SOUTHERN COOPERATIVE SERIES BULLETIN 47

GENETICS AND CYTOLOGY OF COTTON
1948-55

REPORT OF COOPERATIVE RESEARCH UNDER
SOUTHERN REGIONAL PROJECT S-1

AGRICULTURAL EXPERIMENT STATIONS OF ALABAMA,
ARIZONA, ARKANSAS, GEORGIA, LOUISIANA, MISSISSIPPI,
NEW MEXICO, NORTH CAROLINA, OKLAHOMA, TENNESSEE
AND TEXAS, AND THE FIELD CROPS RESEARCH BRANCH,
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GENETICS AND CYTOLOGY OF COTTON

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The “Amendment of the Bankhead-Jones Act and the Agricultural Marketing Act of 1946” was passed by the United States Congress in 1946 “to provide for further research into basic laws and principles relating to agriculture . . . .” Title I, Section 963 authorized allotments “to the states for cooperative research in which two or more state agricultural experiment stations are cooperating to solve problems that concern the agriculture of more than one state.” Project 1 of the Southern Region (S-1), currently titled “Genetics and Cytology of Cotton,” was activated in 1948. Progress made under this project is summarized in this bulletin, which has been prepared under the direction of T. R. Richmond, who served informally as coordinator of the project until 1954, at which time he was appointed part-time coordinator on a formal basis.
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Report of Cooperative Research Under
Southern Regional Project S-1

INTRODUCTION

Cotton improvement in the United States began in the early part of the colonial era. Except for a wild species (Gossypium thurberi) in southern Arizona and possibly a few wild or semiwild forms presently classified as Gossypium hirsutum var. punctatum in southern Florida and northern Arizona, there is no evidence of there having been indigenous cottons within the present boundaries of the United States. The parental stocks from which the cultivated varieties of American Upland cotton arose were introduced from southern Mexico and Central America, an area familiar to cotton scientists as the “center of origin” of Upland cotton (Gossypium hirsutum). Some of the introductions were made directly from the center of origin and others were obtained from foreign countries, principally in the Mediterranean region, where they had been established from seed collected in or near the center of origin by Spanish explorers.

Natural selection must have played an important part in separating the adapted from the unadapted types, not only in respect to the earlier introductions but to all of the material introduced subsequently. Selection also has been practiced by man since the beginning of cotton production in the United States. By saving seed from the choice or best adapted plants, the more progressive cotton growers were able to accelerated the process of natural selection. As new stocks were introduced and as the cotton growing area moved westward, the process of adaptation to new ecological and cultural situations was repeated.

At the turn of the century, when the boll weevil began its spread over the Cotton Belt and threatened to wipe out the entire cotton industry, sufficient genetic variability remained in the then current agricultural varieties to make possible the selection of new types which could be grown eco-
nomically under weevil conditions. The main feature of these new types was the early-maturing, rapid-fruiting habit which, in contrast to the old late-maturing and indeterminate plant types, produced a satisfactory crop during the early and mid parts of the growing season and thus escaped, to a considerable extent, the damaging effects of the weevil which characteristically occurred in great numbers late in the season.

As cotton production expanded, problems with insect pests and diseases multiplied, and increasing numbers of enduses for cotton indicated the need for new and extended properties of raw lint. Shifts in production methods resulted in a need for special characters in cotton that would adapt varieties to mechanized production and harvesting. These developments suggested that further progress depended on (1) the introduction of new germplasm into the primary breeding material and (2) the development of more control and precision in the breeding program. It was apparent immediately that research along these lines depended on the availability of basic genetic information and materials.

Early genetic work in cotton, as in most of the other major crop plants, dealt with simple characters, most of which were of no direct economic value. Geneticists then, as now, found it difficult to bridge the gap between basic information and practical application. Though the literature on cotton genetics prior to the nineteen-forties is impressive, it seems safe to say that research in this particular field had not kept pace with similar research in other major crops. Research in the cytology of cotton was even more retarded.

In the late 1930's, as a result of the work of Skovsted in Trinidad and Beasley in the United States, the amphidiploid nature of cultivated cotton was established and a firm foundation was laid for cytogenetic work on the genus *Gossypium*. World War II prevented the natural development that would have followed. During the war years, the British closed their station at Trinidad and published a summary of the outstanding work in "The Evolution of *Gossypium*”. With the end of World War II, conditions were favorable for the development of a program on fundamental research in cotton genetics in the United States.

ORGANIZATION OF THE PROJECT

Formal organization of regional research in cotton genetics was initiated in the fall of 1946. A "Memorandum of Understanding" was entered into by 11 state agricultural experiment stations and the Division of Cotton and other Fiber Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture (now, Cotton Section, Field Crops Branch, Agricultural Research Service, USDA). Experiment stations of the following states signed the memorandum of understanding: Alabama, Arizona, Arkansas, Georgia, Louisiana, Mississippi, New Mexico, North Carolina, Oklahoma, Tennessee and Texas.

The original master project statement, written in 1947 and designated as S-1, was entitled: "National Cooperative Research in Plant Science for Improvement of Cotton". It was organized in two sections: Genetics and Breeding. Since it was felt that the breeding research, as outlined in the original project, was more properly a function of the individual states and not a function of a regional endeavor, the activities outlined under the breeding section were never authorized under Project S-1. When the master project was revised in 1962 the breeding section was omitted. The revised project bears the simple but inclusive title, "Genetics and Cytology of Cotton". It updates phases of research in progress, specifies more clearly the work proposed for the future and outlines in more detail the duties and functions of the cooperating states and federal agencies.

With the master project as an over-all guide in defining responsibilities of workers, and with annual meetings of the technical workers to improve communication, a well coordinated regional program of cotton genetics research has been in progress since 1948. This report summarizes the major accomplishments of that program.

COLLECTION, MAINTENANCE AND DISTRIBUTION OF BASIC EXPERIMENTAL MATERIAL

One of the primary requirements for the operation of a fundamental research project is the availability of basic experimental materials. The basic materials used in this proj-
ect are the various types and kinds of cotton (both cultivated and wild) such as species, interspecific hybrids, primitive stocks, foreign types, genetic lines and obsolete cultivated varieties. Fortunately, there were a number of stocks available when the project was initiated. For several years prior to 1942, when World War II forced its closing, the Bureau of Plant Industry of the U. S. Department of Agriculture operated a cytotogenetics unit at Riverside, California. This unit supplied a number of species and interspecific hybrids to workers in several state and federal experiment stations. During the period 1936 to 1941, J. O. Beasley, working at the North Carolina and Texas Stations, adapted the colchicine technique to cotton and demonstrated how certain sterile hybrids could be made fertile by doubling the number of chromosomes. Beasley and other workers who used the technique produced several primary interspecific hybrids.

Several years before Regional Project S-1 was initiated, J. W. Neeley assembled a large number of genetic stocks and other Upland breeding material. These stocks formed the nucleus of the present collection in Mississippi.

Colleagues in foreign countries, particularly British workers in the Empire Cotton Growing Corporation, supplied many basic stocks. Collections in southern Mexico and Central America, the center of origin of cultivated American Upland cotton, by T. R. Richmond and C. W. Manning in 1946, by S. G. Stephens in 1947 and by J. O. Ware and C. W. Manning in 1948, contributed significantly to the basic materials of this project.

Under Regional Research Project S-1, the collection, maintenance, primary screening for useful characters and distribution of basic stocks has been organized and systematized. The main purpose of the collection was to provide a reliable source of viable seed, or other propagating materials, of basic genetic and breeding stocks. At the same time the collection was designed to insure against loss of stocks or unnecessary duplication and to provide a means of screening the material for useful characters or properties. To eliminate the practice of haphazard collections at all of the participating stations, the Texas Agricultural Experiment Sta-

Figure 1. Races of G. hirsutum. (a) laijolium, (b) morrilli, (c) palmeri, (d) richmondii, (e) punctatum, (f) marie-galante.
tion was assigned major responsibility for the different species, interspecific hybrids and primitive races of cotton and the Mississippi Delta Branch Experiment Station was assigned prime responsibility for the principal commercial varieties, genetically marked stocks, inbred lines of Upland cotton and obsolete agricultural varieties. Other stations have assembled such stocks as are required for their individual problems. During the 7 years this project has been in operation, the number of stocks in the collection has increased steadily, thanks to the cooperation of colleagues both in this country and abroad. The collection at the Texas Station now contains all of the recognized cotton species (20), 48 subspecies or variations of the type species, 55 basic polyploids and 400 primitive and miscellaneous stocks. Several of the races of *Gossypium hirsutum* are shown in Figure 1. The Mississippi collection contains more than 800 stocks of modern and obsolete varieties of Upland cotton, and genetic types.

An effort is being made to reduce the stocks in the collections to a manageable or practical number by establishing standard or primary types and discarding those stocks which are duplicates or which resemble the standards within the limits of experimental error. This is being accomplished by taxonomic analysis and by evaluating them for agronomic characters, fiber properties, disease resistance, etc.

“The Regional Collection of Upland Cotton”, which catalogued agronomic characters and fiber properties of 477 stocks, was issued by the Mississippi Delta Branch Station in 1949. Supplementary information was released in 1950 and an enlarged and reorganized catalogue was issued in 1953. In 1949 the Texas Station issued a “Catalogue of *Gossypium* Stocks” listing the species, taxonomic varieties and races, interspecific hybrids, haploids and primitive stocks of which seed or propagating material were available for distribution. These catalogues provide cotton breeders with a ready reference to basic stocks available, materials which they could not obtain otherwise without extensive and time consuming research. Since this project has been in operation 620 and 1,485 requests for seed have been filled by the Texas and Mississippi stations, respectively.

At the time of the organization of the Regional Research Project S-1, it was recognized that it would be highly desirable to have a tropical garden of *Gossypium* species and photoperiodic types which are sensitive to length of day. Present commercial cottons have been developed over the centuries from perennial shrubs found in or near tropical deserts. These types, when brought to the temperate zone of the American Cotton Belt, will not bloom during the long days of summer; they flower only when the days are short, i.e., during the winter. Whenever collections are made in the tropics, perennial, photoperiodic types predominate. Evaluation and maintenance of such stocks under the cultural conditions found in the United States are extremely difficult and, therefore, attempts were made to establish a tropical location. Through the efforts of the Division of Cotton and Other Fiber Crops, BPISAE, informal cooperation was established with the Federal Experiment Station in Puerto Rico at Mayaguez from 1948 to 1950. The collections from Southern Mexico and Central America (1946-48) were grown for two seasons near Mayaguez and the material evaluated.

In the spring of 1950, through the National Cotton Council, a tropical station was established at Iguala, Mexico, primarily for the purpose of accelerating breeding progress by growing a second generation in a year. In cooperation with the Agricultural Research Service of the U. S. Department of Agriculture and Regional Research Project S-1, a garden in Iguala, Mexico has been established which now contains all the wild *Gossypium* species. This is the only living collection of *Gossypium* species now growing outdoors in the Western Hemisphere.

The species garden at Iguala is providing an adequate supply of seed for experimental work. Furthermore, it is possible to make certain crosses in Iguala that are extremely difficult under greenhouse conditions. A new species of *Gossypium*, the first described in 25 years, has been grown in Iguala, and a description of this species as *Gossypium lobatum* is now in press.

In addition to the species garden, the Iguala station is being used for the evaluation of photoperiodic types, for
genetic studies of photoperiodic material and for accelerating character transference into Upland stocks.

**CYTOGENETICS OF SPECIES AND INTERSPECIFIC HYBRIDS**

New or special characters can be transferred to or incorporated in cultivated American Upland varieties only if fertile hybrids are obtained. Thus, the cytogenetic phases of this project involve studies of species relationships, mechanisms which underlie species isolation and prevent efficient recombination of their germplasm,\(^1\) differences between chromosome sets, differentiation of individual chromosomes\(^2\) within and between species, problems of fertility, and the inheritance of new characters or properties. For a proper comparison of species differences and similarities, it is essential to know the nature of the barriers between species, the genetic and cytological similarities among species and the detailed differentiation of individual chromosomes within species, especially the American cultivated ones.

**SPECIES CLASSIFICATION AND COMPATIBILITY**

Twenty species of *Gossypium* are now being grown under greenhouse culture or in a tropical garden. The leaf types in Figure 2 illustrate the variation among the species. Most of these have been tested in crosses with each other, and their crossing behavior can be grouped into the following six types:

1. Bolls mature, seeds good, hybrids viable - e.g., *hirsutum* x *raimondii*
2. Bolls mature, seeds good, hybrids die - e.g., *hirsutum* x *gossypioides*
3. Bolls mature, seeds mostly empty; occasional good seed give viable hybrids - e.g., *thurberi* x *sturtii*
4. Bolls mature, seeds mostly empty; occasional good seeds give hybrids which die - e.g., *arborum* x *gossypioides*; *hirsutum* x *davidsonii*

5. Bolls mature, seeds all empty - e.g., *thurberi* x *davidsonii*
6. Bolls fall - e.g., *raimondii* x *stocksi*

The following genome\(^3\) groups have been established from earlier work:

A Asiatic species - e.g., *G. arboresum*
B African species - e.g., *G. anomalum*
C Australian species - e.g., *G. sturtii*
D American wild species - e.g., *G. thurberi*
E Arabian seacoast species - e.g., *G. stocksii*

The American cultivated species are tetraploids combining the A and D genomes.\(^4\)

Classification of new species of *Gossypium* into genome groups is keeping pace with their introduction into greenhouse culture. Two new species recently assigned to genome groups are *G. gossypioides* (D\(_4\)), and *G. robinsonii* (C\(_2\)).

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\(^1\)Hereditary material.
\(^2\)Carriers of the factors of heredity; can be seen under a compound microscope.
\(^3\)Chromosome sets or groups.
In general, hybrids of species with similar chromosomes usually are viable, have regular chromosome pairing and are fertile, as *thurberi x raimondii* or *hirsutum x barbadense.*

Conversely, many hybrids between species with unlike genomes are sterile because the chromosomes fail to pair (Figure 3a). In such cases, fertility can be produced by treatment of the hybrid with the drug colchicine, which doubles the number of chromosomes. When each chromosome has a mate, regular pairing occurs and fertility ensues. In rare cases, doubling of the number of chromosomes occurs spontaneously (Figure 3b). Figures 4a and 4b show the flowers of a hybrid before and after chromosome doubling.

In other cases, viability, chromosome pairing and fertility can each be reduced independently by genetic factors. The newly introduced species *G. gossypioides* (Figure 5) clearly illustrates these phenomena. For example, the hybrid *thurberi x gossypioides* dies even though the chromosomes are similar. The hybrid *raimondii x gossypioides* has regular pairing, but is virtually sterile. The hybrid *hirsutum x gossypioides* has regular pairing between D genome chromosomes,

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**Figure 3.** Chromosome pairing in hybrids of *G. davidsonii x G. anomalum.* (a) Sterile hybrid showing 4 pairs and 18 single chromosomes. (b) Fertile hybrid with all except 2 chromosomes paired.

**Figure 4.** Flowers of hybrids of *G. davidsonii x G. anomalum.* (a) Sterile flower of F₁ hybrid. (b) Fertile flower of hybrid after doubling of the number of chromosomes.

**Figure 5.** Flower, leaf and bud of *G. gossypioides*, a species recently introduced from Mexico.
but dies at the time of blossoming. The hybrid of **barbadense** x **gossypioides** is highly vigorous, but pairing between D chromosomes is greatly reduced. Figure 6 compares the chromosome pairing in the last two hybrids. Proper association in pairs of chromosomes, Figure 7a, is a requisite for complete fertility; such pairing insures their regular distribution into

![Figure 6. Comparison of chromosome pairing in two hybrids involving G. gossypioides. (a) F₁, *hirsutum* x *gossypioides*, 13 pairs of D chromosomes and 13 unpaired A chromosomes. (b) F₁, *barbadense* x *gossypioides*, pairing reduced between D chromosomes, giving 4 pairs and 31 single chromosomes.](image)

functional pollen and egg cells. Complete sterility occurs when large numbers of unpaired chromosomes are present as in Figure 7b. Partial sterility, brought about by irregular distribution of paired chromosomes, can occur when more than two chromosomes are associated (Figure 7c).

Some hybrids break down in the early embryonic stage and careful study reveals whether they can be saved by sterile culture on a nutrient medium (Figure 8). Other hybrids make successful seedlings but are retarded in growth or they may grow vigorously at first, and then die like the row of hybrids in Figure 9. Embryological investigations revealed why it is possible to cross successfully Upland (4n) with Asiatic cottons (2n), when the former is used as the female parent while the reciprocal cross usually fails. In the latter type of cross (2n x 4n) the nutritive tissue in the ovules, the endosperm, breaks down very early in development due to irregular nuclear divisions and the embryo degenerates for lack of food. In 4n x 2n crosses the endosperm is capable

![Figure 8. Planting hybrid embryos in sterile nutrient agar.](image)
of vigorous development if the egg accidentally fails to develop into an embryo, but normally the developing embryo causes the death of the endosperm which in turn leads to starvation of the embryo. However, this fatal process can be modified by using two kinds of pollen on the same Upland flower: its own Upland pollen plus Asiatic pollen. The Upland pollen will produce normal Upland seeds in the fertilized boll, and in locations adjacent to them hybrid seeds are capable of some growth. Apparently, a necessary substance diffuses from the Upland seed to the hybrid seed near by. The thus favored hybrid seeds often develop sufficiently to be artificially nurtured to maturity, or even may grow to maturity by themselves, depending upon the Upland variety used as mother. The contrasting behavior between 4n x 2n and 2n x 4n crosses just described seems to be a general rule in cotton hybridization. If the plant with the larger chromosome number is used as the male parent, e.g., in 4n x 6n crosses, the endosperm fails very early whereas 6n x 4n crosses result in some viable seed.

THREE-SPECIES TETRAPLOIDS

With the demonstration that the American cultivated species are amphidiploids, with genomes similar to those of

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*The term "ploid" with various prefixes is used to denote certain chromosome conditions with reference to number and sort. In cotton the basic number is 18; thus ha-, di-, tri-, tetra- and hexa- prefixed to ploid indicate, respectively 1, 2, 3, 4, and 6 times the basic number.
Asiatic cultivated (A) and American wild species (D), it became more important to obtain all possible combinations of A and D species. It is possible to cross many A and D species directly. When such a cross cannot, or has not, been obtained, an alternative approach is made. It has proved possible to obtain hybrids involving certain D genomes which have not been crossed directly with the Asiatic species by crossing hexaploids of *hirsutum-arboreum* (or *herbaceum*) with the D diploids concerned, namely, *G. armoyrianum, G. harknessi, G. raimondii* and *G. aridum*. Except for segregation involving the A<sub>1</sub> and A<sub>2</sub> genomes in the hexaploid, such three-species tetraploids are equivalent to the “F<sub>1</sub>” hybrids obtained by crossing synthesized AD tetraploids, e.g., *arboreum-thurberi*, with *G. hirsutum*. When, as in the cases so far mentioned, only A and D genomes are involved, these hybrids serve as basic breeding stocks from which genic material can theoretically be readily incorporated into *G. hirsutum*. Chromosome pairing is similar in all. Flowers of three three-species tetraploids, shown in Figure 10, serve to illustrate genetic differences between them; the hybrids also show differences in other characters.

Including the original three-species tetraploid, *arboreum-thurberi-hirsutum*, the AD hybrids presently at hand make available for selection in breeding programs such characters as the following: angular leaf spot resistance, fiber strength, pink bollworm resistance, hirsute leaves for resistance to jassids, glabrous leaves, small deciduous bracteole and drought resistance. Morphological characters of interest primarily in genetic studies also are available.

**TRISOMICS, TETRASOMICS AND MONOSOMICS**

**Intra-hirsutum**

Multiple and simple trisomics have been obtained from colchicine-produced polyploids of *G. hirsutum*. Selfing, and crossing of trisomics *inter se*, have given rise to tetrascines and to double trisomics. Tetrascines, plants with four instead of two chromosomes of a kind, have a more pronounced effect than simple or doubled trisomics on fertility, plant mor-

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The term “*omic*” with various prefixes is used to denote the number of chromosomes of the same kind present in the material.
Phology and other properties (Figure 11). Among the trisomic lines studied, trisomics involving large (A) chromosomes are recovered more frequently, and have a slightly higher transmission rate; such lines show a slightly higher viability than those involving small chromosomes, presumably of the D genome. There is evidence from hybrid and intraspecific *hirsutum* trisomics and tetrasomics that genes for asynapsis (reduced chromosome pairing) are present on chromosomes of the A₂ and D₂ genomes, and on A₈ and D₈ chromosomes of *hirsutum*.

Selfing and intercrossing of trisomic and tetrasomic lines with the recovery of tetrasomics and double trisomics, often of unequal size, are evidence that the n + 1 condition is transmitted through the pollen as well as through the ovule.

**Hybrid**

When hexaploids produced from F₁ hybrids of *G. hirsutum* x diploid species are backcrossed to *G. hirsutum*, lines with one or more chromosomes from the diploid species can be recovered. Examination of hybrid trisomic lines involving each of nine diploid species has shown that one extra chromosome may affect the shape, color and texture of leaf and bracteole, the size and color of floral parts, the size and shape of boll (Figure 12) and the color of fiber and seed coat. By selfing trisomic lines, plants with 54 instead of 52 chromosomes can be obtained. Lines with an extra pair of chromosomes from *G. herbaceum*, *G. arboreum*, *G. anomalum*, *G. karknessi*, *G. raimondii* and *G. stocksii* have been developed. These are partially fertile and partially stable. The effect of adding an extra chromosome is as a rule more marked the more distant the relationship between species.

![Figure 13. Chromosome pairing in tetrasomics. (a) Plant with an extra pair of chromosomes showing 25 pairs and one ring of 4. (b) Disturbed pairing showing many unpaired chromosomes.](image)

Chromosome pairing in most trisomics and tetrasomics is normal. The extra chromosomes in tetrasomics may associate as a pair, as a chain of three plus one unpaired chromosome, or as a ring of four (Figure 13a). In some cases, the extra chromosomes may cause reduced chromosome pairing, as shown in Figure 13b.

**Monosomics**

Plants lacking one chromosome of a pair have occurred spontaneously, following irradiation, and as a result of non-disjunction in trisomic and translocation lines. Some are morphologically different from normal (Figure 12e). Ten transmissible monosomics have been studied, and from tests of monosomics x genetically marked lines, and x translocations, it has been possible to identify particular chromosomes with marker genes, and to identify and number certain chromosome arms (Figure 14).
through the use of inbred seed. Since they eliminate genetic variability, doubled haploids are valuable as “living yardsticks” in all kinds of laboratory and field experimentation. Seven doubled haploids of Upland cotton, one of Pima 32, and several of Sea Island have been produced. At least two of the doubled haploids of Upland have good yield and other good agronomic qualities. There is a growing use of doubled haploids of cotton by geneticists, cytologists, agronomists, physiologists, pathologists and soil scientists.

**TRANSLOCATIONS**

**Multivalents in hybrids**

Many F₁ hybrids between species of *Gossypium* often show association of several chromosomes at metaphase. In some cases these are due to differences in end arrangement of the chromosomes, i.e., to translocations. In hybrids of *hirsutum-herbaceum*, for example, two rings of four chromosomes are formed, and in hybrids of *hirsutum-arboreum*, a ring of four and a ring of six. The segregation of the chromosomes of these multivalent configurations has been studied in derivatives of *hirsutum-arboreum* hexaploids, and in progenies from *arboreum-thurberi-hirsutum* and *hirsutum-arboreum-harknessii* tetraploids. It has been shown that the differential chromosomes are readily transmitted through both male and female gametes. As with induced translocations, balanced heterozygotes only are recovered through the male; through the female, duplication-deficiencies also are recovered. This difference in transmission offers a means of distinguishing balanced translocations heterozygotes from duplication-deficiencies which might otherwise be confused.

It has been possible to isolate the differential chromosomes from *G. arboreum*, which form the ring of four and the ring of six with *G. hirsutum* chromosomes, in *G. hirsutum* background. Likewise, the differential chromosomes from *G. herbaceum* which form one of the two rings of four with *G. hirsutum* have been isolated. In crosses with induced translocations, it is possible to determine when two multi-

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**Figure 14.** Chromosomes of three species and diagrams of multiple associations formed in hybrids.

**Haploids**

Occasionally, perhaps once in about 50,000 or 100,000 times, one Upland cotton seed contains twin seedlings. Usually one seedling is normal and the other is very small and weak-growing. Small twin seedlings are often fatherless plants with just half the normal number of chromosomes. These plants, with just one complete set of genes and chromosomes instead of the normal two sets, are called haploids. Haploids are of great genetic interest because their chromosome number can be doubled by the use of the drug colchicine to produce genetically pure, true-breeding strains of cotton. These doubled haploids can be maintained and multiplied

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8Conditions in which a part of one chromosome becomes attached to another (non homologous) chromosome.

9Reproductive cells.
valent configurations have chromosome ends in common and when they involve completely independent chromosomes. In this manner, it is possible to arrive at tentative designations by number of the chromosome ends of tested translocations. To obtain the observed multivalents in *hirsutum-herbaceum* and *hirsutum-arboresum* only five chromosome parts are involved. The arms of the first five chromosomes have therefore been numbered as shown in Figure 14.

These particular multivalents, since they are known to involve chromosomes from the Asiatic species, serve to identify other chromosome arms pairing directly with them as also being A chromosomes. Examples of how such tests are made are given in Figure 15.

![Diagram of chromosomes with numbered ends and multiple associations formed when certain known chromosomes are combined.](image)

Figure 15. Diagram of chromosomes with numbered ends and multiple associations formed when certain known chromosomes are combined. (a) Heterozygous 2B-1 translocation. (b) Homozygous 2B-1. (c) Homozygous duplication-deficiency from 2B-1. (d) Multiple association formed when one D chromosome pairs with (c). (e) *hirsutum-herbaceum* ring of 4. (f) Multiple association formed from (b) x (e).

### Induced Translocations

Rearrangements of chromosome segments, recognized by the association of four or more chromosomes at metaphase of meiosis, have been recovered following irradiation of seeds by x-rays, gamma rays and neutrons. Similar changes have been produced by treatment of the growing plant with radioactive cobalt. Less frequently, spontaneous changes in chromosome rearrangement have been recovered.

One induced translocation has been of particular interest in the identification of chromosomes. It is a very unequal reciprocal translocation, which gives an asymmetrical configuration at metaphase when heterozygous (Figure 15(a)). Because it is viable when homozygous (Figure 15(b)), all outcrosses carry the translocation as heterozygotes, which means that only small progenies need be grown and analyzed.

### Identification of Chromosomes

To determine whether A- or D-genome chromosomes were involved in the translocation 2B-1, a homozygous duplication deficiency (Figure 15(c)) from 2B-1 was crossed to *G. raimondii*, a diploid species of the D genome. In this cross, pairing took place between 2B-1 and one of the D chromosomes of *G. raimondii* to form a trivalent with the large translocated fragment (Figure 15(d)). From this configuration, it was known that one of the 2B-1 chromosomes was a D chromosome; the other must therefore be an A chromosome. Had both chromosomes in 2B-1 been A chromosomes, or both D chromosomes, the pairing would have been otherwise.

When homozygous 2B-1 (Figure 15(b)) was crossed to the ring of four chromosomes isolated from *hirsutum-herbaceum* (Figure 14), an asymmetrical chain of six chromosomes was observed (Figure 15(f)). This association showed that the A chromosome in 2B-1 was one of the chromosomes involved in the *hirsutum-herbaceum* ring of four.

Since both chromosomes of 2B-1 have been assigned to their respective genomes, and the chromosome arms have been numbered, this translocation, and others with known chromo-

*Biological processes preceding the formation of gametes.*
some ends, are being used as standards for identifying additional chromosome rearrangements.

MECHANICS OF INTERSPECIFIC INHERITANCE

It is important to know how the desirable characters from the wild species are inherited in backcrosses to cultivated cotton. This is the most technical and the least explored aspect of the problem of transferring characters from one species or type to another. While the mechanics of inheritance within a given species are well known, interspecific hybrids are still enigmatic from this point of view. To understand their inheritance attention must be focused on the genetic characters in question and at the same time on the behavior of the chromosomes involved. Study often is complicated by the formation not only of pairs but of associations of many chromosomes (Figure 7c) which, of course, affects the transmission of genes located in them. To simplify the construction of a model of inheritance in various interspecific combination, characters which are controlled by single genes are used. Some such characters are petal spot (Figure 16), or

petal color, leaf shape, lint color, etc. Thus far, these studies have enabled the geneticist to distinguish between certain hybrid combinations which permit a reshuffling of the genes with relative ease and others which are more refractory. These investigations give an idea of the frequency with which new combinations of characters can be expected and which species combinations may be most useful.

Segregation in Amphiploids

One phase of interspecific hybridization is concerned with the amount of recombination between the genes of the two parent species of fertile polyploid hybrids. It is assumed that this recombination is a function of the amount of interspecific chromosome pairing which occurs and therefore of the degree similarity, or homology, of the chromosomes of the parent species. Such studies have considerable theoretical interest, as they reflect upon the evolutionary divergence of the various species of Gossypium, and the kind and amount of changes which have taken place in the evolution of the genus. They also are of practical import as they permit predictions of the frequencies with which desirable recombinations (e.g., G. hirsutum yield factors and lint strength genes from G. thurberi) can be obtained in the initial breeding populations. A sizeable body of data has been accumulated; these indicate that there is no hindrance at all to random recombination of the chromosomes of G. arboreum and G. herbaceum since the amphiploid segregates in a strictly Mendelian fashion (gametic ratios approximately 5:1 for five loci investigated). In contrast, amphiploids between G. hirsutum and G. anomalum were almost stable and permitted the extraction of only rare recombinants (5 loci). Other combinations produced ratios between these two extremes; the gametic output from G. hirsutum-raymondii amphiploids varied between 8:1 and 12:1 (5 loci) while that from 6n G. hirsutum-thurberi gave much wider ratios ranging from 24:1 to 47:1 (2 loci). The genetic results have been corroborated by cytological evidence as the number of multivalent figures, which were necessarily composed of chromosomes from both parental species, was proportional to the amount of genetic segregation. This indicates that the much more economical cyto-

Figure 16. Petal spot segregation in a hybrid involving G. raymondii.
logical study of allopolyploid combinations may be substituted for the genetic investigation of segregation intensities in amphiploid hybrids where breeding results are the object.

GENETIC INVESTIGATIONS

Fundamental studies on the inheritance of various characteristics of cotton provide information and materials that make the work of breeding better varieties more effective. The cotton geneticist deals largely with observable or measurable differences among plants growing in the field, nursery and greenhouse. Examples of common agronomic characters of the cotton plant are yield, boll size, lint percentage and leaf shape. Differences exhibited among plants in respect to a character, or a group of characters, result from variations in the environment (soil, rainfall, fertilizer, etc.) in which the plants are grown or the differential action of genes and chromosomal irregularities, or both. Distinction between environmental and genetic factors in the evaluation of characteristic differences among plants is one of the major problems of the geneticist. If a character is conditioned by one gene (or perhaps two or three) it is said to be simple or qualitative in its inheritance; if it is conditioned by several or a large number of genes it is said to be complex or quantitative in its inheritance. Thus, another primary problem of the geneticist is to determine by genetic analysis whether a given character is inherited according to the qualitative or the quantitative scheme.

In cotton there are several instances of complexes of minor genes (called modifiers) which give the quantitative type of genetic expression and which act to modify the expression of a major gene which is inherited in a simple fashion. Experiments conducted under this project have contributed to a better understanding of the nature and function of modifying complexes and have provided useful guides to more efficiency in breeding programs.

SIMPLE MENDELIAN CHARACTERS AND MARKER STOCKS

Most of the simply inherited characters that have been recognized so far in cotton are of little or no economic value.

Notable exceptions are certain characters for resistance to the fusarium wilt and bacterial blight diseases. Qualitative characters, though they would be called freaks or rogues in a commercial field, are highly prized by the geneticist. Study of their genetic action affords a better understanding of the behavior of those economic characters which are controlled by a large number of genes. Furthermore, simple characters are valuable as markers of chromosomes; they afford a method of identifying the effects of genes carried on specific chromosomes which contributes greatly to practical plant

Figure 17. Examples of cotton characters which are inherited in a simple Mendelian manner. a. okra leaf, b. cup leaf, c. cluster, and d. crinkled mosaic.
breeding. Examples of several such characters are shown in Figure 17.

More than a dozen new qualitative characters have been analyzed since this project was initiated. These have contributed to studies of linkage or association with an extensive list of other simply inherited characters discovered by earlier workers. Considerable progress has been made in the establishment of multiple marker stocks which combine two or more qualitative characters into one pure breeding plant or family of plants, thus providing useful and economical stocks for more complex genetic research. For example, (1) linkage tests are made to determine the degree of association of characters or whether the genes responsible for the characters are located on different chromosomes or on the same chromosome; (2) the ratios in which the characters are recovered in certain interspecific hybrids reveal the complex inheritance in such material and furnish information on how to handle characters in practical breeding programs; (3) where the chromosomes are actually observed under a microscope, it has been possible to associate a particular genetic character with a certain chromosomal configuration, and thus tag a specific chromosome with a known marker gene.

Cluster Growth Habit

Genetic analysis of 13 stocks which exhibited a cluster growth habit showed that they could be divided into two classes or groups. In one the fruiting branches terminate in a cluster of two or more fruit forms apparently arising from the same nodal position, and in the other the fruiting branches are shortened and usually a few normal and a few shortened nodes arise alternately on the main stem. There were six stocks in the first or "true cluster" group and seven in the second or "semi-cluster" group.

There was evidence of a single gene for true cluster and another for semi-cluster and the two appear to be allelic\(^9\) with semi-cluster dominant.

The semi-cluster growth type has become increasingly more important during recent years as interest increases in types of cotton adapted to harvesting with the mechanical stripper. If, as indicated here, the semi-cluster type is the expression of a single gene, the plant breeder has at his disposal a valuable character that is relatively simple to handle in developing new stripper types of cotton.

Dwarf

Four Upland dwarfs, Shafter red-dwarf, Simpson red-dwarf, Ligon-lintless dwarf and York-mutant dwarf, were tested for allelomorphism by intercrossing and by outcrossing the F\(_1\)'s to a very tall, upright parental stock. (For examples, see Figure 18). There was some evidence that the first two of the stocks listed were conditioned generally by the same gene, but it appears that the other two were non-allelomorphic with each other and with each of the two red-dwarfs. Modifier action possibly differentially affected the size of the dwarfs. Where "normal" cotton plants grew to a height of 36 inches, the Simpson red-dwarf averaged 12 inches or less and the York-mutant dwarf about 24 inches. The other two ranged between these limits.

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\(^9\)An allele is an alternative form of a gene.
Red Plant Color

An allelomorphic study of the 13 plant color lines (Arizona red plant, DeRidder red leaf, intense red plant, intense red okra leaf, McNamara winesap, Mississippi red leaf, New Mexico red leaf, Oklahoma purple leaf, Acala red plant, red okra green covered seed, red okra nankeen naked seed, Sacaton winesap and Stoneville red plant) revealed that red plant color in each of the 13 stocks is conditioned by the same major gene. Visible differences in intensity of red color around the lines appear to be results of modifiers.

Louisiana Brown Lint

Louisiana brown lint, an Upland stock found among the Acadians of Louisiana, contained two types of seed cover, fuzzy (covered) and non-fuzzy (naked). This naked-seed character is recessive to covered. Earlier work indicated that the recessive, naked-seed character of the Louisiana brown lint was monogenic, but further study has shown that two or more genes are involved. Modifiers presumably are responsible for the higher level of lint quantity in recessive Louisiana brown than that found in dominant naked-seeded stocks. These modifiers for lint quantity may be of practical value when transferred to commercial cottons.

Delta Smooth Leaf

Inheritance of leaf pubescence has been studied in crosses involving Delta Smooth Leaf, a variety of Upland cotton with relatively few leaf and stem hairs, with normally pubescent Upland varieties. Results suggested a 3:1 ratio although variation in the segregating generations was discontinuous. It was concluded that a major gene dominant for high pubescence was involved, and that modifying genes caused the discontinuous variation. The frequency of recovery of extreme smoothness varied with different pubescent parents and in one case no segregates as smooth as Delta Smooth Leaf were recovered.

INHERITANCE OF COMPLEX (QUANTITATIVE) CHARACTERS

Research in the field of quantitative inheritance has been greatly increased and accelerated under this project. Since the lint or fiber is the most valuable product of the cotton plant it is not surprising that many of the experiments have involved the genetic analysis of such fiber characters as lint percentage, length, strength, fineness and maturity. Studies also have been conducted on boll size, maturity, growth habit and plant type. These experiments have involved both intervarietal and interspecific hybrids. They have yielded information on gene action, heritability and associations among characters which is needed in planning and conducting practical breeding programs.

Statistical analysis of the variability of several important economic characters in parental lines, and in hybrid combinations, has provided a body of information from which more reliable estimates can be made of the progress to be expected when a given character is selected in successive breeding generations. Such information also makes it possible to compare the efficiencies of alternative selection procedures. In most cases characters studied in crosses between species give the same general pattern of genetic behavior as found in crosses between varieties. However, the interspecific material differs from the intervarietal material in several important respects, particularly in the probability of occurrence of recombinations of desired characters and the rate of genetic advance.

FIBER PROPERTIES

A wide range of variability in fiber length, strength and fineness exists in cotton. There are the short, coarse cottons of Asia and the long, fine cottons of Egypt. American Upland varieties fall somewhere between these two extremes. At a lower level of magnitude there is considerable variation among the Upland varieties in respect to fiber properties. The species hybrids and primitive cottons add to the total genetic variability in the genus, Gossypium.

It is difficult to predict what "new" combination of fiber properties would result in improved spinning performance and higher quality end products. As a beginning certain primary stocks with unique combinations of fiber properties are being developed. As these objectives are reached, the quality
of the cotton is evaluated in manufacturing performance tests. The performance tests furnish sound breeding objectives, and the primary stocks serve as basic material to be used by plant breeders in an attempt to develop commercial varieties with improved quality. The relative values of fiber length, strength and fineness for a commercial variety of American Upland cotton and six types in process of development as shown in Figure 19.

An experimental strain, Able-51, with a Pressley Strength Index of about 10.75 was developed by backcrossing and selection from *G. arboreum-thurberi-hirsutum* hybrid. A cross was made between Able-51 and Empire, a commercial variety of *G. hirsutum*, and appropriate populations were grown for a study of the inheritance of lint strength, lint length, lint fineness, lint percent, seed index and lint index. All charac-

![Figure 19. Graphic comparison of seven fiber types extracted from interspecific hybrid material.](image)

ters gave a quantitative type of inheritance indicating that several genes were involved in each.

### Inheritance of Fineness of Fiber in Upland Cotton

A genetic analysis was made of both perimeter and wall thickness of fiber in a cross between a very coarse fibered strain, Florida 1377, and a very fine fibered strain, DPL 45-867. The components of fiber fineness were measured by means of the arealometer. The Florida 1377 parent proved to have larger perimeter (mean = 55.8) and thick fiber walls (mean = 4.62) while the fine fibered DPL 45-867 had medium perimeter (mean = 48.0) and thin fibered wall (mean = 2.40). The segregations observed indicated quantitative inheritance of fiber perimeter. A heritability estimate of 51 percent was obtained from regression of means of the 56 *F*<sub>3</sub> lines on their respective *F*<sub>2</sub> phenotypes. This heritability estimate is sufficiently high to permit effective selection for large or small perimeter among single plants. As was the case for perimeter, inheritance was quantitative and heritability of wall thickness was moderately high, being estimated as 43 percent from regression of *F*<sub>3</sub> means on *F*<sub>2</sub> phenotypes. This indicates that selection for any degree of wall thickness among single plants, as in *F*<sub>2</sub>, should be reasonably effective in obtaining lines with the desired wall thickness.

Although a low but significant negative correlation occurred between perimeter and wall thickness of fiber in *F*<sub>2</sub>, there was no correlation between these two traits among the *F*<sub>3</sub> lines. Consequently, it was concluded that no genetically controlled association existed between perimeter and wall thickness.

### Inheritance of Fiber Density on the Seed in Upland Cotton

Relative density of fibers on the seed is of considerable importance because of its relationship to fiber production. It plays a major role in the expression of such conventional traits as lint percentage and lint index. A low but highly significant positive correlation was found between density of fiber, called lint density index, and yield of lint per acre. Lint density index was expressed as the weight of fiber in grams from 100 square centimeters of seed surface.
Among varieties and strains of Upland cotton, lint density index varies from about 3.5 to 6.0. Several genetic studies have been made of the behavior of this trait in crosses between parents which differed considerably in lint density. Results of the various studies have been in general agreement. The following conclusions have been drawn, usually based on results of three or more experiments:

1. Lint density index is a typical quantitative character, with absence of dominance and strong influence of environment.

2. Large parental differences appeared to be governed by a comparatively small number of genes.

3. Heritability of lint density index, based on regression of F₃ line means on F₂ plant values has been approximately 50 percent, indicating that about half of the variation among single plants is genetically controlled.

4. Lint density index is a major component of lint percentage and lint index. High positive correlations are found consistently among these traits.

5. Differences in lint density among plants, lines or strains are due almost entirely to variations in number of fibers per unit of seed surface area and variations in fiber length and weight fineness have no detectable influence.

**RESPONSE TO LENGTH OF DAY**

Many primitive cottons brought to the United States from Central America fail to set fruit when grown during the long days of summer in Cotton Belt latitudes. These cottons will fruit when grown during the short days of winter in the greenhouse. Such types commonly are called short-day, or photoperiodic, plants. Other cottons, such as the cultivated American Upland varieties, are not sensitive to the changes in length of day between summer and winter. Such types are called day-neutral cottons. The photograph in Figure 20 shows what happened when a short-day cotton, *G. hirsutum* var. marie-galante, and a day-neutral stock, Deltapine 14, were crossed and a study made of photoperiod response during the summer growing season:

Figure 20. Flowering response of a cross between a day-length sensitive stock and a commercial Upland variety during the long days of summer in the American cotton belt. (a) Sensitive parent *marie-galante*. (b) Day-neutral Upland parent. (c) F₁ hybrid. (d) Range of flowering in F₂. (e) F₁ backcrossed to *marie-galante*. (f) F₁ backcrossed to Upland variety.
G. hirsutum race marie-galante set no fruit during the long days of summer. The commercial Upland parent was not sensitive to length of day and set fruit normally. The F₁ hybrid produced an occasional flower. The F₁ hybrid crossed back to marie-galante produced no fruit. The F₁ hybrid crossed back to the commercial Upland flowered normally.

Although no simple genetic explanation can account for these results, the experiment demonstrated that flowering response is inherited and that short-day plants can be used in a breeding program in the Cotton Belt.

GENETICS OF DISEASE RESISTANCE

The breeding of disease resistant varieties is considered the most practical method of combating plant diseases. Resistance to several cotton diseases has been found and, particularly in the cases of fusarium wilt and bacterial blight, the resistance has been established in commercial varieties. There are, however, a number of diseases which cause economic damage to cotton for which satisfactory resistance either has not been found or has not been transferred to productive commercial varieties. Since even the disease resistant varieties are never completely resistant or immune, there still exists a need for additional types and expressions, and a better understanding of the nature of resistance.

The regional cotton collections offer the best known material in which to search for disease resistance characters. This material is being screened as rapidly as facilities and finances will permit and fundamental information on the genetics of disease resistance is being developed in cooperation with plant pathologists.

The Search For Nematode Resistance

The fusarium wilt-nematode complex of cotton has long been considered the most serious disease of cotton in the rainbelt. This disease causes losses in the lighter soils from Virginia to the 40-inch rainfall line extending north and south through East Texas. Breeders have reduced serious wilt losses by developing wilt-resistant varieties. Further progress in improving resistance to these diseases is consider-
ed possible in most areas by improvement in nematode resistance, particularly root-knot resistance. Root-knot-nematode resistance also is needed in certain areas of the irrigated southwest where yields are reduced in the sandier soils.

The S-1 collection of species, sub-species and varieties was tested on a heavily infested soil at the Plant Breeding Unit at Tallahassee, Alabama, in an attempt to discover a better source of root-knot resistance for improvement of commercial varieties. One promising source of high root-knot resistance was discovered in a line of G. barbadense var. darwinii. This line was hard seeded and had a short-day flowering habit. However, it crosses readily with commercial types and a breeding program is well underway to transfer the resistance. The distribution of both wilt and root-knot resistance in cotton was determined in these studies.

Among a large number of varieties and strains tested for resistance to root-knot nematode under field conditions in Louisiana, Clevewilt 6 appeared to be the most tolerant. Data obtained from a cross of this variety with a susceptible stock, Deltapine 15, under greenhouse conditions indicated that inheritance of root-knot nematode resistance probably is quantitative in nature and that heritability of reaction is low.

Fusarium Wilt

Resistance to fusarium wilt appeared to be controlled by a single major gene and a number of modifiers in a cross of Half and Half (susceptible) and Delfos 425 (resistant). Delfos 425 is highly resistant to wilt under exposure to surface feeding nematodes, but is susceptible under root-knot nematode conditions. No root-knot nematodes were present in the soil used in this study. It appeared that the modifying genes contributed to the high resistance of Delfos 425, and they would require attention in a breeding program.

Bacterial Blight

Three pure breeding lines of cotton resistant to the bacterial blight disease were intercrossed and outcrossed to susceptible stocks to determine the genetics of the character. Inter crossing demonstrated that the same genic make-up conditioned resistance in each of the three lines. The outcrosses
showed that one major gene was involved, susceptibility being dominant. Though none of the lines is advanced sufficiently in yield and other economic characters to qualify as an agricultural variety they and their derivatives provide a new source of breeding material with a high degree of resistance to bacterial blight.

**CHARACTER TRANSFERENCE, BREEDING METHODOLOGY AND THE DEVELOPMENT OF PRIMARY BREEDING STOCKS**

The variability present in and among cotton species, primitive types, non-commercial stocks and foreign varieties presents the possibility of developing valuable primary breeding stocks by the transference of characters to cultivated Upland types or by desirable recombination of characters through special hybridization schemes. Research in this field involves (1) the location of characters of economic value, (2) determination of the fertility of the hybrids and the mode of inheritance of the characters in question, and (3) the devising of techniques and methods for the transference and recombination of the desired characters.

A considerable part of the research under the Regional Project S-1 has been devoted to an attack on fundamental breeding problems in interspecific hybrids. A number of species combinations have been made and their progeny searched in varying degrees for characters of economic value. To date the greatest effort has been spent on the investigation of certain fiber properties and disease resistance characters in a hybrid which combines three species (American Upland, Arizona Wild and Asiatic Cultivated). From this and other hybrids investigated it has been learned that the experimental methods to be employed in character transference and recombination must be adapted to the character and hybrid in question.

**D₂ Smoothness**

It has been possible to transfer a satisfactory degree of leaf smoothness from a wild American species, *Gossypium armourianum* (D₂), to a productive Upland type by orthodox backcrossing methods. Plants with D₂ Smoothness have smooth (hairless) stems, leaves and bracts (Figure 21). The character is conditioned by one dominant gene; it is easy to use in a cotton breeding program and may help in solving the trash and lint-cleaning problems of mechanically harvested cotton. D₂ Smoothness is not closely associated with any obvious deleterious plant, seed or lint characteristic. Although this new characteristic was first found in 1951 it is already established in fairly good agronomic strains. Seeds and pollen have been released to cotton breeders and geneticists.

**Deciduous Bract**

Much of the foreign matter in hand-picked cotton, and more especially in mechanically harvested cotton, is bract trash. Types which shed their bracts (Figure 22) have been extracted from interspecific hybrid material. These hybrids involve Upland cotton, an Asiatic cotton, and the wild, lint-
less American species, *G. armouriannum*, which normally sheds its bracts. Deciduous bract is conditioned by one recessive gene. Progress has been made in moving this character from the original hybrid into commercial varieties of Upland cotton. In addition to reducing the amount of bract trash in cotton lint, this characteristic possibly may aid in the control of pink bollworm.

**Selection Indices**

The development of selection indices which may improve substantially the precision and efficiency of cotton breeding techniques is the primary objective of a series of investigations being conducted. Various selection indices have been constructed, several of which may enable cotton breeders to increase their efficiency of selection for a trait such as yield by as much as 15 percent. To develop and evaluate such indices, experiments have been designed to provide information on the magnitude, nature and interrelations of the genetic and environmental variations in the various plant characters under consideration. In addition to yield, the traits being studied include its quantitative components and certain fiber properties.

Environment greatly influences the expression of a trait such as yield, making it necessary to evaluate material over a series of locations and years to identify correctly the superior yielding genotypes. Other traits such as lint percentage, seed index, lint index and the various fiber properties are quite highly heritable, however, and may be selected for rather efficiently on an individual plant or single plot basis. Genotypic correlation studies have shown that certain of these latter traits are associated closely with yield performance; thus, such traits, which may be influenced less by environment than is yield itself, may well serve as better indicators of high yield than yield measurements *per se*.

### Association of Economic Characters With Yield of Fiber

Approximately 100 randomly chosen F3 lines from a cross between the Wilds and Half and Half varieties grown in a replicated field design were measured for yield of fiber and for the following characters which were presumed to be components of yield: (1) number of bolls per acre, (2) number of seeds per boll, (3) seed index, (4) lint index, (5) lint percentage and (6) lint density index. The objective was to discover an index (or component) of yield which was affected less by environment than is the per acre yield of fiber at the end of the season and would, therefore, be a more reliable indicator of true (genetic) yield. While three characters (number of bolls per acre, seed index and lint percentage) were significantly associated with yield, only lint percentage can be considered less subject to environmental influence than is yield itself. Selection for high lint percentage, therefore, may be expected to result in higher yield in these experiments.

A significant negative correlation was found between yield and fiber length, indicating it would be difficult to obtain a high yielding strain which possessed the fiber length of the Wilds parent. On the other hand, there was no association (a non-significant correlation coefficient) between yield and strength of fiber, indicating there should be no
special difficulty in combining the fiber strength of Wilds
with high yield.

**Effect of Recurrent Selection on Gene Frequency**

Recurrent selection is a procedure that has been used
effectively in corn breeding to increase the frequency or
concentration of superior genes in a heterozygous population
without rapid loss of genetic variability. Within a few years
recurrent selection has become a commonly used, important
technique in corn breeding. On the basic of genetic theory,
the method also seemed sufficiently promising for cotton to
warrant fundamental studies for measuring its effectiveness
in modifying gene frequency.

Studies with one cycle of recurrent selection have been
completed for two crosses. The economic characters segre-
gating in these crosses included fiber length and strength, lint
percentage, and seed size. The major results were:

1. In both crosses the average level of expression of the
characters involved was considerably higher in the recurrent
selection population than in F2.

2. The various intercrosses among F2 lines varied greatly
in superiority. Some intercrosses were distinctly superior
to all others. If recurrent selection is used as a tool in cotton
breeding, selection should be confined to the few outstanding
intercross populations.

3. The selection of parents for intercrossing will be
more effective if based on a progeny test rather than on
individual plants.

4. Properly applied, recurrent selection should be a
highly effective method in cotton breeding, especially for
crosses in which the parents differ in respect to a large num-
ber of important genes.

**Pedigree and Recurrent Selection**

High fiber strength derived from species hybrid material
tends to be associated with small bolls, low lint percentage,
nonfluffy locks and low yields. In an effort to eliminate
undesirable features and to develop strains with combina-
tions of good agronomic properties, various breeding sys-
tems have been used. Two years of pedigree selection were
more effective in moving the mean of fiber strength, in both
high and low directions, than one cycle of selection and inter-
crossing by the recurrent selection procedure. However,
pedigree selection for high fiber strength resulted in plants
with longer lint, finer lint, smaller bolls, lower lint percentage,
less fluffy locks and lower yields than selections for low
fiber strength. All plants and fiber properties were fixed
in relatively homozygous lines by pedigree selection, while
recurrent selection preserved a "pool" of variability of eco-
nomical characters which provides opportunity for further
selection of desirable combinations.

**Methods of Pollination**

Six varieties were self-pollinated by the following meth-
ods or devices: wire strung tags, kraft paper bags, and
cloth bags. Self-pollination by these methods was compared
to normal open-pollination and to open-pollination plus hand
pollination with "foreign" pollen. There was little difference
among the methods of self-pollination in terms of percentages
of flowers set, but the self-pollinated group averaged 13% less than the open-pollinated group. The introduction of
"foreign" pollen, which apparently fortified natural pollina-
tion, consistently gave a small increase in the percentage of
flowers set. The self-pollinated group averaged seven seeds
per boll less than the open-pollinated group. The degree of
inbreeding in this preliminary study was not associated with
the percentage of flowers set or the number of seeds per
boll. It was concluded that self-pollination reduced both the
percentage of flowers set and the number of seeds per boll.
This reduction in seed number was associated more with the
method or mechanics of self-pollination than with inbreeding
alone. The small increase over natural open-pollination when
"foreign" pollen was applied tends to bear out this conclusion.

**Primary Breeding Stocks**

As a direct result of experiments planned for the specific
purpose of developing stocks with new or improved economic
characters, or as "byproducts" of basic genetic experiments
involving useful economic types, several primary breeding stocks are available. In these stocks one or more new or improved fiber properties, leaf characters, boll types, plant structures or disease resisting characters are established in relatively true breeding lines. The production, vigor and other agronomic characteristics of these lines vary considerably. In all cases, however, the stocks are fully fertile in crosses with cultivated Upland varieties. They show significant improvement in all economic characters when compared with the early generation material from which they were extracted. Several of the new primary stocks are being tested in yield trials. Though few if any will prove suitable for direct release to farmers as agricultural varieties, they will serve as the nucleus of an increasing reservoir of special characters from which plant breeders, both public and private, may obtain up-graded breeding material.

**INSTRUMENTATION**

Research designed to develop new methods, improve established methods and to test alternative methods is an essential part of this project.

Workers at the Tennessee Agricultural Experiment Station have had major responsibility, under this project, for developing instruments and machines for testing and evaluating various properties of cotton fibers. Since this project has been in operation these workers have: (1) improved the Arealometer, an instrument for measuring the fineness or coarseness of cotton fibers, (2) developed the Stelometer, for determining the strength and elongation of cotton fibers, (3) developed the Speedar, for rapid measurements of fiber fineness and compressibility and (4) developed the Lint Percener for determining the percentage of lint (fiber) obtained from a given sample of seed cotton without the necessity of determining the separate weight of seed cotton or the lint and seed fractions. The instruments provide a means of evaluating new or unusual fiber properties and having been designed to handle small samples rapidly, make it possible to increase greatly the amount and scope of genetic research on the inheritance of fiber properties.

Figure 23. Fiber testing instruments. (a) Arealometer. (b) Stelometer.
Arealometer

The fineness and cross-sectional shape of cotton fibers are measured on the Arealometer, Figure 23a. A predetermined weight of cotton is placed in the instrument and compressed until its resistance to the flow of air through it matches a standard resistance. The fineness of the plug of cotton then is read from a calibrated drum. When the cotton is matched with a higher resistance, there is an apparent but spurious increase in fineness. The difference between the readings at the two compressions is a measure of the immaturity or shape of the fibers. From these two measured properties, fineness and immaturity, approximate values of other properties such as weight per inch, perimeter and wall thickness may be calculated.

Stelometer

The Stelometer, Figure 23b, is a pendulum-type fiber bundle breaker, equipped with scales to read force to break and elongation at break. The head is adapted to accept standard Pressley clamps at both zero and 1/8 inch jaw spacings. The constant rate of loading is controlled by a hydraulic cylinder attached to the frame.

Speedar

The Speedar, Figure 24a, is an air flow instrument for measuring the fineness and compressibility of cotton. The instrument furnishes its own air supply by means of a weighted piston falling in a cylinder. Samples between 5 and 10 grams may be tested by a simple adjustment which changes the size of the cotton chamber to fit the sample size. The fineness scale is calibrated in units of area fineness—i.e., square millimeters of surface area per cubic millimeter of fiber volume, but can also give readings in terms of any other comparable fineness units or fineness index. The packing modulus scale indicates the force necessary to compress the sample to a standard density.

Lint Percenter

The Lint Percenter, Figure 24b, is a balance calibrated in percentage. A sample of ginned lint is hung on the hooks

Figure 24. Fiber testing instruments. (a) Speedar. (b) Lint perc.
on one arm of the balance while the seeds from which it was
ginned are placed in a pan attached to the other arm. The
scale indicates directly the percentage of lint, thus eliminating
the time-consuming weighings and calculations required in
the methods now being used.

ANNOTATED BIBLIOGRAPHY

The number and quality of scientific papers is one of
the most reliable measures of progress under a fundamental
research project. Regional Research Project S-1 has been
exceptionally productive in this respect. Papers and theses
reporting research conducted wholly or in part under this
project are listed below. An annotation accompanies each
reference to provide somewhat more information on the na-
ture of the research reported than may be gained from the
title alone.

ALI, MAHBUB. The effect of reciprocal crossing on the cytological
and morphological features of G. hirsutum and G. barbadense hy-

The direction of a cross did not affect morphological charac-
ters or chromosome pairing as a general rule. There were
several cases where reciprocal crosses differed significantly
but the differences were not of great magnitude.

BISHR, M. A. Inheritance of perimeter and wall thickness of fiber
in a cross between two varieties of Upland cotton. Ph. D. Disserta-
tion, Louisiana State University, 1954.

The genetic analysis of the two components of fiber fineness—
perimeter and wall thickness—in a cross between a fine fibered
strain, DPL 45-867, and a coarse fibered strain, Pla. 1377, is
reported. Analysis in F<sub>2</sub> showed that the apparent negative
correlation between these characters in F<sub>2</sub> was non-genetic.

BRADFORD, W. W. An inheritance and cytological study of angular
leaf spot resistance in the F<sub>2</sub> generation of a Gossypium three-

In F<sub>2</sub> progenies of G. arboreum-thurberi-hirsutum the number
of days required for appearance of disease symptoms was found
to be closely correlated with final disease grade. The results
indicated that resistance was due to one pair of dominant major
genes which was influenced by modifiers in this complex hy-
bрид.

BREAUX, R. D. A genetic analysis of the major components of yield
University, 1954.

A study of four yield components was made in an F<sub>2</sub> population
consisting of 98 lines derived from a cross between the Wilds
and Half and Half varieties. It appeared that selection for
high lint percentage among single plants and lines would have
been effective in selecting high yielding lines while selection
for large seed would have reduced yield.

Fertile branches, in which the number of the chromosomes was doubled, developed without treatment on two otherwise sterile F₁ hybrids of Gossypium. The new forms are comparable to new species, which combine the characteristics of the two parent species.


New 52-chromosome hybrids which combine three species of Gossypium were obtained by crossing 78-chromosome hybrids of American and Asiatic cultivated with wild 26-chromosome species. Several hybrids have chromosome complexes similar to those of American cultivated and provide new breeding material.


The crossing behavior of a newly introduced Mexican wild species, G. gossypioides, is reported.


G. gossypioides, a wild species which gives inviable hybrids with many species, gives viable hybrids with G. raimondii. Leaf shape and color of pigment glands offer proof that the plants are hybrids. The hybrid nature of plants of another cross which die early is shown by the color of glands in the cotyledons.


Chromosome pairing is described in hexaploid (78-chromosome) hybrids of American cultivated (52-chromosome) x each of nine diploid (26-chromosome) species, and in 17 combinations of two diploids.


Plants homozygous for red leaf color yielded less than the heterozygous plants, and the homozygous green plants yielded more than the two pigmented classes. Plants with fuzzy seed yielded more than plants with naked seeds.


The meaning of cotton fineness and immaturity, and of how the arealometer measures them, is discussed.


A study of seed size in two crosses between the very large seeded Tuxulta variety and the small seeded varieties Half and Half and Delta Smooth Leaf is reported.


The effectiveness of the pedigree and recurrent selection systems of breeding for high and low fiber strength is compared in progenies derived from the three-species hybrid, G. arboreum-thurberi-hirsutum.


For estimates of the amount of natural crossing among genetic stocks of cotton in an isolated plot to be unbiased, the population of pollen vectors operating therein must be assumed to be operating at random. Three independent lines of evidence are presented which verify this assumption.


Genetically unlike stocks of cotton differed significantly in amounts of natural crossing. Techniques for measuring such differences are presented and discussed.


In controlled pollinations, pollen from certain genetic stocks seems to be superior to other types in effecting fertilization. Results also are presented concerning the effects of applying different types of pollen on the same stigma at different time intervals.


From a study of G. herbaceum, G. arboreum, G. anomalum, G. hirsutum and their hybrids, it was concluded that G. arboreum
is an evolutionary side branch rather than the progenitor of American Upland cotton.


Hybrids between a strain of G. arboreum and Upland die around blooming time, but the expression of the lethal character depends on temperature.


Fingernail polish is suggested as a sealer for microscope slides.


Artificial polyploids supply sensitive material for genetic studies of homologies and structural dissimilarities of species.


The inheritance of the factors causing "red lethals" in Asiatic-Upland cottons is analyzed. Because of sterility complications polyploids are used and segregation patterns of artificial polyploids are described. The function of interspecific lethals in isolating species is discussed.


The range in lint length, strength, and fineness, and in seed index, and lint percentage in strains of Upland cotton in the regional collection is described.


A new member of an allelic series including normal, okra, super okra, and Sea Island leaf shapes is described and given the name sub-okra. The locus is identified with the D genome.


A simply inherited abnormal bract type, useful as a genetic marker, is described.

HERTEL, K. L. Fiber strength and extensibility as measured by the Stelometer. The Cotton Research Clinic. (A research publication of the National Cotton Council of America), 1953.

Some of the difficulties connected with accurate determinations of breaking strength and elongation of fiber bundles are dealt with. The Stelometer was designed to overcome some of these difficulties, and some results obtained with the instrument are given.


The development of the Arealometer is reviewed. The principles and methods used in calibrating it to measure surface fineness and immaturity of cotton are described in detail.


The development of the Speedar, a self-contained air flow instrument for rapidly measuring the area fineness of cotton and its compressibility or packing modulus, is described.


Data in F2 from a cross of Delta Smooth Leaf with Stoneville 2-B indicated segregation for one major pair of genes, with dominance of pubescence, and one or more minor or modifying genes for the smooth leaf condition.


The relation of yarn strength to twist multiplier was determined for various cottons whose length, fineness and frictional properties had been measured.


The development of a chart for finding the twist multiplier which will produce yarn of maximum strength is discussed. The chart shows the relationship between the twist multiplier, mean length and fineness.


The F2 and F3 progenies of G. arboreum-thurberi-birsutum were extremely variable in plant habit, seed cotton production,
and all lint properties. There is an opportunity to develop from this material new combinations of lint length, strength, and fineness which should be stabilized into relatively true breeding stocks.


A mutant was designated cup leaf because the adaxial surface of the leaf curved into a concave form. Cup leaf is controlled by a single incompletely dominant gene which is independent of the gene for frigo bract.


In intraspecific backcrosses involving certain marked stocks of G. hirsutum, the marker genes were recovered as expected on the basis of random recombination. The pubescent gene, Pb, was independent of the genes for red plant body, okra leaf, petal spot, brown lint, and naked seed.


Significant deviations in the recombination fractions were observed within the second backcross interspecific progenies, but not within the intraspecific progenies.


The application of foreign pollen to stigmas of unemasculated flowers before normal receptivity resulted in a significant increase in mean number of seed per boll, but the foreign pollen did not fertilize an appreciable number of the seed which were set.


Early and current work on heterosis in cotton are reviewed and methods of hybrid seed production and the possibilities of commercial utilization are discussed.

LUND, ZANE F. and JAMES R. MEYER. Development of smooth leaf cotton. Service Sheet 428 of Mississippi State College Agricultural Experiment Station and in Mississippi Farm Research, May, 1954.

Smooth strains selected from Delta Smooth Leaf cotton are described and the progress is transferring D2 Smoothness from the species, G. armouriunum, to Upland cotton is reviewed.


A genetic analysis of seed index, lint density index, or the weight of lint per unit of surface area of the seed, lint index and lint percentage was made in F1 and F2 of a cross between the Upland varieties, Half and Half and Wilds.


Linkage was tested in segregating populations involving nine monogenic characters.


Segregation in hexaploids leads to variation in tetraploids derived from them. The variation in multivalent formation due to heterozygous translocations, duplication-deficiencies, and pairing between chromosomes of the A and D genomes leads to further cytological as well as genetic segregation.


A second case of somatic reduction is described in a mosaic-forming three-species hybrid between American cultivated, American wild and Australian wild cottons, having 78 chromosomes. The mutant branches had 69 chromosomes in their pollen mother cells. Meiotic analysis revealed that most of the lost chromosomes were probably members of the D group.


An unequal exchange of arms between two chromosomes of American cultivated cotton, induced by irradiation, in which almost the whole arm of one chromosome exchanged places with a very short segment of another chromosome, was used to illustrate two methods in which the chromosome anatomy of Gossypium may be investigated and compared.

Irregular distribution of chromosomes during cell divisions is thought to be the cause of mosaic sectors in leaves and petals of certain multiple species hybrids. The degree of mosaicism increases with the number of chromosomes and the number of species involved.


Study of the chromosome number and configuration in the progeny of plants with a radiation-induced chromosome rearrangement has demonstrated that plants with parts of chromosomes missing or in duplicate are viable. Such plants are useful in testing for the location of marker genes on particular chromosomes.


Rearrangements in the chromosomes of the A chromosome sets of American Upland and the two Asiatic cultivated species of cotton account for all the multiple chromosome configurations found in hybrids involving these species. In three-species hybrids involving American wild species in addition, pairing between the A and D sets of chromosome leads to additional multiple chromosome configurations.


Progenies of plants from irradiated seed of a genetic marker line showed a high frequency of chromosome rearrangements, and a high transmission rate of duplications and deficiencies of chromosomes.


Hybrids of G. gossypioides with two other wild species and with the two American cultivated species show several ways in which species are kept separate.

MEYER, JAMES R. Species, the raw materials for future cottons. Mississippi Farm Research, April, 1952.

Cotton species have many desirable properties of value to a cotton breeding program.


The pentaploid method for the transfer of genes from diploid species to isogenic strains of Upland cotton is described.


The possibility of transferring valuable plant and fiber properties from wild species of cotton to deal with the specific breeding problems in Upland cotton is discussed.


A method for determining the optimum number of replicates and locations for providing adequate data on lint yield performance where the total number of plots or total cost, respectively, is held constant, is described.


All characters showed a quantitative type of inheritance. Heritability estimates and the correlations among the characters were calculated.


Intercross populations resulting from one cycle of recurrent selection were compared with F2 from a cross of DPL 14 and AHA 6-1-4, using lint percentage and fiber strength to measure the effectiveness of recurrent selection.


Postfertilization sterility was ascribed to infertility of male and female gametes, and aberrant development of nucellus, endosperm and zygote.


Thirteen red leaved varieties are shown to contain allelic genes for red plant color.

Two genetic systems control the quantity of lint on seeds of American Upland cotton. One is a single major gene for presence or absence of lint, which also controls the presence (fuzzy) or absence (glabrous) of seed fuzz. The other system involves lint quantity modifiers which are able to function in the presence of the major lint quantity gene and can be detected directly on a homozygous seed coat background.


Breeding problems, systems and special methods are reviewed.


Breeding methods and special characters of breeding value are reviewed and discussed.


There was no consistent difference in yields between seed mixture entries and the weighted mean yields of component pure stocks; however, the strength of fiber was significantly higher in the mixtures than in the pure stocks.


A study of fiber strength, using the Pressley strength tester, was made in F2 and F3 of the above cross. The high strength of AHA 50 behaved as a typical quantitative character. It was concluded that the mean difference in the parents of approximately 2.5 Pressley Index units was probably governed by no more than 4 or 5 pairs of genes.


The inheritance of fiber length from a cross of Wilds and Half and Half was studied in F2 and F3 generations. Fiber length was highly heritable and conditioned by at least three pairs of genes.

STAFFORD, T. J. Inheritance of strength and perimeter of fiber in a cross between two varieties of American Upland cotton. Ph. D. Dissertation; Louisiana State University, 1953.

Fiber strength and perimeter were studied in F2 and F3 of a cross between Half and Half and Wilds. Heritability for fiber strength was about 50 percent. The striking parental difference in fiber strength was governed by relatively few genes.


A very simply designed apparatus for adding seitz-filtered components aseptically to embryo culture media is illustrated and explained.


Spectrophotometric analysis suggest that the leuco substance present in the flower petals of Asiatic cottons is a common precursor of the two plant pigments, anthoxanthin and anthocyan. The precursor is convertible to either pigment by a single genetically controlled chemical step.


The importance of collecting mutant genes into multiple marker stocks for the purpose of allocating genes to their correct sub-genomes in Upland cottons is stressed. Methods of utilizing multiple marker stocks in combination with synthetic amphidiploids for this purpose are presented.


Interspecific backcrosses involving G. hirsutum and G. barbadense show a tendency for genes from the donor parent to be transmitted less frequently than alleles from the recurrent parent. There is a cumulative tendency for the recurrent parent genotype to be recovered more rapidly than expected as a result of random segregation and recombination.


Critical evidence is presented that the complementary genes responsible for the “corky” character in certain interspecific crosses are not located at independent loci.


The cytogenetic evidence concerning the nature of species differentiation in Gossypium is reviewed.


Since the red and cluster loci in cotton represent a linkage group which is common to the amphidiploids and their nearest
diploid relatives, they offer a unique opportunity for a study of the evolution of specific genes. A comparative study of their properties suggests that differentiation could have occurred at the diploid level, and there is no evidence that new properties were developed, as far as these loci are concerned, subsequent to amphidiploidy.


The possibility that duplication is a step in the evolution of new genes is considered in relation to the data available on pseudo-alleles, repeats, and duplicate series in cotton and other organisms.


The shortcomings of current methods of measuring natural crossing are pointed out, and possible methods of improvement are suggested.


Seeds were exposed in the stratosphere and subsequently planted. This paper reports the genetic changes which took place.


The two yield constituents, seed index and lint density index, or weight of lint per unit surface area of seed, were studied in $F_1$, $F_2$, and $F_3$ populations of five crosses. Seed index and lint density index were not correlated, but there was a high positive correlation between number of fibers per unit area of seed surface and lint density index.


Study was made in $F_1$ and $F_2$ of a cross between the short, coarse fibered strain Fla. 1377 and the long, fine fibered strain DPL 45-887. Heritability and correlation analyses showed that it would be difficult to combine long staple with coarse fiber, but easy to retain the parental combinations.


Estimates of genetic variation within and between five commercial varieties of American Upland cotton were made for four characters: seed index, boll size, lint percentage, and yield. Genetic variation was found within a variety and between varieties, but not for all characters.


The effect of open-pollination and self-pollination on the characters studied, though occasionally significant, usually were so small in relation to differences among varieties with respect to the same characters that open-pollinated seeds may be used with confidence, for at least four successive years, as a source of seed stock for performance trials.


The inheritance of photoperiodic response in G. hirsutum race latifolium (Hutchinson) was investigated in a series of greenhouse and field experiments.


In a lethal combination of a line of G. arboresum and Upland cotton, the lethal effect occurs in hybrid tissue grafted upon normal as either root or shoot and lethality is therefore not due to abnormal translocation of nutrients.


In G. hirsutum x arboresum hybrids the endosperm develops normally at the beginning but stops after a while and fails to nourish the hybrid embryo in those crosses where hirsutum is used as the female parent. In reciprocal crosses the endosperm is highly abnormal from the beginning and never becomes cellular.


The inheritance of the reaction to root-knot nematode was studied in a cross involving Cleveland 6 (moderately resistant) and Deltapine 15 (susceptible). Based on heritability estimates it was considered that selection for resistance in $F_1$ would not be effective; but selection in $F_2$ should be reasonably effective.