

BASIC GENETIC RESEARCH IN *GOSSYPIMUM*

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Abstract

Work on cotton taxonomy dates back to the 18th century when Linneaus delineated the genus *Gossypium* and described the four cultivated species *Gossypium arboreum* L. and *Gossypium herbaceum* L. of the Old World and *Gossypium barbadense* L. and *Gossypium hirsutum* L. of the New World. Over the ensuing years many species of *Gossypium* were described by various workers. In the second decade of the 20th century, chromosome numbers began to have impact upon the delineation of species in *Gossypium*, heralding in a more conservative approach to taxonomy and a diminishing number of species.

The study of cytology and cytogenetics gained momentum in the 1930's and more precise relationships among the then known species of *Gossypium* were established. Important findings were that the New World tetraploid ($2n=56$) species had descended from crosses of Old World cultivated diploid cottons ($2n=13$) and New World wild diploids ($2n=13$). Chromosomal sizes and pairing affinities in interspecific crosses led to a system of genomic classification, A, B, C, D, etc. Thus, the New World tetraploid species were designated AADD; the Old World cultivated diploids, AA, and the New World wild diploids, DD. Other significant cytogenetic work involved the recovery of monosomics in the AADD cottons, the use of dominant markers to find the diploid species most closely related to the tetraploids, and the use of teleosomes to locate genes on chromosomes.

Genetic studies in cotton began as early as 1906 and remain important in cotton research. Early research focused mostly on the recovery of genetic markers and the establishment of linkage groups, although genetic studies on resistance to blackarm, or angular leaf spot, began in 1939. Later, attention focused more and more on the genetics of economic characters.

Traits such as fiber yield and components, and fiber properties, are called quantitative characters; i.e. variances for the characters contain measurable genetic and environmental components. The results of many studies showed much additive, less dominance, and occasional epistatic variance.

Glandless cottons, differing from normal cottons by alleles at two loci, bear seeds free of the toxic terpenoid aldehyde substance, gossypol. Cottons bearing genes that impart higher than usual terpenoid aldehyde levels in flower buds

were shown to be resistant to bollworm larvae. Glandlessness, which involves several genes, disrupts oviposition by bollworm imagoes and reduces plant debris in ginned lint. The D_3 complementary lethality system has been suggested as a method for isolating cotton cultivars grown for special purposes, such as glandless seed.

In this short treatise I shall discuss the taxonomy, cytogenetics, and genetics of the genus *Gossypium*. Over the years there has developed an interdependence between the three areas of study in seeking the parameters that define the genus and the species included within it. That is to say, there has been positive feedback between the three.

Fryxell (1979) reviewed the taxonomy of *Gossypium*, identifying the contributions, both important and trivial, of various workers. In the late 18th century, Linneaus delineated the genus *Gossypium* and described five species, including the four cultivated taxa, *Gossypium arboreum* L. and *Gossypium herbaceum* L. of the Old World and *Gossypium barbadense* L. and *Gossypium hirsutum* L. of the New World.

Todaro (1877) published the first thorough interpretation of the genus *Gossypium*. Watt (1907) published a major landmark in *Gossypium* taxonomy "The Wild and Cultivated Cottons of the World." Besides cataloging many species of *Gossypium*, Watt's book is a storehouse of historical and botanical information, including illustrations of type specimens.

Denham (1924) found that Old World cultivated cottons had $2n=26$ chromosomes, whereas New World domesticates had $2n=52$, the latter seeming to be tetraploids. Thus was the study of cytology poised to influence cotton taxonomy.

Zaitzev (1928) took full advantage of Denham's findings to formulate his own notions about the relationships among cultivated cottons. First, he divided domesticated cottons into two groups based upon chromosome number and place of origin. He then subdivided the two groups into four distinct groups. Although Zaitzev withheld taxonomic judgement about these groupings, his conclusions were to prove seminal for later workers. Zaitzev died at the age of 42 and it fell to this favorite student, F. M. Mauer, to publish in 1954 a monograph based on Zaitzev's work.

Hutchinson, Silow, and Stephens (19947) published the first "modern" monograph on *Gossypium*. Each of Zaitzev's subgroups was recognized as a single taxon, the four cultivated species of Linneaus. In all, five tetraploid species were listed. The wild diploid species known at the time were described, and most of the tetraploid species recognized by Watt (1907) reduced to racial status. Fryxell (1979) recorded 39 species of *Gossypium*, six of which were tetraploids.

Harland (1939) reviewed genetic research in *Gossypium*. Such work began as early as 1906 and accelerated in the 1920's and 30's. Characters studied included the crinkled dwarf mutant, plant color, lint color, plant pubescence, branching patterns, and chlorophyll mutants. Knight (1939) began his monumental work on the genetics of blackarm resistance, which was to span more than 20 years.

Cytological and cytogenetic work in *Gossypium* gained momentum in the 1930's. Skovsted (1937) made many interspecific crosses in *Gossypium* and studied chromosomal morphology and behavior. He found that in crosses between cultivated tetraploid cottons and cultivated diploids, the large chromosomes of the latter paired with the 13 largest chromosomes contributed to the resulting triploid by the 4n parent, excluding the 13 smaller chromosomes present. When he crossed a tetraploid cotton with a wild American diploid taxon, the 13 smallest chromosomes contributed by the 4n parent paired with the chromosomes contributed by the wild diploid. Skovsted hypothesized that the New World tetraploid cottons arose from crosses of an Old World cultivated diploid with a wild American diploid. Webber (1939), pursuing similar studies, was not as certain, having tentatively concluded that the 4n cottons were autopoloids.

Beasley (1940 a, b) produced an allotetraploid by crossing *G. arboreum* with *G. thurberi* Tod. and doubling the chromosome number of the hybrid with colchicine. The resulting 4n plant was fully fertile as female, occasionally fertile as male, and crossed readily with *G. hirsutum* to produce a tri-species hybrid. Skovsted's hypothesis concerning the origin of the tetraploid cottons was confirmed. Later Beasley (1942) published findings, based upon relative chromosome sizes, and pairing affinities in interspecific crosses, in which he introduced chromosomal formula groupings, A, B, C, D, etc. The Old World cultivated cottons were listed as AA, the New World wild diploids as DD, and the tetraploid cottons as AADD.

Stephens (1949) conceived a method for allocating dominant genetic markers to genomes in tetraploid cottons. A marked AADD stock was crossed with either an AA or DD diploid. A hexaploid stock was then prepared and crossed with a 4n plant with a recessive allele at the locus of the marker in question. Presence or absence of segregation would identify the genome in which the marker was located. If the chromosomes of a 2n taxon were the precise homologues of one set in a 4n species, there should be random pairing within the group of four homologous chromosomes associated with the marker and a segregation ratio of five dominant to one recessive. Thus, there developed a method for testing the relatedness of A and D genomes of diploids with homologues in the 4n species.

Phillips (1963) did most of the work cited above and found that the AA species displayed a segregation ratio with *G. hirsutum* and *G. barbadense* that averaged between 5 and 6

to 1. The DD diploid, *G. raimondii* Ulb., showed the closest affinity with the AADD species at 9.6 to 1. Gerstel and Sarvella (1956) concluded, based upon chromosomal end arrangements, that *G. herbaceum* was more closely related to the tetraploid cottons than *G. arboreum*. Therefore, *G. herbaceum* and *G. raimondii* have been accepted as the putative parents of the tetraploid species.

Further cytogenetic and genetic work was summarized by Endrizzi, Turcotte, and Kohel (1985). Seventeen of the possible 26 monosomics in AADD cottons were recovered and characterized. Teleosomes were used to locate genes in particular chromosomes, and mutagenic agents were used to produce mutations and chromosomal aberrations. Several linkage groups were discovered, some duplicated in tetraploid cottons.

Quantitative inheritance studies in cotton were pioneered by Miller, Williams, Robinson, and Comstock (1958) and developed further by many workers. The progress was summarized by Meredith (1984). Most economic characters of cotton, fiber yield and components, and fiber properties are determined by multifactors of quantitative expression; that is to say the variances generated by contrasts have genetic and environmental components. Additive effects are defined as the average of contributions of the genes involved, dominance as interallelic interactions, and epistasis as non-allelic interactions.

Meredith pooled the results of 18 experiments and found that when additive effects were set at 100, and dominance calculated as a percentage of additive effects, significant additive effects were found for all characters sampled, and significant dominance effects occasionally were found. Significant epistatic effects seemed to be rare.

Some crosses showed a high level of specific combining ability for fiber yield indicating that dominance effects were frequent enough to justify seeking ways to produce productive hybrids. However, the lack of a suitable cytoplasmically sterile male line (see V. Meyer, 1975) and the problems of transfer of cotton pollen have proven to be formidable obstacles.

Beginning about 1960 much genetic research shifted to a search for major characters that promoted agronomic fitness, McMichael (1960) published on the genetics of glandless cotton. The combined effects of two alleles, gl_2 and gl_3 , removed all pigment glands from the plant, including embryos, thus rendering the seeds free of the toxic terpenoid aldehyde substance – gossypol.

Lee (1962) used McMichael's glandless stocks to separate the genes that imparted glands to leaves and cotyledons. One allele, $G1_2$, seemed somewhat more expressive than the other, $G1_3$. Lee, Cockerham, and Smith (1968) crossed stock of two *G. hirsutum* cultivars homozygous for various combinations of $G1$ and gl alleles as a 2x2 diallel set and

determined the level of gossypol associated with seeds of each genotype. The Gl_2 allele contributed about twice as much gossypol as Gl_3 , likewise, acted in an additive manner, but that in *G. barbadense* the two alleles were associated with similar levels of gossypol. Overall, the *G. barbadense* cultivars assayed produced more gossypol in seeds than the *G. hirsutum* cultivars examined earlier.

Lukefahr and Martin (1966) selected a stock, XG-15, from the progeny of a cross of a Deltapine (Upland) cultivar and Socorro Island Wild, a race stock of *G. hirsutum*, GS-15 proved to be very high in flowerbud terpenoids and was resistant to early instar *Heliothis* spp. larvae. Wilson and Smith (1977) and Lee (1978) showed that the high terpenoid level in the flowerbuds of XG-15 was conditioned by an allele at the Gl_3 locus acting in concert with other alleles, including Gl_2 . One conspicuous expression of the special allele was pitted or rugate boll surface. The high terpenoid allele was particularly expressive when acting in the monomeric state in *G. barbadense* background. Earlier Wilson and Lee (1971) challenged early instar budworm (*Heliothis virescens* F.) larvae with all of the possible combinations of leaf gland alleles in cotton seedlings. Damage was negatively correlated with gland number, and the relationship was virtually linear.

Reduced pubescence on cotton plants has attracted the attention of cotton breeders and research workers because of the potential for reducing plant debris in ginned lint. Lukefahr, Houghtaling, and Cruhm (1975) showed that glabrous plant interferes with oviposition by imagoes of bollworms (*Heliothis* spp.). J. Meyer (1957) transferred a smoothness allele from *G. armourianum* Kearney to *G. hirsutum* and designated the character Sm. Lee (1968) found that the distribution of trichomes on the veins and margins of the leaves and petioles of *G. hirsutum* was inherited in a predictable sequence and named two genes that when acting in concert removed all pubescence from the plant.

Several genes affect pubescence abundance and distribution on cotton plants. Lee (1985) compiled the genetic knowledge of the distribution and modification of trichomes in *Gossypium* spp. and wrote a review in which he advocated a change in the genetic nomenclature for pilosity grade. Instead of Sm for plant smoothness, the symbol T for trichomes was advanced. Alleles were tentatively assigned to five loci.

Gossypium davidsonii Kell. and *Gossypium klotzsdhianum* Anders., the D_3 diploids of Beasley (19492) are unusual in that these species rarely cross successfully with AA, AADD, and other DD taxa, the hybrid embryos becoming moribund before full-term. Among the collections of S. G. Stephens were some wild accessions of *G. barbadense* that were fully compatible with D_3 . Lee (1981a) using Stephens' material bred a D_3 compatible glandless line of *G. barbadense*. During attempts to transfer leaf gland alleles

from D_3 into *G. barbadense*, he accidentally introduced a complementary lethality factor. The lethality gene was fixed in *G. barbadense* background and the genetics of D_3 complementary lethality solved.

In domestic stocks of *G. barbadense* and *G. hirsutum* there are two alleles, Le_1 and Le_2 that interact with the D_3 lethality gene to impart embryonic or seedling lethality. Compatible tetraploid stocks harbor the alleles, le_1 and le_2 . The combination of the D_3 lethal with Le_1 causes earlier seedling death than when the gene is combined with Le_2 . Lee (1982) showed that the Le alleles are linked with the Gl alleles, Le_1 with Gl_2 in the A genome and Le_2 with Gl_3 in the D genome. Lee (1981b) proposed the D_3 lethality combination as a way to isolate cottons grown for special purposes, such as glandless seed or to separate *G. barbadense* from *G. hirsutum*.

Cotton genetic research seems to be taking the directions workers were groping for when I retired in 1987, namely, the route of biochemical resolution. Hopefully, such studies will support, or if needed, redirect our notions about taxonomy. Perhaps most crucial of all is to get a more precise handle on characters that contribute to productivity and quality so that these might be more easily manipulated. I think we will see a continuing stream of foreign germplasm, such as Bt, in the ongoing battle against adversities. One question: how much genetic junk can a cotton plant tolerate and still perform at a satisfactory level?

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