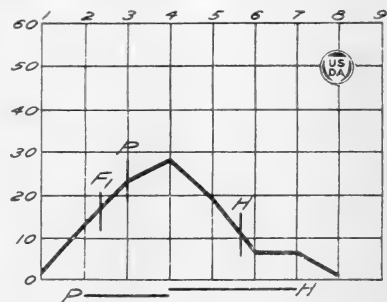


FIG. 36.—Boll apex index: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

It will be seen from Table 6 that the four F_2 parents which had shown complete absence of the spot gave spotless F_3 progenies except that one individual each in progenies 161 and 123 showed presence of

the spot. It should be noted, however, that the whole of progeny 161 and part of progeny 123, including the individual showing presence of the spot, were grown from open-pollinated seed. While all the plants which were graded in these two progenies were judged from their general appearance to have originated from self-fertilized ovules, the possibility exists that the individual in each of these progenies

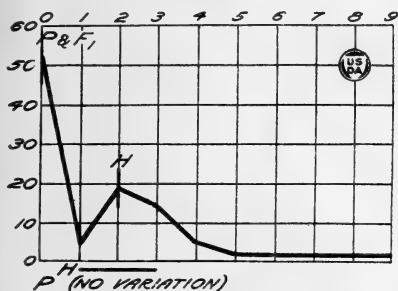


FIG. 37.—Midlock furrow index: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

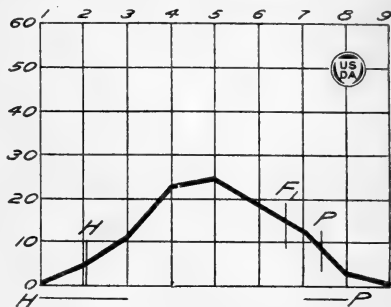


FIG. 38.—Fiber length: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

which showed presence of the spot may have resulted from cross-fertilization.¹⁸

It is interesting that there were two entirely spotless F_3 progenies (Nos. 19 and 171) the F_2 parents of which had been recorded as showing presence of the spot. The mere trace (grade 1) recorded for F_2 plant No. 19 may have been due to mistaking discoloration due to an extraneous cause for presence of the red pigment, but this could

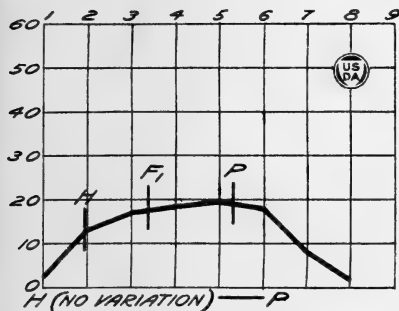


FIG. 39.—Fiber color: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

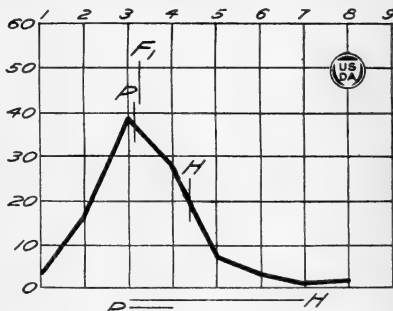


FIG. 40.—Lint index: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

not well have been the case with F_2 plant No. 171, which was graded No. 3.

Only two of the F_3 progenies, Nos. 44 and 29, appeared to be homozygous for presence of the spot. In all the other progenies one

¹⁸This was probably the case with the plant in progeny 123 which was graded No. 5 in respect to petal spot, this individual having been decidedly aberrant in respect to leaf index and vein angle also.

or more of the plants were graded 0. It has been pointed out, however, that this character varies on the individual plant, and it is also more or less influenced by soil variations. It is not unlikely that if a larger number of flowers had been examined on each of the F_3 plants graded 0 the "zero" individuals in some of these progenies would have been found to show a faint development of the spot in some of the flowers.¹⁹

The fact that notwithstanding this uncertainty in regard to the grading of some individuals a close approximation to a 3 to 1 ratio for presence and complete absence of the petal spot was obtained in F_2 makes it likely that such errors as may have occurred in the grading offset each other, the population having been a fairly large one ($n=215$). That the grading was, on the whole, satisfactory is indicated by the high parent-offspring correlation between the grades for petal spot of 22 F_2 individuals and the mean grades of their F_3 progenies, the coefficient of correlation having been 0.86 ± 0.037 .

Taking as one population the F_3 progenies from F_2 individuals which had shown some degree of

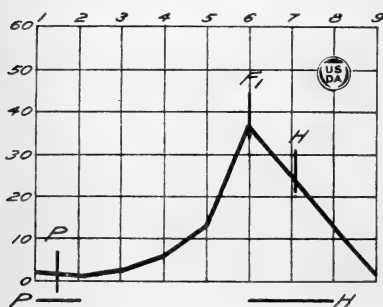


FIG. 41.—Seed fuzziness: Frequency distribution of Holdon \times Pima F_2 cotton plants, by grades, as used in computing the correlations. The ordinate figures indicate the number of plants as a percentage of the total population.

development of the petal spot, but excluding progenies 44 and 29, which were homozygous for presence of the spot, and progenies 19 and 171, which were graded as entirely spotless, the total numbers of spotless and of spotted individuals were, respectively, 88 and 180. This is far from being a 1 to 3 ratio, the deviation from the expected percentage of spotless having been 7.8 ± 1.9 per cent; but in view of the likelihood that the number of spotless individuals would have been found to be smaller if larger numbers of flowers had been examined the supposition that complete absence of the spot, as compared with its presence, is a simple recessive character can not be regarded as disproved.

That the degree of development of the petal spot, when present, is conditioned by modifying factors seems to be satisfactorily established by the evidence from both F_2 and F_3 .

ANTHER COLOR.

The frequency distribution for anther color in F_2 (fig. 29) is interesting because of the failure to recover the very pale anther color, or rather pollen color, of the Holdon parent. The golden yellow color of the Pima parent was partly dominant, as is shown by the position on the F_2 frequency curve of the F_1 mean and by the fact that the mode in F_2 was only one grade lower than the Pima mean. It is possible but not probable that the apparent bimodality of this

¹⁹ Balls (2, p. 367) met with the same difficulty in classifying plants in regard to this character and attributes an excess of "spotless" in F_2 to the fact that "it was common to record a plant once or twice as spotless and then find a flower appearing which bore a faint spot on one or more petals."

curve may have been a result of insufficiently accurate grading, the difference between any two successive grades having been slight. Assuming that two modes actually occurred, a very close approximation to a 3 to 1 ratio is obtained by grouping together as "yellow" those individuals whose pollen equaled or surpassed in intensity of color that of the first generation (grades 4 to 6) and grouping as "pale" the individuals which had lighter colored pollen than F_1 (grades 2 and 3). The numbers in the two classes are 156 and 59, while the expectation would have been approximately 161 and 54.

On the assumption that both absence of the petal spot and pale color of the anthers are simple Mendelian recessives, 1 individual in 16 should have presented this combination. The actual number was 15 in an F_2 population of 215, or 1 in 14.3. The departure from the expected ratio was not significant.

MIDLOCK FURROW INDEX.

Indication of segregation in a definite ratio is afforded also by the character midlock furrow (fig. 37), which was present in the Holdon parental population and absent in the Pima parental population and in F_1 . Examination of the boll photographs showed that the presence or absence of the midlock furrow could be determined definitely in 181 F_2 individuals, of which 94 showed no trace of the furrow, while in the remaining 87 plants it was present in varying degrees. On the basis of a 9 to 7 dihybrid ratio, assuming absence of the furrow to result from the combination of two dominant factors, the proportion of individuals without furrow should have been 56 per cent. The actual percentage having been 52 ± 2.5 , the departure from the expected ratio was not significant.

DATA OF THE HOLDON-PIMA HYBRID COMPARED WITH EVIDENCE FROM OTHER SOURCES OF MENDELIAN SEGREGATION IN COTTON HYBRIDS.

Cotton hybrids have been studied from a Mendelian point of view by Balls, Fletcher, Fyson, Harland, Leake, Leake and Prasad, McLendon, and Shoemaker. It is in order to consider the evidence of definite segregation obtained by these investigators, especially in regard to characters determined on the upland-Egyptian hybrid which is the subject of this bulletin.

LEAF SHAPE.

Two expressions of leaf shape were the subject of investigation in the Holdon-Pima hybrid. These were leaf index (width as a percentage of the length) and leaf-lobe index (distance to the upper sinus as a percentage of the length), this being an expression of the depth of lobation. The mean leaf index of F_1 was higher than that of either parental population, the leaves having been relatively as well as absolutely wider than in Pima. The mean leaf lobe index of F_1 was almost exactly the same as that of Pima, the more deeply lobed parent. In F_2 the curves representing the frequency distributions for both indices resemble normal frequency curves (figs. 10 and 11), indicating that several factors are involved in each of these characters. Similar, but not identical, leaf characters studied by others have shown evidence of more definite segregation.

Leake (30, pp. 14, 15) devised an expression of leaf shape which he termed the "leaf factor" and which integrates the breadth of the lobes and the depth of the lobation.²⁰ His data indicate that in crosses of *Gossypium indicum*, which has a

²⁰ The leaf factor is the length of the midvein minus the distance to the upper sinus divided by the maximum width of the terminal lobe.

deeply and narrowly lobed leaf, with *G. arboreum* or *G. neglectum*, species which have broader and shallower lobes, the F_1 is exactly intermediate. In a later paper (31, pp. 225-230, Table 14) similar results in F_1 and a close approximation to a 1:2:1 ratio in F_2 are reported. There was a high parent-offspring correlation between F_2 and F_3 . Furthermore, F_2 individuals which had a leaf factor closely approaching that of one or the other parent gave strong evidence of homozygosity in their F_3 progenies while progenies of intermediate F_2 plants showed segregation similar to that of the F_2 population.

Fyson (26, pp. 11-15) crossed two distinct species grown in India, one having broadly and shallowly lobed leaves, the other deeply and narrowly lobed leaves, and obtained only the latter type in F_1 . The distribution in F_2 was not recorded, but of 13 F_3 progenies 5 showed only the deeply and narrowly lobed type, 4 progenies showed practically only the broadly and shallowly lobed type (84 in a total of 85 individuals), and 4 progenies, when combined as one array, gave a 3 to 1 ratio with the deeply and narrowly lobed type predominating. Similar behavior continued in the fourth and fifth generations, some of the dominant type breeding true and others segregating in approximately a monohybrid ratio, while the recessive type (broadly and shallowly lobed) bred true with a few exceptions, which the author attributes to accidental cross-pollination.

Shoemaker (36), crossing two upland cottons, one being an "okra leaf" (deeply and narrowly lobed) type segregated from the King variety and the other being the Edson variety with relatively shallow and broad lobes, obtained an intermediate F_1 and close approximations to a 1:2:1 ratio in F_2 and in the F_3 progenies of intermediate F_2 individuals. His results, although based upon grading rather than measurement, accord therefore with those of Leake.

McLendon (34, pp. 169-185), crossing narrowly lobed types ("okra leaf," sea island) with broad-lobed varieties of upland cotton and making his classifications by inspection rather than by measurement, obtained results similar to those of Leake and Shoemaker.

Balls (6, p. 158) used the same expression for depth of lobation as the writer's leaf lobe index and obtained results with an upland-Egyptian hybrid similar to those here described for the Holdon-Pima cross, the Egyptian (deeply lobed type) being dominant in F_1 and no segregation in a definite ratio being discernible in F_2 .

LEAF BLADE COLOR.

The character leaf blade color, as was explained on a preceding page, could not be graded satisfactorily in the Holdon-Pima hybrid, the difference between the parent varieties being only that between a lighter and a darker shade of green. Other investigators have studied hybrids of which one of the parents had red color in the foliage, and their results may be considered briefly.

Leake (31, pp. 214-215, Table 6, p. 246) found in various crosses involving a red-leaved and a green-leaved type that the red color was dominant but with diminished intensity in F_1 and that very close approximations to a monohybrid ratio for presence of the red color as contrasted with its absence were obtained in most of the F_2 progenies. There was, however, wide variation in the intensity of the red color in different F_2 individuals in which red was present. The behavior, therefore, was similar to that of the character petal spot in the Holdon-Pima hybrid.

McLendon (34, pp. 169-178), in crosses of the Willetts Red Leaf variety of upland cotton with upland varieties having green leaves, concluded that F_1 was intermediate and that the segregation in F_2 indicated a 1:2:1 ratio. F_3 progenies from red-leaved and from green-leaved F_2 individuals appeared to be homozygous, while in progenies of intermediate F_2 individuals the three types segregated, but usually not in very close approximation to the 1:2:1 ratio. In crossing a broad-lobed, red-leaved type (Willetts) with a narrow-lobed, green-leaved type ("okra leaf") he obtained an intermediate expression of both characters in F_1 and recovered in F_2 the nine types, in approximately the proportions to be expected when both characters give a monohybrid ratio and the heterozygotes can be distinguished.

LEAF CALLUS COLOR.

In the Holdon-Pima hybrid the F_1 and F_2 means were approximately intermediate although nearer that of the Holdon parent, and there was no indication of a plurimodal frequency distribution in the second generation. (Fig. 14.)

Balls (4, p. 24), studying this character in upland-Egyptian crosses, found an intermediate condition in F_1 . Classifying an F_2 population as "spotted," "intermediate," and "no spot" he obtained a close approximation to a 1:2:1 ratio. Three F_3 progenies of intermediate F_2 plants also gave close approximations to this ratio. In a later publication (6, p. 133) Balls states that "extracted full spot and spotless breed true, without known exceptions."

PETIOLE HAIRINESS.

In the Holdon-Pima hybrid the F_1 mean for petiole hairiness indicated a slight tendency to dominance of the practically glabrous condition of the Pima parent. The F_2 frequency curve (fig. 15) was extremely skew, approximately two-thirds of the population having been as glabrous or nearly as glabrous as Pima, while a few individuals were much hairier than the Holdon parent.

Balls (4, p. 25), working with an upland-Egyptian cross, reported that the glabrous condition of the Egyptian parent was dominant in F_1 . An F_2 progeny contained 111 glabrous and 37 hirsute individuals—an exact 3 to 1 ratio—and in another F_2 progeny the numbers were 58 glabrous and 17 hirsute. Of four F_3 progenies of F_2 individuals which had been classed as glabrous, two contained only glabrous individuals, while the other two each contained a few hirsute individuals. In a later publication (6, pp. 140, 141) Balls states that complete dominance of the glabrous condition does not occur in F_1 and that the segregation in F_2 and later generations is such as to indicate that several factors are concerned. Certain F_5 families are stated to have "bred true to new types of hirsuteness."

McLendon (34, p. 185), dealing with upland-sea-island hybrids, reports the hairiness of the upland parent to be incompletely dominant in F_1 and that the F_2 frequency distributions extended "from one extreme to the other."

PETAL COLOR.

Petal color, in the Holdon-Pima hybrid, gave an intermediate and uniform F_1 and a unimodal frequency curve in F_2 , extending from one to the other parental extreme. (Fig. 26.) The F_2 mode was intermediate, but the number of individuals which had the petals lighter colored than the intermediate shade greatly exceeded the number having deeper yellow petals.

Fletcher (18), crossing a red-flowered with a yellow-flowered Indian cotton, obtained in F_1 approximately equal numbers of reds and yellows. Second-generation progenies of red F_1 's comprised 428 red-flowered and 114 yellow-flowered individuals (ratio 3.75 to 1) while F_2 populations grown from yellow F_1 's comprised 474 yellow-flowered and only 12 red-flowered individuals. Balls (2, p. 367) is doubtless correct in his interpretation of this result that the red-flowered parent was heterozygous, containing a factor for yellow, and that the presence of a few red-flowered individuals in the F_2 populations from yellow-flowered F_1 's was due to accidental cross-pollination. Fletcher states that in crossing yellow-flowered with white-flowered varieties he found yellow to be completely dominant.

Fyson (20), crossing a yellow-flowered with a white-flowered Indian cotton, also reported complete dominance of the yellow color in F_1 . The segregation in F_2 was not fully worked out, but taking all progenies as one array, 729 individuals were classed as yellow, 156 as "pale," and 411 as white, a distribution which arouses the suspicion that either the classing was faulty or much accidental cross-pollination had occurred. F_3 progenies of yellow-flowered F_2 individuals were uniformly yellow in some cases, while in other cases segregation in a ratio of approximately three yellow to one white was recorded. Progenies of white-flowered F_2 individuals were white flowered, with a few exceptions attributed by the author to accidental cross-pollination.

Balls (4, pp. 36, 37) found that in a hybrid of upland with Egyptian cotton petal color was intermediate, or "lemon," in F_1 , while two second-generation progenies were classified as 16, 36, 17 and 21, 51, 23 yellow, intermediate, and white, respectively, these figures indicating a 1 : 2 : 1 ratio. F_3 progenies of some of the F_2 individuals were grown, but the populations were far too small to give trustworthy data. In a later publication by the same author (6, pp. 134-138) it is suggested that in the petal color of upland-Egyptian hybrids "not less than three pairs of allelomorphs may be involved." It is stated also that F_1 is always intermediate and that white-flowered F_2 individuals always breed true while yellow-flowered F_2 individuals breed true in some cases but segregate in others. Balls points out that in the second generation there is always an excess of the paler shades, as was found by the writer to be the case in the Holdon-Pima hybrid.

Leake (31, pp. 212, 213, and Table 1, p. 244) reported that in a hybrid between a yellow-flowered and a white-flowered Indian cotton F_1 was "all yellow flowered." In an F_2 population of 161 individuals the ratio of yellow flowered to white flowered was 2.1 to 1. Progenies of white-flowered F_2 individuals bred true, while the progenies of yellow-flowered F_2 gave the following data: 5 F_3 progenies (as one array) 65 yellow, 0 white; 6 F_3 progenies (as one array) 34 yellow, 11 white. The author suggests that the excess of white-flowered individuals in F_2 , which gave a 2 to 1 rather than a 3 to 1 ratio, may be correlated with the fact that in India white-flowered races are always the hardier.

Two crosses made by Leake between Indian cottons having, respectively, deep-yellow and pale-yellow petals are reported (31, p. 213) to have shown full dominance of the deep yellow in F_1 . The numbers of deep yellow and of pale yellow in F_2 indicate ratios of 2.4 to 1 and 1.4 to 1, respectively. The author remarks that these cases of petal color were the only ones "in which complete dominance has been observed in the cottons under consideration."²¹

Leake reports (31, pp. 241, 242) a correlation, to which he says no exception has been found, between size and color of petal, white petals being always much smaller than yellow petals. It is interesting to note in this connection that in the second generation of the Holdon-Pima hybrid the coefficient of correlation for corolla length and petal color was 0.214 ± 0.048 , indicating that there is a tendency for long petals to be associated with pronounced yellow color and vice versa. Individual cases occurred, however, in which large corollas were very light colored and small corollas were deep yellow, and these combinations persisted in F_3 .

That red color in the vegetative organs and in the petals may be dependent upon the same factor is indicated by data recorded by Leake for Indian cottons. When a red-leaved, red-flowered type was crossed with a green-leaved, yellow-flowered type (31, pp. 216, 217) there was partial dominance of red in both organs in F_1 and a 3 to 1 ratio in F_2 for presence contrasted with absence of red. Crossing a red-leaved, red-flowered type with a green-leaved, white-flowered type (31, pp. 217, 218, Table 7, p. 247, pl. 35),²² he found that in F_1 there was partial dominance of the red in both organs, but the petals of the first-generation flowers were red and yellow, rather than red and white.

In F_2 six types were obtained, in the following proportions:

	Number.
Petals red, leaf all red	89
Petals red and yellow, leaf veins red	193
Petals red and white, leaf all red	30
Petals red and white, leaf veins red	78
Petals yellow, leaf green	96
Petals white, leaf green	25

The ratio is therefore approximately 3:6:1:2:3:1. The data from F_3 progenies of individuals representing all six types in F_2 conformed remarkably well to the expectation. Leake interprets these results as attributable to the presence in the red-leaved parent of a factor for red color in the leaf and the petal which is dominant in respect to its absence and of a factor for yellow color in the petals which is also dominant to its absence, the green-leaved, white flowered parent having carried the recessive factors for both colors. The results indicate, although it is not expressly so stated, that both dominant factors (R and Y) must be present, the former in double dose, in order to produce a solidly red-colored petal.²³

McLendon (34, pp. 191-198) reported that in hybrids of sea-island cotton with upland varieties, F_1 was intermediate in petal color. The data as presented indicate that in F_2 the full yellow color of the sea-island parent was not recovered and that a much greater number of individuals had intermediate colored (pale yellow) petals than white petals.

Harland (22) describes crosses among types of cotton grown in the West Indies representing six different grades of petal color, from white (pale cream) to a pronounced yellow. "A cross between any two of the above shades gave an intermediate F_1 . In all F_2 families the parental and F_1 color types appeared, but there may have been other intermediate color forms" (p. 15). In a cross of white with yellow of grade 3, the F_2 ratio appeared to be 4.4 yellow to 1 white. In progenies of eight yellow-flowered F_2 individuals only yellow flowers appeared in F_3 . Progenies of 27 other yellow-flowered F_2 's contained both yellow and white flowered individuals, the totals for all heterozygous progenies as one array having been 477 yellow and 180 white. The departure from a 3 to 1 ratio is not significant. Progenies also were grown of 11 white-flowered F_2 individuals, of which 6 bred true, while 5 progenies, taken as one array, comprised 150 white-flowered and 11 yellow-flowered plants, the occurrence of the latter, in Harland's opinion, being attributable to accidental cross-pollination.

²¹ In a later publication (32, p. 126) it is stated that "yellow is dominant both to pale yellow and to white." This was not the case in the upland-Egyptian cotton hybrids studied by Balls and by the writer.

²² This cross is further discussed and illustrated by Leake and Prasad (32, pp. 128-132, pls. 14-18).

²³ Reference to Leake's table 7 shows that the departure from a 9:3:3:1 ratio is not very great if the classes are arranged as follows: Containing both R and Y, 282 individuals; containing R but not Y, 108 individuals; containing Y but not R, 96 individuals; containing neither R nor Y, 25 individuals. Compare also Leake and Prasad, 32, p. 131.

PETAL SPOT.

The behavior of petal spot in the Holdon-Pima hybrid (fig. 27) indicated dominance of the presence of the spot but in a reduced condition in F_1 and a 3 to 1 ratio for its presence as contrasted with its complete absence in F_2 , the degree of development when present being apparently conditioned by modifying factors.

Balls (4, pp. 37, 38) reported that in an upland-Egyptian hybrid of which the Egyptian parent had a fully developed spot and the upland parent none, the distributions in two F_2 populations of full, intermediate, and no spot, respectively, were: 23-42-31 and 11-22-18. These figures indicate a 2 to 1 rather than a 3 to 1 ratio if presence of the spot in any degree be contrasted with its complete absence. Small F_2 progenies of four F_2 individuals gave the distributions shown in Table 7.

TABLE 7.—Distribution of petal spot in the progenies of four F_2 individual upland-Egyptian cotton hybrids.

F_2 parent.	Full spot.	Inter- mediate spot.	No spot
Full spot.....	6	0	0
Intermediate spot.....	2	12	1
Do.....	1	2	1
No spot.....	0	0	7

In a later publication (6, pp. 138, 139) it is stated that "spotless" breeds true, while "full" may either breed true or break, and intermediates break in at least two different ways. Probably there are again two allelomorphic pairs concerned."

McLendon (34, pp. 185-190), crossing sea-island cotton, which has spotted petals much like those of Egyptian cotton, with spotless varieties of upland cotton, found that in F_1 the spot was intermediate in size and intensity. In most of the F_2 progenies the ratio of individuals having the petals spotted in any degree to those having spotless petals was less than 3 to 1, but in a few progenies this ratio was closely approximated or was even exceeded.

Leake and Prasad (32, pp. 127, 128) reported results from crossing a Chinese cotton having no petal spot with an Indian cotton possessing a well-developed spot which indicate complete dominance of the spot in F_1 .

ANTHER COLOR.

Anther color in the Holdon-Pima hybrid showed partial dominance in F_1 of the yellow color of the Pima parent, and the mode in F_2 was even higher than the F_1 mean. There was some indication of a bimodal distribution in the second generation (fig. 29), the pale color appearing to be a simple recessive.

Balls (4, p. 38) described the first generation of an upland-Egyptian hybrid as having anthers of a "pale yellow" color as contrasted with "rich yellow" in Egyptian and "buff" in upland. In F_2 and F_3 his classification was admittedly unsatisfactory, but the same type of segregation as he obtained for petal color was indicated. In another publication (6, pp. 140, 141) he states that a 1:2:1 ratio was obtained in F_2 and concluded that only one pair of allelomorphs was involved in this case.

McLendon (34, pp. 191-198) in his sea-island-upland hybrids obtained results for anther color similar to those which he obtained in regard to petal color, and in fact his data as presented would indicate that the same factor determines the color of the petals and the anthers. On the other hand, complete independence of the factors for yellow color in the two organs was indicated in the Holdon-Pima hybrid, the F_2 coefficient of correlation of petal color and anther color having been 0.087 ± 0.050 .

BOLL LOCK NUMBER.

The average per plant of the number of locks of the boll was exactly intermediate in F_1 of the Holdon-Pima hybrid, and the F_2 distribution (fig. 32) was unimodal and fairly symmetrical, the evidence indicating that several factors are involved in this character.

Balls (6, pp. 163-166) presents evidence concerning this character in hybrids between upland and Egyptian and between different varieties of Egyptian cotton which points strongly to the same multiple factor interpretation.

BOLL SHAPE.

Shape of the boll, as expressed by the boll index (diameter relative to length), gave a frequency distribution in F_2 of the Holdon-Pima hybrid (fig. 35) which indicated that this character involves several factors.

Balls (6, pp. 162, 163) records similar behavior of the boll index character in upland-Egyptian hybrids studied by him.

McLendon (34, pp. 200-205), working with sea-island-upland hybrids, concluded that the short thick type of boll is recessive, although he did not find the long, slender type to be fully dominant. But his evidence of a monohybrid ratio of 3 intermediate to 1 short and thick is not convincing, especially when it is considered that his classification was made by inspection rather than by measurement.

BOLL SURFACE

Satisfactory grading with respect to boll surface, if it can be regarded as a single character, was not found to be practicable in the Holdon-Pima hybrid, although the parent varieties differed conspicuously.

Balls (4, pp. 59, 60), while recognizing the probable complexity of the character, dealt with it in studying an upland-Egyptian hybrid, reporting an intermediate F_1 and an approximately 1:2:1 segregation in F_2 into upland type (smooth), F_1 type (intermediate), and Egyptian type (pitted). He states also that F_3 progenies of two smooth and of one pitted F_2 plant bred true. In a later publication (6, p. 142), however, he states that this apparently simple type of inheritance did not hold good upon further study of the F_3 data.

McLendon (34, pp. 205-210) found that in sea-island-upland hybrids F_1 was intermediate, while the data for numerous F_2 populations show ratios varying from 1:1 to 29:0 for pittedness as contrasted with smoothness.

FIBER LENGTH.

The first generation of the Holdon-Pima hybrid had a mean fiber length which approached the mean of the longer fibered (Pima) parent while F_2 gave a unimodal and nearly symmetrical frequency curve, indicating that several factors are involved (fig. 38).

Balls (4, pp. 6, 7, 77-80) obtained data from an upland-Egyptian hybrid from which he deduced a 3 to 1 ratio for length of fiber, long being dominant. He reports cases of intensification in crosses of Mit Afifi Egyptian with a short-staple cotton, F_1 having considerably longer fiber than the Egyptian parent.

McLendon (34, pp. 211-217), studying length of fiber in hybrids of sea-island with upland varieties, obtained an intermediate and rather variable F_1 . Several of his F_2 frequency curves are strongly bimodal, with long fiber in excess, while other F_2 populations gave plurimodal curves.

FIBER COLOR.

In the Holdon-Pima hybrid the F_1 was approximately intermediate in color of fiber, and the frequency curve of F_2 was unimodal and fairly symmetrical, although flatter than the curves for most of the characters (fig. 39).

Balls (4, pp. 4, 80, 81), crossing a brown-fibered with a white-fibered cotton, reports a distribution in F_2 of 30 brown, 66 cream, and 32 white. In a hybrid of Mit Afifi Egyptian, which has much browner fiber than the Pima variety, with a white-fibered upland cotton, F_1 was intermediate (cream colored), and an F_2 segregation into 12 brown, 21 cream, and 11 white was recorded. It is evident, however, that the segregation was not so sharp as this classification would indicate, for in discussing the results in F_3 one of the F_2 parents is described as "creamish" and another as "whitish." An F_3 progeny of 30 individuals from a brown-fibered F_2 plant showed only brown fiber, but with more variation in the intensity of the shade than occurred in the Mit Afifi parent of the hybrid. In a later publication (6, p. 146) it is implied that the inheritance of this character is more complex than was supposed at first to be the case.

SEED FUZZINESS.

The entire fuzziness of the upland parent was almost completely dominant over the partial fuzziness of the Egyptian parent in the first generation of the Holdon-Pima hybrid. The frequency curve of the second generation (fig. 41) was unimodal, and the mode coincided with the F_1 mean. Several factors appear to be involved.

Fletcher (18) records dominance of the fuzz in a cross of a fuzzy-seeded with a naked-seeded cotton. On the other hand, Fyson (20), crossing a smooth-seeded tree

cotton, stated to have been *Gossypium peruvianum*, with a fuzzy-seeded American upland variety, reported (p. 5) dominance of the smooth-seeded condition, and stated (p. 19) that the same relation obtained in crossing two nearly related Indian cottons which had, respectively, smooth and fuzzy seeds. In subsequent generations of the latter hybrid some of the naked-seeded parents bred true, others segregated irregularly, while most of the fuzzy-seeded parents gave only fuzzy seeds in their progenies. Fyson (20, p. 26) notes, however, that there was variation in the degree of fuzziness, and it is doubtful that the inheritance was of a simple type.

Balls (3, p. 21), in a hybrid between an entirely fuzzy-seeded upland cotton and an Egyptian variety which had only a little fuzz on the seeds, found that F_1 was entirely fuzzy like the upland parent and that the F_2 population comprised 147 plants that were entirely fuzzy seeded and 8 plants resembling the Egyptian parent. Apparently both the uplandlike and the Egyptianlike F_2 plants bred true or very nearly so in F_3 . Similar data are presented in a later publication (4, pp. 71-74) and are interpreted as pointing to a dihybrid ratio (15 to 1), although the evidence is not conclusive. In crosses between two Egyptian varieties differing in the amount of fuzz on the seed, Balls (6, p. 143) reported that "in all cases they have given a simple 3 to 1 ratio, more fuzz being dominant over less fuzz and expectation has been fulfilled in F_3 ,"²⁴

McLendon (34, pp. 220-225) reported that in his hybrids of the smooth-seeded sea-island cotton with fuzzy-seeded upland varieties, fuzziness was dominant. His F_2 populations, classified simply as fuzzy and smooth, show great diversity in the proportions of the two classes and afford little evidence of definite segregation.

EVIDENCE FROM F_3 OF SEGREGATION IN THE HOLDON-PIMA HYBRID IN CHARACTERS NOT GIVING DEFINITE MENDELIAN RATIOS IN F_2 .

It has been shown that the second generation of the Holdon-Pima hybrid afforded no satisfactory proof of segregation in definite ratios except possibly in the characters petal spot, anther color, and mid-lock furrow index. It remains to consider whether the third generation yielded evidence that segregation of a less definite type had taken place in F_2 in regard to other characters. Eighteen of the characters which were determined on the parental and F_2 progenies in 1919 were also determined on 22 F_3 progenies grown in 1920. One of these characters, petal spot, gave evidence of definite Mendelian segregation and has been considered in that connection. The other 17 characters gave unimodal frequency distributions in F_2 . The size of the F_3 progenies varied from 8 to 46 individuals, but it was not possible to determine all of the characters on every plant of each progeny. No character was determined in any progeny on less than seven individuals.

Evidence of segregation in F_2 was sought by comparing for each character (1) the means of the several F_3 progenies as to the significance of their differences, (2) the means of the F_3 progenies with the values given by their respective F_2 parents, and (3) the coefficients of variation of the F_3 progenies with those of the parental and F_2 populations.

COMPARISON OF THE F_3 PROGENY MEANS.

Table 8 shows for all characters determined in F_3 ²⁵ the means of the F_3 progenies which gave, respectively, the highest and the lowest mean, and the means of the populations representing the parent varieties which were grown in the preceding year.

²⁴ This simple type of Mendelian inheritance was not encountered by the writer in crosses between two varieties of the Egyptian type of cotton (Pima and Gila) which differed rather markedly in the degree of fuzziness of the seed coat. Six grades, including the parental extremes, were distinguished in F_2 , and the frequency curve for that generation was unimodal and very nearly symmetrical. The indication, therefore, was that more than two factors were concerned.

²⁵ Including, for the sake of completeness, the character petal spot, which is not further considered in this connection.

The highest and the lowest F_3 progeny mean differed very significantly for every character, the difference having amounted to 12 to 50 times its probable error. These data point strongly to the conclusion that segregation had taken place in F_2 .

For 11 of the 18 characters the highest F_3 mean was either higher than or did not differ significantly from that of the parental population which gave the higher mean, while for the other 7 characters the highest F_3 mean was significantly lower than the higher parental mean. For 14 of the 18 characters the lowest F_3 mean was either lower than or did not differ significantly from that of the parental population which gave the lower mean, while for the other 4 characters the lowest F_3 mean was significantly higher than the lower parental mean.

TABLE 8.—Means for 18 characters of the F_3 hybrid progenies having, respectively, the highest and the lowest mean and means of the parental populations of Pima and Holdon cotton.

Character.	Hybrid F_3 (1920).			Parental (1919).	
	Highest mean.	Lowest mean.	Difference divided by its probable error.	Pima	Holdon.
Axis:					
Length.....	201.5±2.90	68.2±4.62	24.4	184.0±4.16	92.0±2.20
Internode number.....	45.9±.48	26.5±.87	19.7	39.0±.30	26.2±.71
Internode length.....	45.0±.66	25.3±1.09	15.5	47.1±.70	35.6±.85
Fruiting branch:					
Length.....	50.9±1.38	121.8±1.91	12.3	72.2±1.56	21.3±1.06
Length, first internode.....	19.5±.65	16.3±.68	14.0	19.0±.60	2.1±.14
Leaf:					
Length.....	163.9±4.54	92.9±2.31	13.9	182.0±1.91	127.0±1.69
Width.....	204.1±6.58	116.5±1.66	12.9	236.0±4.90	143.0±4.10
Index.....	139.5±1.36	107.4±1.97	13.4	130.0±2.36	113.0±2.80
Lobe index.....	56.0±.96	30.5±.97	18.7	36.1±.61	45.9±.75
Vein angle.....	107.0±1.27	72.6±2.11	14.0	103.4±2.14	94.5±1.10
Callus color.....	7.9±.08	2.2±.08	50.4	2.1±.02	6.7±.06
Petiole hairiness.....	6.6±.11	1.1±.03	48.3	1.0±0	5.2±.08
Petal:					
Color.....	3.8±.06	1.2±.04	36.1	5.0±0	1.0±0
Spot.....	6.6±.19	0 ± 0	34.7	6.5±.19	0 ± 0
Boll:					
Length.....	40.4±.80	21.7±.89	15.6	47.5±.41	45.1±.42
Diameter.....	28.4±.28	16.3±.49	21.4	27.6±.13	38.2±.23
Index.....	85.6±1.07	65.7±1.21	12.3	58.2±.49	84.7±.70
Lock number.....	3.9±.03	3.1±.01	25.3	3.0±.01	4.4±.01

¹ Progeny No. 140, on which these characters were not measured, was of the extreme cluster type and would doubtless have given lower values.

PARENT-OFFSPRING CORRELATIONS OF F_2 AND F_3 .

The coefficients of correlation between the means of the F_3 progenies and the values of the F_2 parents of these progenies, computed for all characters determined in F_3 , are given in Table 9. The average of the coefficients of correlation for the 17 characters which did not show segregation in definite ratios in F_2 is 0.66. That for leaf width is only 2.8 times its probable error, but for all other characters the coefficient is not less than 4 times its probable error. This criterion, therefore, yields additional evidence that segregation had taken place in F_2 .

TABLE 9.—Coefficients of correlation between the F_3 progeny means and the values of the corresponding F_2 parents of the Holdon-Pima cotton hybrids.

Character.	Coefficient of correlation.	Character.	Coefficient of correlation.
Axis:		Leaf:	
Length	0.79±0.054	Vein angle	0.84±0.042
Internode number55±.100	Callus color77±.058
Internode length74±.065	Petiole hairiness78±.056
Fruiting branch:		Petal:	
Length57±.099	Color65±.083
First internode61±.090	Spot86±.037
Leaf:		Boll:	
Length46±.113	Length75±.064
Width35±.126	Diameter50±.108
Index63±.087	Index63±.087
Lobe index87±.035	Lock number81±.049

COMPARATIVE VARIABILITY OF THE F_3 PROGENIES AND OF THE F_2 AND PARENTAL POPULATIONS.

Table 10 gives, for each character determined in F_3 in respect to which definite Mendelian segregation was not shown in F_2 , the coefficient of variation (of measured characters) or standard deviation (of graded characters) of the most variable and of the least variable F_3 progeny grown in 1920 and the corresponding constants for the parental and F_2 populations grown in 1919. In the last three columns of the table are shown the significance of the differences, as expressed by the value obtained by dividing the difference by its probable error, between the most variable and least variable F_3 progenies, between the most variable F_3 progeny and the F_2 population, and between the least variable F_3 progeny and the parental population which was the less variable as regards the character in question.

The data given in Table 10 permit the following conclusions, the expressions "most variable" and "least variable" referring always to the individual character and not to the general variability of the population:

The coefficients of variation or standard deviations of the most variable and of the least variable of the F_3 progenies differed significantly for all characters, the value obtained by dividing the difference by its probable error ranging from 3.4 to 9.6.

The coefficient of variation or standard deviation of the most variable of the F_3 progenies was higher than that of the F_2 population in respect to all characters, although for only 3 characters were the differences apparently significant.

The coefficient of variation or standard deviation of the least variable of the F_3 progenies differed significantly from that of the less variable parent in respect to only 3 of the 18 characters, the least variable F_3 progeny showing significantly less variability for 1 character and significantly greater variability for 2 characters. In respect to the 2 latter characters, the least variable F_3 progeny was not significantly more variable than the more variable parent.

The assumption seems justifiable that if segregation has taken place in F_2 the progenies of second-generation individuals at either extreme of the F_2 distribution should be less variable than progenies of individuals representing the F_2 mean. As expressed by Freeman (19, p. 20):

If the differences in the means of the F_3 cultures * * * are due to genetic causes, one would expect the intermediate cultures to be more variable than the extremes, thus assuming that the extreme cultures are more nearly homozygous than those which are intermediate.

This test was applied to the 22 F_3 progenies of the Holdon × Pima hybrid. The results are stated in Table 11, which shows, for each of

the 17 characters determined in F_3 which did not show definite segregation ratios in F_2 , the extremeness of the individual or individuals among the 22 F_2 parents which had, respectively, the highest and the lowest value for the character in question, the coefficients of variation or standard deviations of the F_3 progenies of these extreme individuals, and the average of the coefficients of variation or standard deviations of the F_3 progenies whose parents had given values nearest the mean of the F_2 population. Extremeness is expressed by taking the difference between the value of the high or low parent individual and the opposite extreme of the whole F_2 population as a percentage of the difference between both extremes of the whole F_2 population. An extremeness of 100 per cent indicates that the parent individual was at one or the other end of the F_2 frequency distribution, while an extremeness of 50 per cent would indicate that the parent individual was close to the mid-point of the F_2 distribution.

TABLE 10.—Coefficients of variation or standard deviations of the most variable and least variable F_3 progenies and of the F_2 and parental populations of Holden-Pima cotton hybrids.

Character.	Coefficient of variation or standard deviation. ¹					Significance of difference in variability (D+E) between ² —		
	F_3 progeny giving—		F_2 (entire population.)	Holdon.	Pima.	Most and least variable F_3 .	Most variable F_2 and F_3 .	Least variable F_2 and less variable parental.
	Highest C or σ .	Lowest C or σ .						
Axis:								
Length.....	31.7 \pm 4.98	6.9 \pm 1.26	22.7 \pm 0.85	13.2 \pm 1.65	11.1 \pm 1.55	4.8	+1.8	-2.1
Internode number.	17.7 \pm 2.29	4.6 \pm .69	12.8 \pm .46	14.9 \pm 1.87	8.5 \pm 1.17	5.5	+2.1	-2.9
Internode length.	20.1 \pm 2.99	8.0 \pm 1.02	14.9 \pm .54	13.2 \pm 1.65	7.2 \pm .99	3.8	+1.7	+ .6
Fruiting branch:								
Length.....	45.9 \pm 7.85	16.9 \pm 3.13	29.6 \pm 1.14	27.2 \pm 3.57	12.4 \pm 1.67	3.4	+2.1	+1.3
First internode..	62.5 \pm 8.67	4.8 \pm .81	33.6 \pm 1.32	33.3 \pm 4.53	16.3 \pm 2.20	6.6	+3.3	-4.9
Leaf:								
Length.....	18.1 \pm 2.23	6.1 \pm 1.03	16.2 \pm .58	7.3 \pm .89	5.2 \pm .72	4.9	+ .8	+ .7
Width.....	23.6 \pm 3.42	9.5 \pm 1.60	21.1 \pm .78	15.9 \pm 1.99	10.2 \pm 1.41	3.7	+ .7	-.3
Index.....	14.3 \pm 1.25	5.9 \pm .89	12.8 \pm .46	13.9 \pm 1.73	8.8 \pm 1.21	5.5	+1.1	-1.9
Lobe index.....	32.6 \pm 4.93	6.8 \pm 1.15	21.7 \pm .80	9.1 \pm 1.11	8.4 \pm 1.16	5.1	+2.2	-1.0
Vein angle.....	16.7 \pm 2.04	6.6 \pm 1.11	12.7 \pm .46	6.4 \pm .78	10.2 \pm 1.41	4.3	+1.9	+ .1
Callus color.....	2.28 \pm .33	.38 \pm .06	1.8 \pm .064	.3 \pm .037	.1 \pm .013	5.7	+1.4	+4.6
Petiole hairiness.....	2.51 \pm .31	.12 \pm .02	1.3 \pm .046	.4 \pm .049	0	7.7	+3.9	+6.0
Petal color.....	1.10 \pm .13	0	.9 \pm .032	0	0	8.5	+1.5	0
Boll:								
Length.....	19.9 \pm 3.48	5.2 \pm .69	11.6 \pm .41	5.1 \pm .62	4.2 \pm .55	4.1	+2.4	+1.1
Diameter.....	22.1 \pm 3.90	3.9 \pm .66	9.2 \pm .33	3.4 \pm .42	2.5 \pm .33	4.6	+3.3	+1.9
Index.....	16.4 \pm 2.08	6.7 \pm .96	12.1 \pm .44	4.5 \pm .55	4.3 \pm .57	4.2	+2.0	+2.2
Lock number....	10.3 \pm .76	2.3 \pm .33	8.6 \pm .30	1.8 \pm .22	1.3 \pm .17	9.6	+2.1	+2.7

¹ For the three graded characters, leaf callus color, petiole hairiness, and petal color, the standard deviations are compared. For all other characters the comparison is of coefficients of variation.

² A plus sign (+) indicates that the first and a minus sign (-) that the second of the populations compared is the more variable.

In many of the characters the most extreme of the 22 parent individuals were comparatively remote from the corresponding extreme of the entire F_2 population. With an extremeness of less than 80 per cent, indicating that the location of the parent individual on the F_2 distribution was more than one-fifth of the distance from the extreme in question, we should not expect to find a marked approach to ho-

mozygosity and hence an appreciably smaller variability in the F_3 progeny than in the progeny of an intermediate F_2 individual. For this reason in cases where the extremeness of the highest or lowest parent individual was less than 80 no data on the variability of the F_3 progenies are given in the table. This leaves 8 characters in respect to which the F_2 parent individual giving the highest value had an extremeness of 80 per cent or greater and 15 characters in respect to which the F_2 parent individual giving the lowest value had an extremeness of 80 per cent or greater.

TABLE 11.—Holdon-Pima cotton hybrids: Relation between the percentage extremeness of the F_2 parent individuals which gave the highest and the lowest values for the several characters and the variability of their F_3 progenies.

[The averages of the coefficients of variation or standard deviations of the F_3 progenies of those F_2 individuals which gave values nearest the mean of the whole F_2 population are stated for comparison. For the three graded characters—leaf callus color, petiole hairiness, and petal color—the standard deviations are compared. For all other characters the comparison is of coefficients of variation.]

Character.	Relative extremeness of F_2 parents which gave the —		Coefficients of variation or standard deviations of F_3 progenies of F_2 individuals which gave the—			
	Highest value.	Lowest value.	Highest value.	Lowest value.	Value nearest the mean of the F_2 population.	
					Average C or σ .	Number of intermediate progenies.
Axis:						
Length.....	86.0	98.5	14.60	31.70	18.10	3
Internode number.....	100.0	95.5	4.60	17.70	10.00	5
Internode length.....	88.5	88.5	14.40	¹ 12.10, 20.10	13.30	3
Fructing branch:						
Length.....	88.0	(-80.0)	¹ 26.50, 34.70	23.30	4
First internode.....	(-80.0)	92.3	¹ 33.00, 55.50	19.20	3
Leaf:						
Length.....	(-80.0)	81.5	13.30	4
Width.....	(-80.0)	81.0	¹ 9.50, 17.30	15.40	4
Index.....	81.0	91.5	6.40	10.60	11.60	4
Lobe index.....	85.5	83.5	6.80	14.60	16.60	5
Vein angle.....	85.0	88.0	7.80	16.70	11.70	6
Callus color.....	87.5	87.5	.89	1.45, 1.43	1.48	4
Petiole hairiness.....	(-80.0)	100.0	² .12 to 1.10	1.32	11
Petal color.....	(-80.0)	100.068	.53	11
Boll:						
Lock number.....	(-80.0)	81.0	12.30, 5.40	7.60	6
Length.....	(-80.0)	(-80.0)	6
Diameter.....	(-80.0)	93.5	6.70	8.60	6
Index.....	(-80.0)	88.0	9.00	11.40	6

¹ Two progenies the F_2 parents of which gave the same value.
² Eight progenies the F_2 parents of which gave the same value.

As compared with the average for the intermediates, the F_3 progeny of the highest F_2 parent gave a lower coefficient of variation or standard deviation for six of the eight characters which met the conditions stated in the preceding paragraph, and the F_3 progeny of the lowest F_2 parent gave a lower coefficient of variation or standard deviation for 8²⁰ of the 15 characters which met the conditions.

Of the seven characters in respect to which the extremeness of both the highest and the lowest F_2 parent was 80 per cent or greater, only

²⁰ Omitting two cases in which there were two F_2 parent individuals which gave the same value, the progeny of one but not of the other having been less variable than the progenies of the intermediate F_2 individuals.

three showed less variability in the progenies representing both extremes of the F_2 distribution than in the progenies of intermediate F_2 individuals. The correlation between the percentage extremeness of the 22 F_2 parent individuals and the size of the coefficient of variation or standard deviation of the corresponding F_3 progenies was determined for the characters in question and gave values for r (coefficient of correlation) as follows:

Leaf index.....	-0.242 ± 0.135
Leaf lobe index.....	- .418 ± .119
Callus color.....	- .106 ± .142

In all cases the correlation is negative, as the theory requires, although only the coefficient for leaf lobe index appears to be significant, being 3.5 times the probable error.

The data as a whole indicate a tendency, although with many exceptions, to less variability in the progenies of extreme than in the progenies of intermediate individuals of the second generation. As far as the evidence goes, it points to a greater degree of homozygosity at both ends of the F_2 distribution and hence strengthens the conclusion that segregation has occurred.

SUMMARY OF EVIDENCE OF F_2 SEGREGATION AFFORDED BY F_3 .

Many of the characters determined on this hybrid of upland and Egyptian cottons are not size characters in the narrow sense, although nearly all of them resemble size characters in showing inheritance of the "blend" rather than of the sharply alternative type. In reviewing the evidence that segregation took place in the second generation, the data will be considered, therefore, in their relation to the eight requirements "which must be fulfilled in order to establish the validity of the multiple-factor theory of size inheritance," as postulated by East (16, pp. 165-167).

(1) Crosses between individuals belonging to races which * * * approach a homozygous condition, should give F_1 populations comparable to the parental races in uniformity.

This condition was fulfilled for the hybrid here dealt with in respect to nearly all of the characters (Tables 2 and 3).

(2) In all cases where the parent individuals may reasonably be presumed to approach complete homozygosis, F_2 frequency distributions arising from extreme variants of the F_1 population should be practically identical.

This point was not adequately tested in the present case, but the evidence, such as it is, indicates that the requirement was met (p. 11).

(3) The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

The Holdon-Pima hybrid gave an F_2 coefficient of variation or standard deviation which was significantly higher than the corresponding constant of F_1 in 37 of the 38 characters compared (Table 2).

(4) When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

For 37 of the 39 characters determined in F_2 of the Holdon-Pima hybrid the frequency distribution of F_2 comprised the means of both grandparental populations, and for 33 characters both extremes of the combined grandparental distributions were recovered in F_2 (figs. 3-41).

(5) In certain cases individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent.

For 31 of the 39 characters the F_2 frequency distribution of Holdon \times Pima extended beyond the combined distributions of the grandparental races in one or both directions. For 3 characters half or more of the F_2 distribution lay outside the combined distributions of the grandparents (figs. 3-41).

(6) Individuals from various points on the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

For all of the characters determined in F_3 the means of the progenies which gave, respectively, the highest and the lowest mean differed by an amount not less than 12 times the probable error of the difference (Table 8). The coefficients of correlation between the F_2 value and the F_3 progeny mean for the several characters ranged from 0.35 to 0.87, the average value of the coefficient having been 0.66. For 17 of the 18 characters the parent-offspring coefficient of correlation was not less than four times its probable error (Table 9).

(7) Individuals from either the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parents to that of the F_2 generation.

The F_3 progenies of Holdon \times Pima which gave, respectively, the highest and the lowest coefficient of variation or standard deviation skewed, for every character, a significant difference in variability. The least variable of the F_3 progenies was significantly more variable than the less variable parental race in only 2 of the characters and was significantly more variable than the more variable parental race in none of the characters. The most variable of the F_3 progenies was at least equal in variability to the F_2 population in all of the characters (Table 10). There was a tendency, although with many exceptions, to less variability in the F_3 progenies of individuals at either extreme of the F_2 frequency distribution than in the F_3 progenies of intermediate F_2 individuals (Table 11).

(8) In generations succeeding the F_2 the variability of any family may be less but never greater than the variability of the population from which it came.

In the present case, for 3 of the characters, the most variable F_3 progeny gave a coefficient of variation or standard deviation which was apparently significantly higher than that of the entire F_2 population (Table 10). To this extent the eighth postulate is not fulfilled. But, as was pointed out by East (16, p. 174), complications due to linkage may affect the result. Furthermore, "when dealing with small populations one should not place too much confidence in the probable error calculated for any particular biometrical constant." The latter consideration should not be overlooked in view of the small size of the Holdon \times Pima F_3 populations.

EXTRAPARENTAL CHARACTERS IN F_2 OF THE HOLDON-PIMA HYBRID.

It was pointed out in discussing the frequency distributions for bract connation index and midlock furrow index that some of the F_2 plants had the margins of their involueral bracts connate to a much greater extent than in Pima, the parent which has the more connate bracts, and that midlock furrows much longer than those of Holdon, the parent in which this character appears, were found in

several of the F_2 individuals (Pl. IX, fig. 7). Extremely narrow corollas were also met with in F_2 , the corolla index (width as a percentage of the length) having ranged as low as 22, while in Pima the minimum was 59 and in Holdon it was 95.

Other extraparental variations, chiefly in characters not determined by measurement or grading, were noted as having appeared in one or more of the F_2 plants. Several of these were so remarkable as to differentiate the plants exhibiting them from any commonly cultivated type of cotton. In some cases the character as a whole, in other cases the degree of its expression, were extraparental. The most striking were:

Excessively numerous vegetative branches or limbs (Pl. XIII, fig. 1).

Absence of a sharp differentiation, at high nodes of the axis, between vegetative and fruiting branches.

Red color present in the stems, leaves, and involucre to a much greater extent than in any individual of the parental populations.

Bluish glaucous color of the stems and foliage (Pl. XIII, fig. 1).

Color of the foliage lighter green than in Holdon (Pl. XII, fig. 2) or darker green than in Pima (Pl. XV, fig. 1). In some of the light-green plants the leaves had a yellowish hue, and in at least one individual (Pl. XXI, fig. 3) a tendency to chlorosis was noticeable.

Leaves thinner than in the Holdon parental race or thicker than in the Pima parental race, being almost coriaceous in some of the F_2 individuals.

Leaves of the middle zone of the axis only three lobed, in one individual some of them entire (Pl. XII, fig. 1; Pl. XIII, figs. 2 and 3; Pl. XVII, fig. 1; Pl. XIX, fig. 1), while in the parent races the corresponding leaves are five lobed.

Deflexed instead of an approximately horizontal position of the whole leaf blade.

Deflexed or pendent position of the terminal lobe only, the rest of the leaf blade being approximately horizontal.

Terminal lobe twisted so as to occupy a plane almost at right angles to that of the remainder of the leaf blade.

Petiole twisted so as to reverse the usual position of the dorsal and ventral surfaces of the leaf blade (Pl. XIV, fig. 1).

Leaf margin sinuate or fluted (Pl. XIII, fig. 2; Pl. XV, figs. 1 and 2; Pl. XVII, fig. 2), characters not expressed in either parental population and but faintly so in F_1 . In the F_2 population 29 of the 215 individuals showed a more pronounced expression of the characters than any of the F_1 , and in several F_2 individuals the crinkled or wavy condition was extremely conspicuous.²⁷

Leaf lobes, especially the terminal lobe, conspicuously toothed or notched, (Pl. XVIII, fig. 1), a character which is frequent in sea-island cotton but of rather rare occurrence in Pima while in Holdon it has not been observed.

Leaf lobes constricted at the base (Pl. XX, fig. 1).

Leaf blade deeply cupped by the upward curving of the margin (Pl. XVII, fig. 2).

Leaf lobes terminating in threadlike tips (Pl. XX, fig. 2).

Extreme hairiness, with the hairs either much longer or much more numerous and feltlike than in Holdon, the hairy parent. In one individual the hairiness extended to the young bolls.

Calyx having one or two excessively long teeth. In one individual a portion of the calyx was transformed into a bractlike structure having two or three teeth.

Outer corners of the petals washed with red. This variation in petal color was not observed in newly opened flowers of the parental varieties, although in both Pima and Holdon when the flowers begin to wither the petals turn red.

Pistil exerted in the bud, a character sometimes associated with malformation of the corolla.²⁸

Stigmas bent (Pl. VIII, fig. 8) sometimes at a right angle to the column.

Occurrence of six-locked bolls, noted in one individual only.

Surface of the boll very rough (Pl. IX, figs. 10, 13, 18), the pits in which the oil glands are situated being very large and deep.

²⁷ Fyson (20, p. 12 and fig. 10) notes the occurrence of waviness of the leaf margin as an extraparental character in a hybrid between two species of cotton grown in India (*Gossypium herbaceum* and *G. pergluctum*).

²⁸ J. H. Kempton calls attention to the fact that exertion of the pistil in the bud is normal in *Thurberia thepsinoides*, a plant allied to *Gossypium* which is native in the mountains of southern Arizona and in adjacent portions of Mexico.

Boll locks strongly concave toward the apex (Pl. IX, fig. 7), a character which is perhaps associated with deficient fertilization.

Constriction of the boll about midway between the base and the apex.²⁹

Boll ending in a long, sharp point (Pl. IX, fig. 6). This character is not nearly so frequent and pronounced as in hybrids between Pima and sea-island cottons.

External grooves which correspond to the partitions between the locks terminating far above the base of the boll (Pl. IX, figs. 16 and 18). In Pima cotton these grooves extend always to the base of the boll and in Holdon very nearly or quite to the base. In the F_2 extreme the grooves terminated at less than two-thirds of the distance from the apex of the boll and in 11 of the 215 F_2 individuals at not more than three-quarters of the distance.

Fuzz or short hairs of the seed coat longer than in the parent variety (Holdon) which has the longer fuzz.

Occasionally two or more of these characters, such as presence of red color in the vegetative organs and also in the petals, were associated in the same individual, but as a rule the extraparental characters seemed to be as independent as were most of the characters expressed in the parents. Many of them were regularly expressed in the offspring from self-fertilized seed. Thus the conspicuous bluish white color of the foliage of plant No. 61 appeared without diminution in all of the 22 plants which constituted its F_3 progeny (Pl. XIII, fig. 1). Other extraparental characters of F_2 individuals which were recorded as having been expressed with great regularity in their F_3 progenies were extreme limbiness, various sorts of pubescence, exceptionally light or dark color of the foliage, exceptional thinness or thickness of the leaves, sinuate or undulate leaf margins, cupped leaves, reduced number of leaf lobes, rough deeply pitted surface of the boll, extension of the boll into a long sharp point, and exceptionally light or dark color of the boll.

Characters of a definitely pathological nature also appeared in F_2 . Various deformities of the reproductive organs were observed (Pl. VIII, fig. 8,) the most serious being imperfect development of the anthers, which will be further considered in the discussion of sterility.

Tomosis, or leaf-cut (Cook, 14), a presumably physiological malady which occurs in Arizona in a high percentage of the very young cotton plants but does not normally persist in the later stages of development, was present in a pronounced degree in 9 of the 215 adult plants of F_2 (Pl. XXI, figs. 1 and 2) and in a less marked degree in several others. The symptoms were crumpling or buckling of the leaves, with failure to develop of a portion of the foliar tissue. Inheritance of a tendency to this condition was clearly shown in F_3 progeny No. 19.

STERILITY IN F_2 AND F_3 OF THE HOLDON-PIMA HYBRID.

A thorough investigation of the manifestations of sterility in the Holdon-Pima hybrid was not undertaken, but it seems advisable to record such observations as were made.

The first generation of hybrids between Holdon and Pima, as between upland and Egyptian cottons in general, is extremely fertile, much more so than either parental variety, and this notwithstanding the fact that there is often a considerable loss from shedding of buds and young bolls, probably caused by the rapid and vigorous growth of the F_1 plants.

²⁹ The occurrence of this character was noted by Marshall (33, p. 61) in the second generation of a hybrid between Egyptian cotton and Hindi, an uplandlike type which occurs as a weed in cotton fields in Egypt.

A very different condition is encountered in the second generation. Absolute sterility was shown by 7 per cent of the F_2 population, 15 of the 215 individuals having produced no seed, even from open-pollinated flowers. Four of these sterile plants developed bolls, which, although containing only shriveled ovules, reached a good size. As compared with the averages for fully developed bolls of the Pima parental race, they had a length of 67 to 82 per cent and a diameter of 90 to 105 per cent. The seedless condition was common to all of the bolls borne by the 4 plants in question. On the remaining 11 sterile plants the bolls did not attain measurable size, although the numbers which had apparently set on these individuals ranged from 31 to 389 and exceeded 100 in 7 of the plants.³⁰

In addition to the 15 completely sterile F_2 plants, a very low degree of fertility was not infrequent, one of the plants having produced only 7 bolls and others very small numbers. Shedding of the flower buds in various stages of their development and of the young bolls was the proximate cause of the low fertility. Deficient fertilization, resulting in a very small number of seeds in the bolls which matured, was also of common occurrence. One obvious cause of deficient fertilization in many of the plants was the imperfection of the anthers (Pl. VIII, fig. 8), especially of the uppermost ones upon which self-fertilization mainly depends. Of 55 F_2 plants (not including any of the 15 completely sterile individuals above mentioned) on which flowers were bagged to prevent cross-pollination, 8 plants produced no seed from such flowers and 9 plants produced fewer than 10 seeds each, or fewer than are usually contained in a single boll from a bagged flower of either parental variety. It is probable that some of the plants of which the anthers were apparently well developed produced defective pollen, but no investigation of this condition was made.

The seeds produced by many of the F_2 plants were of low viability, and there was a heavy mortality in the seedling stage among the F_3 hybrid progenies. Unfortunately, adequate data on this point were not obtained, but in approximately 25 per cent of the hills which were planted with selfed seed of the F_2 parents not a single plant developed beyond the seedling stage, although three or four seeds had been planted in each hill.

The 22 F_2 plants of which F_3 progenies were grown had differed considerably in fertility, as is indicated by the fact that in the number of bolls of all sizes counted on October 15 they ranged from 55 to 326 and averaged 167. The average number of bolls per plant in the F_3 progenies was in every case much smaller than the number borne by the corresponding F_2 parent, the average for approximately 400 plants in the 22 F_3 progenies having been only 27, with a minimum of 17 and a maximum of 50 bolls. The very low fertility of the F_3 populations may have been due partly to the fact that these progenies were grown on the same land on which the F_2 was grown the year previous, and the soil may have become partially exhausted. The weather conditions also were less favorable for cotton in 1920 than in 1919. It is highly improbable, however, that these were the sole causes of so great a decline in fertility from the F_2 to the F_3 .

³⁰ The highest number of bolls on any F_2 plant was 406.



FIGS. 1 AND 2.—THE EFFECTS OF TOMOSIS, OR LEAF-CUT.

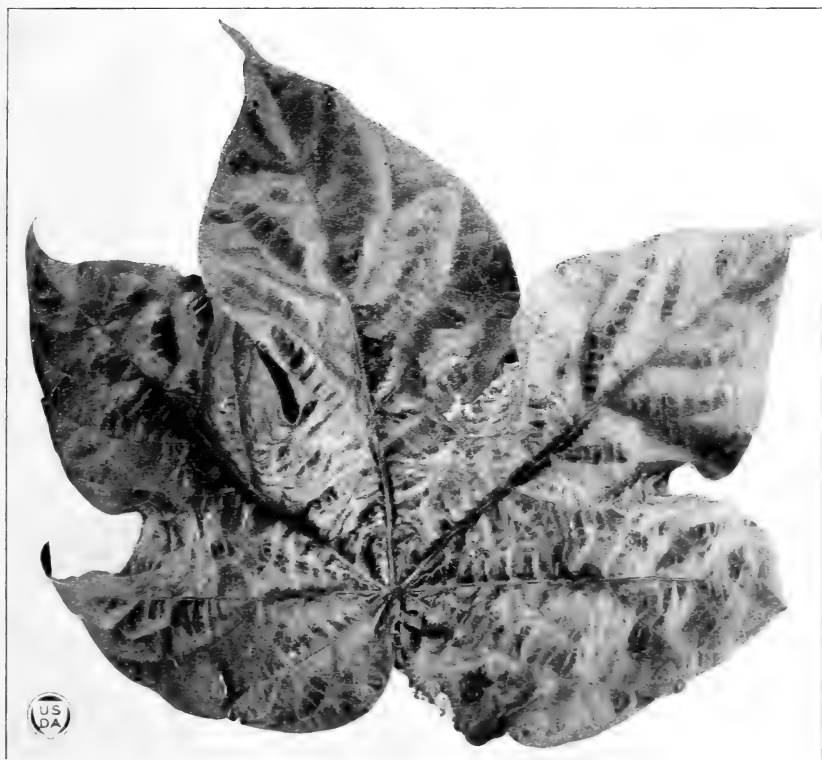


FIG. 3.—A COARSE TYPE OF LEAF WITH BROAD AND SHALLOW LOBES.

Color very light green, almost chlorotic.

LEAVES OF HOLDON \times PIMA COTTON, F₂. PATHOLOGICAL TYPES.



The fact is rather remarkable, considering the high parent-offspring correlations in other characters, that no correlation was found to exist between the number of bolls borne by the F_2 parent and the average number per plant in the corresponding F_3 progeny, the value of r having been 0.095 ± 0.143 . One of the most fruitful of the F_2 parents, the one which gave the largest F_3 progeny, produced offspring of which 23½ per cent were completely or almost completely sterile, only 1 of the 21 other F_3 progenies having shown a higher percentage.³¹ Of the 22 F_3 progenies, 9 contained from 3 to 38 per cent of completely sterile individuals which matured no seeds, and most of these progenies contained also a certain percentage of plants which matured only a very few (not more than 5) bolls. In 4 progenies from 6 to 10 per cent of the plants were nearly sterile, but none was completely so. In the remaining 9 progenies none of the plants was recorded as sterile or nearly so.

It is of interest to consider whether there was any relation between the relative sterility of these F_3 progenies and the relative variability of their morphological characters. The correlations were determined between the coefficients of variation or standard deviations for the 18 characters measured or graded on these populations (see Table 5) and the percentages of sterile or nearly sterile individuals. Positive and presumably significant correlations were found in the following cases:

Axis internode length	$r = 0.545 \pm 0.101$
Fruiting branch length	$r = .513 \pm .108$
Fruiting branch, first internode length.....	$r = .854 \pm .040$
Leaf length	$r = .379 \pm .123$

Positive correlations also occurred between the relative sterility and the variability in respect to callus color and petal spot, but the coefficients of correlation in these cases were only 2.6 and 2.3 times the respective probable error. The four length characters, high variability in respect to which proved to be associated with a marked tendency to sterility, are all intercorrelated, doubtless physiologically.

Especially noteworthy is the very high positive correlation in the case of the length of the first internode of the fruiting branch, the character which showed the greatest range in variability among the several F_3 progenies. It is fairly obvious that the presence of factors making for sterility might affect injuriously the development of the fruiting branch as a whole and hence might increase the variability of this organ, but it is not apparent why variability in the first internode of the branch should be so much more closely correlated with a tendency to sterility. At any rate, the conclusion may be drawn that variability in the length of the internodes, branches, and leaves, characters which might be expected to respond most readily to the influence of unfavorable growth factors, is more closely associated with a tendency to sterility than is the variability in color characters, hairiness, and size and shape of the bolls.³²

³¹ On the F_2 plant referred to (No. 40), 280 bolls of all sizes were counted on October 15 as compared with a maximum of 406 and an average of 167 bolls per plant in the entire F_2 population. This individual was the tallest of the 215 plants in the F_2 population and was characterized by numerous, nearly erect vegetative branches. The F_3 progeny was remarkably uniform and closely resembled the parent individual except in the marked tendency to sterility and to a diseased appearance of the foliage.

³² Kottur (29) found that in a hybrid between *Gossypium herbaceum* and *G. neglectum* F_1 showed the same kinds and degree of sterility as the parent species and F_2 and F_3 a greater amount. He describes a form of complete sterility accompanied by vegetative peculiarities (abnormal leaf color, etc.) not seen in the parents nor in F_1 but affecting about 7 per cent of the F_2 individuals and from 0 to 20.5 per cent of the individuals in different F_3 progenies.

The various manifestations of sterility in the second and third generations of this hybrid may be summed up as follows:

Failure of the seeds to germinate or of the plants to grow beyond the seedling stage.

Abortion of the flower buds in various stages of development, so that few or no flowers arrived at anthesis.

Imperfect development of the anthers and pollen, sometimes to the point of absolute self-sterility.

Shedding of the young bolls a few days after anthesis, so that few or none reached maturity. This occurred in some plants on which a large number of flowers had reached anthesis.

Complete seedlessness, although the bolls attained a good size.

Seeds matured, but in much smaller number per boll and per plant than in the parental races.

The frequency of partial or complete sterility, together with the appearance of numerous characters not expressed in either parental race, some of which were of an abnormal or even pathological nature, are proof of the wideness of the cross between upland and Egyptian cottons. Crosses between two varieties within the Egyptian type (28) on the other hand, showed no reduction of fertility and no expression of extraparental characters.

CORRELATION OF CHARACTERS IN F_2 OF THE HOLDON-PIMA HYBRID.

The coefficients of correlation for all possible combinations of 38 characters were determined on the 180 individuals of the F_2 population on which all of the characters had been determined. The correlations involved all measured or graded characters in respect to which the means of the parental populations differed by an amount equal to three and one-half or more times the probable error of the difference, with the exception of leaf width.³³

The coefficients of correlation were calculated by the Jennings formula (24, pp. 416, 417), using sorting and tabulating machines in the manner described by Collins and Kempton (9, pp. 5, 6). The total number of coefficients of correlation determined was 703. of which 93 may be regarded as significant, having been not smaller than 0.172. The number of individuals having been 180, a coefficient of 0.172 is 3.5 times its probable error.

Table 12 gives the significant coefficients of correlation, the probable errors being omitted because the number of individuals is in all cases the same. The plus and minus signs in the column headed "Expected sign" show whether a positive or a negative correlation is to be expected if the characters are associated in the hybrid as they are received from the parents; in other words, if coherence occurs. The sequence of the characters in both the first and second member of the pair is the same as that followed in the definitions on pages 7 to 11 and in Table 1, which gives the statistical constants. Axis and branch characters are placed first, followed by the leaf, bract, flower, boll, and seed characters. Therefore, if it is desired to examine all correlations involving, for example, bract length, this character will be found as the second member of the pair in each

³³ Leaf width is represented in a way by leaf index or relative width. Two characters, pedicel length and bract number of teeth, in respect to which the parental means of 1919 did not differ significantly, were nevertheless included in the correlations, the means of the parental populations of 1917 and 1918 having differed significantly and in the same direction in both years.

correlation of which an axis or leaf character is the first member, while bract length becomes the first member in correlations with other bract characters and with the flower, boll, and seed characters.

TABLE 12.—Coefficients of correlation in the second generation of the Holdon-Pima hybrid which are regarded as significant, having amounted to three and one-half or more times the probable error of the coefficient.

[The signs given in the column headed "Expected sign" show whether a positive or negative correlation was to be expected if coherence occurred. For pedicel length and bract number of teeth the "expected" signs indicate the relations of the means of the Holdon and Pima populations grown in 1917 and 1918. For all other characters the relations of the parental means of 1919 are indicated.]

Character pair.	Correlation.		Character pair.	Correlation.	
	Expected sign.	Coefficient.		Expected sign.	Coefficient.
Axis length and—			Petiole hairiness and—		
Internode length.....	+	+0.831	Bract:		
Internode number.....	+	+ .715	Connation.....	-	-0.247
Fruiting branch:			Tooth spread.....	-	- .187
Length.....	+	+ .620	Pedicel length and—		
Internode.....	+	+ .226	Bract:		
Leaf extension.....	+	+ .172	Length.....	+	+ .208
Pedicel length.....	+	+ .218	Number of teeth.....	+	+ .312
Bract:			Bract length and—		
Number of teeth.....	+	+ .198	Bract number of teeth.....	+	+ .187
Dentation.....	-	+ .257	Calyx dentation.....	-	+ .195
Fiber color.....	+	+ .178	Boll:		
Internode length and—			Length.....	+	+ .186
Internode number.....	+	+ .300	Diameter.....	-	+ .187
Fruiting branch:			Bract connation and—		
Length.....	+	+ .596	Calyx glands.....	+	- .253
Internode.....	+	+ .307	Lint index.....	-	+ .178
Leaf length.....	+	+ .199	Calyx dentation and—		
Pedicel length.....	+	+ .259	Petal spot.....	-	- .220
Bract dentation.....	-	+ .181	Boll length.....	-	+ .174
Internode number and—			Midlock furrow.....	+	+ .230
Fruiting branch length....	+	+ .388	Calyx glands and—		
Callus color.....	-	+ .182	Petal color.....	+	- .200
Bract:			Stigma index.....	+	+ .242
Number of teeth.....	+	+ .201	Boll index.....	-	+ .187
Dentation.....	-	+ .250	Corolla length and—		
Boll apex.....	-	+ .213	Corolla index.....	-	- .485
Fruiting branch length and—			Petal:		
Fruiting branch internode.	+	+ .362	Color.....	+	+ .214
Leaf length.....	+	+ .214	Spot.....	+	+ .244
Pedicel length.....	+	+ .183	Stamen length.....	+	+ .242
Bract:			Pistil length.....	+	+ .470
Length.....	+	+ .178	Boll apex.....	-	- .185
Number of teeth.....	+	+ .184	Corolla index and pistil length.	-	- .243
Dentation.....	-	+ .201	Petal color and—		
Calyx dentation.....	-	- .201	Pistil length.....	+	+ .197
Boll diameter.....	-	+ .182	Fiber length.....	+	+ .277
Fruiting branch internode and—			Stamen length and—		
Bract number of teeth.....	+	+ .210	Anther color.....	-	- .254
Boll length.....	+	+ .179	Pistil length.....	-	+ .197
Midlock furrow.....	-	- .195	Stigma index.....	-	- .246
Leaf length and—			Boll diameter.....	+	+ .180
Lobe index.....	-	- .264	Anther color and stigma index.	+	+ .222
Leaf extension.....	-	- .282	Pistil length and—		
Bract length.....	+	+ .301	Stigma index.....	+	+ .466
Boll diameter.....	-	+ .205	Lock number.....	-	- .182
Leaf index and—			Boll apex.....	-	- .212
Lobe index.....	-	- .183	Stigma index and lock number.	-	- .216
Vein angle.....	+	+ .750	Lock number and—		
Leaf extension.....	+	+ .502	Boll diameter.....	+	+ .202
Lobe index and vein angle....	-	- .422	Midlock furrow.....	+	- .193
Vein angle and—			Boll length and—		
Leaf extension.....	-	+ .566	Boll:		
Petal color.....	+	+ .197	Diameter.....	-	+ .289
Leaf extension and—			Index.....	-	- .703
Bract length.....	-	- .200	Apex.....	-	- .504
Fiber color.....	-	+ .186	Fiber length.....	+	+ .175
Callus color and—			Boll diameter and—		
Petiole hairiness.....	+	- .297	Boll index.....	+	+ .376
Calyx glands.....	+	+ .186	Lint index.....	+	+ .214
Corolla index.....	+	- .218	Boll index and boll apex.....	+	+ .448
Boll:			Boll apex and fiber length....	+	- .172
Diameter.....	+	+ .208	Fiber length and fiber color....	+	- .230
Index.....	+	+ .187			

The only significant correlations, not of an obviously physical nature, between characters that may be regarded as especially important from an agricultural point of view are the positive correlations between boll length and fiber length and between boll diameter and lint index. In both cases the coefficient of correlation is small. The existence, in upland cottons, of a small degree of correlation among certain characters of practical importance is indicated by results obtained by Hodson (23).

Many of the characters here dealt with are doubtless correlated physically or physiologically (8. p. 436), the correlation involving either a mathematical necessity or a tendency presumably common to different parts of the plant, e. g., to greater or less length in several organs. It is, however, impossible to determine the category of the correlation merely by inspection of the list of character pairs. As Collins has pointed out (8, pp. 438, 439), comparison of the coefficients of correlation in the F_2 population with those obtained in the parental populations (if approximately homozygous) or in F_1 is the only available means of distinguishing genetic from physical or physiological correlation.

It is regrettable that this test could not be applied satisfactorily in the present case because of the very small size of the parental and F_1 populations grown in 1919 for comparison with the F_2 . An F_1 of 24 individuals was grown in 1920 and the coefficients of correlations were computed for most of the character pairs for which they had been computed in F_2 , but a comparison of correlations based upon determinations made in different seasons would be of doubtful value. Furthermore, the F_1 showed almost no variation in respect to several of the most interesting characters, so that many of the possible correlations could not be determined by the "product-moment" method. For these reasons it was decided not to attempt a detailed comparison of the F_1 and F_2 correlations.

Of the 93 presumably significant correlations in F_2 , as given in Table 12, 66 have signs indicating coherence, i. e., a tendency for the characters to be associated in the hybrid in the same manner as they had been received from the parents. For the remaining 27 significant correlations the sign of the correlation indicates the opposite tendency or disherence. These disherent correlations are listed in Table 13.

TABLE 13.—*Significant and disherent correlations in F_2 of the Holdon-Pima cotton hybrids.*

[The value $r \div E$ is that obtained by dividing the coefficient of correlation by its probable error.]

Correlation.	$\frac{r}{E}$	Correlation.	$\frac{r}{E}$
Axis length and leaf extension.....	3.5	Callus color and corolla index.....	4.5
Axis length and bract dentation.....	5.5	Bract length and calyx dentation.....	4.0
Internode length and bract dentation.....	3.7	Bract length and boll diameter.....	3.9
Internode number and callus color.....	3.7	Bract connation and calyx glands.....	5.4
Internode number and bract dentation.....	5.3	Bract connation and lint index.....	3.6
Internode number and boll apex.....	4.4	Calyx dentation and boll length.....	3.5
Fruiting branch length and bract dentation.....	4.2	Calyx glands and petal color.....	4.2
Fruiting branch length and boll diameter.....	3.7	Calyx glands and boll index.....	3.9
Leaf length and boll diameter.....	4.3	Corolla length and stamen length.....	5.1
Leaf index and leaf extension.....	13.2	Stamen length and pistil length.....	4.1
Leaf vein angle and leaf extension.....	16.7	Boll lock number and midlock furrow.....	4.0
Leaf extension and fiber color.....	3.9	Boll length and boll diameter.....	6.3
Callus color and petiole hairiness.....	6.5	Fiber length and fiber color.....	4.8
Callus color and calyx glands.....	3.9		

A few of the disherences listed in Table 13 may be explained as due to physical or physiological correlation. This is certainly true of the correlations leaf index with leaf extension index and leaf vein angle with leaf extension index, both of which gave positive and very significant coefficients in F_1 , as well as in F_2 . It is probably true also in the following cases, for the F_1 coefficients, although apparently not significant, were of the same sign as the F_2 coefficients:

- Bract length with boll diameter.
- Corolla length with stamen length.
- Boll length with boll diameter.

It is evident that the list of disherences may be reduced slightly by allowing for intercorrelation. This applies to the correlations with bract dentation of axis length, internode length, internode number, and fruiting branch length, these stem-and-branch characters being intercorrelated positively. There remains, however, nearly a score of disherences which can not be explained away thus easily. A striking example is the correlation of callus color with petiole hairiness. The Holdon parent being characterized by a highly colored callus and by hairy petioles, the correlation in F_2 , if of a genetic nature, should have been positive, but it proved to be both negative and highly significant, the coefficient having been 6.5 times its probable error. It does not seem probable that physiological correlation as ordinarily understood is involved in this case.

No recognized principle in genetics seems adequate to explain the occurrence of disherence, of which so many apparently significant examples were encountered in this cotton hybrid. It may be noted that Collins and Kempton (9, pp. 33, 34) were confronted with the same dilemma in studying the correlations of characters in a hybrid of teosinte and maize.

TABLE 14.—Significant and coherent correlations in F_2 of the Holdon-Pima hybrid which are not apparently physical or physiological.

[The value $r \div E$ is that obtained by dividing the coefficient of correlation by its probable error.]

Correlation.	$\frac{r}{E}$	Correlation.	$\frac{r}{E}$
Axis length and fiber color	3.7	Corolla length and petal spot	5.2
Fruiting branch length and calyx dentation	4.2	Corolla length and boll apex	3.8
Fruiting branch internode and midlock furrow	4.0	Petal color and fiber length	6.0
Vein angle and petal color	4.1	Stamen length and anther color	5.4
Callus color and boll diameter	1.3	Stamen length and stigma index	5.2
Petiole hairiness and bract connation	5.2	Stamen length and boll diameter	3.7
Petiole hairiness and bract tooth spread	3.9	Anther color and stigma index	4.6
Calyx dentation and petal spot	4.6	Pistil length and lock number	3.7
Calyx dentation and midlock furrow	4.8	Pistil length and boll apex	4.4
Calyx glands and stigma index	5.1	Boll length and fiber length	3.6
Corolla length and petal color	4.5	Boll diameter and lint index	4.5

The cases of significant coherence become reduced to 22 if correlations of a more or less obviously physical or physiological nature be omitted. These 22 correlations are listed in Table 14. To what extent they are of a genetic rather than a physiological nature it is impossible to judge in the absence of direct evidence. A positive correlation between such characters as corolla length and petal spot would seem to belong to the genetic category, but it happens that in connection with another investigation the relation between this pair

of characters was worked out on a Pima population of considerable size, with the result that a positive and significant correlation was detected. For these 22 examples of coherence the coefficients of correlation are uniformly small, the largest having been only 0.277 ± 0.046 . This would indicate, on the assumption of genetic correlation, that the linkage is weak and that there is a high percentage of crossing over.

It may be objected that the product-moment method of determining the coefficient of correlation is inapplicable to characters in respect to which there was segregation in definite ratios, these having been petal spot, anther color, and midlock furrow index. These three characters showed no significant fourfold correlations with one another. In order to ascertain whether there were other correlations involving these characters which had not been revealed by the product-moment method, the F_2 population of 180 individuals was divided into two groups for petal spot, anther color, and midlock furrow, respectively, the basis of the groupings being indicated in the discussion of Mendelian segregation (pp. 21 to 27), and the means of the larger and of the smaller group were computed for each of the remaining characters. In every case where the means of the two groups differed significantly the correlation was worked out by the biserial method. This procedure subtracted none from the list of significant correlations as given in Table 12, and added the following:

Petal spot and petiole hairiness, coefficient of biserial correlation	-0.294 ± 0.063
Petal spot and lint index, coefficient of biserial correlation ..	$-.283 \pm .064$
Midlock furrow and leaf extension, coefficient of biserial correlation	$-.208 \pm .061$

The correlations of petal spot with petiole hairiness and with lint index are in the nature of coherences, while that of midlock furrow with leaf extension index is a disherence.

Coherence of characters in cotton hybrids has been noticed extensively in the writings of O. F. Cook (11, 12, 13, 15), who defines coherence as—

A condition in which characters derived from one parent remain together in expression instead of being expressed in chance combinations as in Mendelian hybrids (12, p. 30).

Combinations in which the parental relations of the characters are reversed are regarded by Cook as being associated with infertility, for he remarks—

Plants with these incongruous combinations of characters are generally infertile and sometimes completely sterile (12, p. 29).

In an earlier publication (11, p. 17) Cook stated:

Incongruities such as flowers of upland shape with the darker Egyptian color are rare and have been found thus far only on plants which are nearly sterile or otherwise definitely degenerate.

Some idea of the frequency of occurrence of this incongruous combination is given in another paper (13, p. 53), the statement being that—

A few hybrid plants, perhaps half a dozen out of as many thousands, have been found with the incongruous combination of Egyptian color with upland form, but these individuals were infertile and abnormal in other respects. The combination of white petals with Egyptian characters is less incongruous and much more frequent, in some Egyptian fields about one plant in a hundred. Some of the white-flowered

Egyptian plants are sterile or otherwise malformed, but many are fertile and apparently normal.

Specific instances of coherence of characters in Egyptian-upland hybrids are mentioned by Cook, although no determinations of the coefficient of correlation were made. One of these is pale color of the petals with an open cuplike corolla, both being upland characters, and the converse, or Egyptian combination (11, p. 17; 15, pp. 42, 43). In the Holdon-Pima hybrid, however, there was no significant correlation between corolla index (width as a percentage of the length) and petal color. Coherence of the three upland characters—short and wide corolla, pale petals, and long filaments—is mentioned by Cook, McLachlan, and Meade (15, p. 43), but in the Holdon-Pima hybrid stamen length was not significantly correlated with corolla index, and for the correlation stamen length with petal color the coefficient was positive instead of negative and was only 0.168 ± 0.049 . A further instance of coherence in the hybrid of two upland characters, pale color of both petals and pollen, is cited by Cook, McLachlan, and Meade (15, p. 44), but there was no significant correlation of petal color and anther (pollen) color in the Holdon-Pima hybrid.

Cook (11, p. 14) directs attention to—

A very general correlation between the shape of the boll and the length of the lint running through all the varieties of cotton that have been studied with this idea in mind, plants with more rounded bolls having shorter lint.

In a later paper (12, p. 30) the statement appears:

The general association of longer lint with more pointed bolls in any particular type of cotton may be connected with the other general fact that the long-linted types of cotton have more gradually tapering bolls than short-linted types of cotton.

The Pima parent of the Holdon-Pima hybrid has more pointed bolls, as expressed by the lower boll apex index, and longer fiber than the Holdon parent; hence, there should be in the hybrid a negative correlation between these characters if the coherence pointed out by Cook obtains in this case. The coefficient of correlation in F_2 , although low, was in fact negative and was apparently significant ($r = -0.172 \pm 0.049$).

It is of interest to consider to what extent the whole series of characters determined on the Holdon-Pima hybrid is connected by mutual correlation (9, p. 34). Coefficients of correlation were determined in F_2 for all possible combinations of 38 characters with respect to which the parental means differed significantly (difference of three and one-half or more times its probable error). Thirty-seven of these characters are involved in a continuous chain of correlations having a value for r of three and one-half or more times the probable error. The only character which appeared to be entirely independent was seed fuzziness, which was significantly correlated in F_2 with no other character.

It seems at first glance remarkable that nearly all of the characters determined in this hybrid should be intercorrelated, in view of the fact that the number of the chromosomes in *Gossypium* is large. Cannon (7, p. 167) determined the number in the haploid stage in the first generation of a sea-island-upland hybrid as 28, while Balls (6, p. 12) working presumably with Egyptian cotton, gives the haploid number as 20. It is to be considered, however, that the coefficients of correlation in the Holdon-Pima hybrid are mostly too small to

afford conclusive evidence of linkage. Moreover, all or nearly all of the characters involve more than one factor, and it is highly probable that the several factors for a given character are distributed in different chromosomes (9, p. 34). Determination of the actual linkage relations in this hybrid would seem to be precluded by the complex nature of the characters.

PRACTICAL SIGNIFICANCE OF THE RESULTS.

Many unsuccessful attempts have been made by practical breeders to obtain a superior type by hybridizing upland with Egyptian or with sea-island cotton. Combination of the large upland bolls with the long silky fiber and the relatively smooth seeds of the Egyptian or sea-island cottons is an attractive goal, but one which doubtless would be very difficult to reach. The difficulty of obtaining and fixing desirable recombinations from hybrids of upland with Egyptian or sea-island cottons has been discussed by Cook (13, pp. 60-64), who believes that one of the most serious obstacles is coherence of the characters:

For three or four generations some individuals continue to show resemblance to the superior first-generation hybrids, but progenies of such plants are diverse, like those that are obtained from the so-called heterozygotes in a typical Mendelian hybrid. The other plants that correspond roughly to the homozygotes of Mendelism return to the expression of the characters of the parental stocks in different degrees and combinations.

The data here presented concerning the correlations of characters in the Holdon-Pima hybrid indicate that freedom of recombination in hybrids between upland and Egyptian cotton is much less restricted than Cook supposed and evidence is also given that even as early as the third generation the new combinations may be relatively stable. On the other hand, it should be pointed out that not one of the 215 F_2 individuals and not one of the F_3 progenies showed any indication of possessing agricultural merit comparable to that of either parent variety. No near approach to a recombination of upland size of bolls with Pima length of fiber and relative smoothness of seeds was detected. The briefest consideration will show that the chance of such a combination appearing in this small F_2 population was exceedingly remote.

Leaving all other characters out of account for the moment, let us assume that the breeder's goal would be attained if the boll diameter of Holdon could be combined with the length of fiber and relative smoothness of seeds of Pima. It may be inferred from the F_2 frequency distributions for these characters (figs. 34, 38, and 41) that full expression of each of them depends upon not less than three factors. On the theory of probability only one in 262,144 individuals, homozygous for the nine factors involved, could be expected in F_2 , and to have a reasonable chance of getting the one homozygous individual, at least three times this number of plants would be required. Even were it practicable to grow so large an F_2 population, discovery of the one desirable plant would be exceedingly unlikely, especially as close examination is required to bring out the fiber and seed characters.

Emerson and East (17, p. 117) have pointed out, however, that the chance of obtaining by hybridization a desired recombination involving numerous factors is not so remote as would appear from calculation of the probability in the second generation. The procedure

recommended is to select in F_2 and later generations those individuals which show the nearest approach to the combination in view and, if there is no indication that the object may be attained by selection alone, to intercross the most promising individuals or families. Another method to be considered in such cases is back crossing with whichever of the parent varieties has the larger number of desirable characters or the characters which had proved most difficult of recovery in F_2 .

The employment of one or all of these methods might bring the combination of upland size of boll with Pima or sea-island length of fiber and relative smoothness of seed within the range of practicability were these the only characters involved. But so far the problem has been stated in its simplest terms. Habit of growth and fertility of the plant and additional properties of the fiber, such as abundance, strength, and fineness, would have to be taken into account in breeding a type of cotton desirable from the agricultural and commercial points of view. It was observed that the few second-generation Holdon \times Pima plants which produced very long fiber were deficient in either the abundance,³⁴ strength, or fineness of the fiber. Probably the most serious obstacle to success in recombining the desirable qualities of such diverse types of cotton is the marked tendency to sterility manifested in the perjugate (second and later) generations. If the great decrease in fertility from the second to the third generation, noted in the case of Holdon \times Pima, is a phenomenon of general occurrence in hybrids of upland and Egyptian cottons, the possibility of developing in this way a satisfactory agricultural variety would seem to be very remote.

Fortunately, the chances are much greater of obtaining desirable recombinations in crosses between more nearly related cottons. The results of an earlier investigation of a hybrid between two varieties of Egyptian cotton proved that segregation in F_2 is comparatively slight and that a cross of this nature does not result in the appearance of extraparental characters, abnormalities, and sterility, as is the case when upland and Egyptian cottons are crossed. The practical breeding work with Egyptian cottons has afforded evidence that it may not be extremely difficult to combine the desired characters of two such varieties in a stable and uniform type.³⁵

It is very clear from the results of this investigation that accidental cross-pollination of such different cottons as upland and Egyptian is sure to depreciate greatly the agricultural value of either type. The extensive segregation must result in a loss of that uniformity in the length and other properties of the fiber upon which its commercial value so largely depends, while the partial or complete sterility of many of the segregates will necessarily reduce the yield.

The recognition and definition of numerous characters in hybrids between upland and Egyptian cottons which are not expressed in either parent, some of these being of a very striking or abnormal description, has a direct application in the practical work of maintaining supplies of pure planting seed. It is evident that a stock of Egyptian cotton can not be regarded as uncontaminated by cross-

³⁴ There was not, however, a significant negative correlation between fiber length and lint index.

³⁵ It is reported by Longfield Smith (37, pp. 5, 6) that in hybridizing sea-island cotton and Sakellariidis Egyptian cotton, a much wider cross than that between any two varieties of the Egyptian type, "the second-generation plants show considerable variation, but when selections are made from these the third generation comes fairly true to seed and further selections continue to come almost true."

pollination with upland cotton merely because definite upland characters are not observed among the Egyptian plants. The occurrence of any peculiarity or abnormality must be regarded as ground for the suspicion that such cross-pollination has occurred and all such variants should be removed when seed-increase fields are rogued.

SUMMARY.

Upland and Egyptian cottons, although both types are possibly of hybrid origin, are comparable to very distinct botanical species in the nature and magnitude of the differences between them.

A genetic study of the kind and degree of segregation in an upland-Egyptian hybrid was undertaken for the purpose of obtaining statistical data as to the nature and behavior of the variants to be expected in fields of either type when exposed to natural cross-pollination by the other. Such information should be useful in determining whether cross-pollination has occurred and as a guide in the work of roguing seed-increase fields.

The Holdon variety of upland cotton, a representative of the Texas big-bolled group, was crossed with the Pima variety of Egyptian cotton, and the resulting hybrid was studied in the first, second, and third generations.

Holdon and Pima differ in respect to a great number of characters, many of which distinguish the two types of cotton in general. By measurement or grading 39 characters were determined in the parental, F_1 and F_2 populations, and showed significant differences between the parental populations.

The first generation of the hybrid showed heterosis or intensification in respect to most of the size characters, the F_1 mean having approximated or surpassed that of the parent which gave the higher value. Of the remaining 21 characters determined in this population, the F_1 mean was approximately intermediate in 9, while a tendency to dominance was shown in 12 characters, the F_1 mean approaching or in some cases surpassing that of one or the other parental population.

The mean of F_2 for all characters in respect to which the parental populations differed significantly either fell between the parental means or did not differ significantly from that of one or the other parental population.

Comparison of the coefficients of variation for measured characters and of the standard deviations for graded characters showed Holdon to be decidedly the more variable of the parental populations. In a large majority of the characters F_1 was less variable than the parental population which gave the higher coefficient of variation or standard deviation for the character in question. F_2 was more variable than the respective more variable parental population in most of the characters and was significantly more variable than F_1 in all but one character.

The relative diversity in F_2 , as compared with that of the parental and first-generation populations, is not fully expressed by comparison of the coefficients of variation or standard deviations for the characters determined. Numerous extraparental characters or expressions of characters appeared in F_2 .

The frequency distributions of F_2 extend to or beyond the extremes of both parental populations in 33 of the 39 characters.

Most of the distributions assume approximately the form of a normal frequency curve, indicating that several factors are involved. Pronounced skewness is shown in several cases, however, and the F_2 modes for a number of characters are much closer to the mean of one than of the other parental population. For corolla index, anther color, and seed fuzziness, the F_1 mean also showed a wide departure from intermediacy in the same direction as the mode of F_2 , indicating partial dominance.

The only fairly clear cases of bimodal distribution in F_2 are given by the characters petal spot, anther color, and midlock furrow index. A monohybrid ratio for petal spot is suggested by the fact that approximately three-fourths of the F_2 individuals showed presence of the spot in greater or less degree, as contrasted with its total absence. In F_1 all individuals showed the spot present, but the great amount of variation in intensity in F_1 and in the portion of the F_2 population in which it was present indicates that several factors are involved in the degree of development of the spot, although its complete absence may be a simple recessive character. Data obtained in F_3 afford further indication, although not complete proof, that absence of petal spot is a simple Mendelian recessive and that modifying factors are concerned in its development, when present. The evidence points to the occurrence of a 3 to 1 ratio for anther color, light color of the anthers being recessive, and of a 9 to 7 dihybrid ratio for midlock furrow index, presence of the furrow being recessive.

Data obtained by other investigators of cotton hybrids give evidence of segregation in definite Mendelian ratios in respect to several characters which did not show discontinuous variation in the Holdon-Pima cross.

Evidence of segregation in characters which did not give definite Mendelian ratios in F_2 is afforded by data obtained in the third generation of Holdon \times Pima. Seventeen characters which did not show definite Mendelian segregation in F_2 were determined in 22 F_3 progenies. For all of these characters the means of the F_3 progenies which gave the highest and the lowest mean, respectively, differed by an amount not less than twelve times the probable error of the difference. There was a high parent-offspring correlation between the F_3 progeny means and the values given by their respective F_2 parents, the average of the coefficients of correlation for the 17 characters having been 0.66 and the coefficients for all but one character having amounted to not less than four times the probable error.

Further evidence of segregation is afforded by a study of the variability of the F_3 progenies. In respect to every character the coefficient of variation or standard deviation of the most variable and the least variable F_3 progeny differed significantly. As compared with the F_2 population, the most variable F_3 progeny was at least equally variable in respect to every character. As compared with the parental population which was the less variable for the character in question, the least variable of the F_3 progenies was significantly more variable in only 2 of the 17 characters. There was a tendency, although with many exceptions, for F_3 progenies of individuals which occupied extreme positions on the frequency distribution of F_2 to manifest less variability than the F_3 progenies of individuals whose position on the F_2 distribution curve was intermediate.

Many of the characters of this cotton hybrid fulfill the requirements laid down by East as necessary to establish the fact of segregation when the frequency distribution of F_2 is unimodal and no definite ratios can be ascertained. These requirements may be paraphrased as follows:

Uniformity of F_1 comparable to that of its parents.

Absence of segregation in F_1 . (This point was not adequately tested in the material here dealt with.)

Variability much greater in F_2 than in F_1 .

Recovery of grandparental types in F_2 .

Deviation in F_2 beyond the grandparental extremes.

Marked differences in the modes and means of F_3 progenies of individuals representing different points on the F_2 frequency curve.

A range of variability in the several F_3 populations, extending from that of the populations representing the original parents of the hybrid to that of the F_2 generation.

Variability in generations succeeding F_2 never greater than that of the preceding generation.

It may, therefore, be concluded that segregation has taken place, the apparent nonoccurrence of definite ratios in F_2 being due to the fact that the characters each involve several factors and to the relatively small size of the population.

Several of the characters determined by measurement or grading showed variation, in the second generation, far beyond the combined ranges of the parental populations. Numerous other characters, not expressed in either parent variety, appeared in F_2 . Some of the more striking of these variations are absent or of very rare occurrence in any cultivated variety of cotton known to the writer. Abnormal or even pathological characters, such as persistence of tomosis in the adult state, partial chlorosis, extrusion of the pistil in the bud, malformation of the corolla, and abortion of the anthers were exhibited by a few of the second-generation plants.

Further evidence of the wideness of this cross between upland and Egyptian cottons is the frequency of sterility. Of the F_2 individuals, 7 per cent were completely sterile, and many more showed a very low degree of fertility. Many of the F_3 progenies, including one of which the F_2 parent had been exceptionally fertile, showed a low average fertility and comprised numerous sterile individuals.

The coefficients of correlation were determined for 703 pairs of characters in the second generation of the Holdon-Pima hybrid. Of the coefficients, 93 were probably significant. Many of the correlations are undoubtedly physical or physiological or are of a secondary nature, resulting from the mutual correlation of several characters.

Of the 93 pairs of characters which showed a presumably significant correlation in F_2 , the coefficient having been at least three and one-half times its probable error, the sign in 66 cases indicated coherence or expression of the characters in the hybrid in the same relation as they were received from the parents. Omitting cases of more or less obvious physical or physiological correlation, the number of significant coherences is reduced to 22. In 27 of the significant correlations the opposite tendency, disherence, was shown. Few of these disherent correlations obviously were of a physical or physiological nature.

The occurrence of disherent correlations, also noted by Collins and Kempton in their study of a hybrid between teosinte and maize, seems contrary to any generally recognized principle of heredity. No adequate explanation of the phenomenon has suggested itself.

In the cases of significant coherence in this hybrid, the smallness of the coefficients of correlation, except where the relation is probably physical or physiological, indicates that the linkage is weak and that the percentage of crossing over is high.

Of the 38 characters whose intercorrelations were determined in F_2 , 37 are connected by coefficients of correlation amounting to at least three and one-half times the probable error. In view of the fact that the haploid number of chromosomes in *Gossypium* is probably not fewer than 20, it may appear surprising that so high a percentage of the characters are associated. It is probable, however, that more than two factors are involved in most of the characters here dealt with, the several factors for each character being in all likelihood distributed in different chromosomes.

It may be inferred from the results of this investigation that, although the data on correlation indicate relative freedom of recombination, the chances are heavily against the isolation and fixation of a productive type of cotton, combining the most desirable characters of both parents, from the segregation products of so wide a cross as that between upland and Egyptian. It is also evident that accidental cross-pollination between these cottons can not but greatly impair both the uniformity and the fertility of either type. Both of these conclusions are in line with the practical experience of cotton breeders.

In roguing seed-increase fields of upland or of Egyptian cotton, the absence of characters definitely associated with the other type should not be regarded as proof that cross-pollination has not occurred. It is advisable to remove all plants which show peculiar or abnormal characters on the suspicion that they are products of accidental hybridization.

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