

Review

Inter-Specific Hybridization in Cotton (*Gossypium hirsutum*) for Crop Improvement

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Abstract: Interspecific hybridization has contributed significantly to land diversity, species evolution, and crops' domestication, including upland cotton, the cultivated form of *Gossypium hirsutum*. Being the world's most important fiber crop species, *Gossypium hirsutum* belongs to the allotetraploid *Gossypium* consisting of six additional tetraploid species. The lint fiber evolved once in diploid parent A-genome species in the *Gossypium*'s history and passed on during hybridization of the A-genome with the D-genome and was maintained in subsequent evolution. The domestication history of *G. hirsutum* involved the collection and use of lint fibers by indigenous people for the purpose of making strings and other textile products; hence, spinnable lint fibers were likely to have evolved under domestication. Crossing with *G. barbadense* has resulted in the development of multiple genetic lines in contemporary upland cotton. However, in later-generation hybrids between *G. hirsutum* and other polyploid species, reproductive barriers such as reduced fertility, segregation distortion, and hybrid breakdown are frequently observed, complicating the task of introgressing new, stably inherited allelic variation from inter-specific hybridization. Recent efforts in molecular genetics research have provided insights into the location and effects of QTLs from wild species that are associated with traits important to cotton production. These and future research efforts will undoubtedly provide the tools that can be utilized by plant breeders to access novel genes from wild and domesticated allotetraploid *Gossypium* for upland cotton improvement.

Keywords: interspecific hybridization; *Gossypium hirsutum*; crop improvement; fiber quality; polyploidization; introgressive breeding



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1. Introduction

Cotton is a food and fiber plant contributing to humanity's fundamental requirements. Cotton fiber, in the form of textile objects, contributes significantly to the comfort, style, and culture of human society. Despite its lack of appeal as a food, cotton is a primary source of vegetable oil, which is used extensively in meals such as baking and frying fats, mayonnaise, margarine, and snack food. Following oil extraction, the seed by-product is used as a raw material in animal feed, fertilizer, and paper. Because of its flexibility, cotton is one of the most important field crops in the world. According to the International Cotton Advisory Committee (ICAC), which collects data on global cotton production, consumption, and commerce, cotton is grown on 36 million hectares in over 100 countries [1]. The top five cotton-producing countries are China, India, the United States, Pakistan, and Brazil, which

account for around two-thirds of worldwide cotton production [2]. Cotton has become the most important natural fiber in the textile industry, as well as a vital agricultural product in the global economy. The annual value of the worldwide cotton crop is estimated to be over USD 30 billion, with lint fiber accounting for 90% of that value [3]. Cotton farming and processing employ about 350 million people worldwide. Cotton's economic importance as a natural fiber for the global textile industry has spurred a lot of interest in improving the crop's inherent genetic potential by breeding cultivars with higher biotic and abiotic tolerance, higher lint yield, and enhanced fiber quality [4].

Cotton's development and progress have benefited greatly from interspecific hybridization. Cotton remarkable as a crop in that four distinct species of the genus *Gossypium* (Malvaceae) were domesticated for lint fiber production on two separate continents [5,6]. As a result, in the textile business, the two allotetraploid species *G. hirsutum* L. and *G. barbadense* L., both native to the Americas, and the two diploid species *G. arboreum* L. and *G. herbaceum* L., both endemic to Africa and Asia, are referred to as "cotton." Allotetraploid *Gossypium* has a single polyploidization history, with progenitors that resemble *G. herbaceum* or *G. arboreum* (A genome) and *G. raimondii* (D genome) merging together [6]. The two allotetraploids now provide the great majority of the world's textile fiber, with *G. hirsutum* accounting for more than 90% of worldwide cotton production [7]. As a result, the focus of this review will be on *G. hirsutum*, popularly known as "Upland" cotton, a cultivated allotetraploid species. Other domesticated and non-domesticated allotetraploid species, on the other hand, will be included since they represent a vast pool of untapped genetic resources for future genetic advancement.

2. Taxonomy of *Gossypium* and Origin of *Gossypium hirsutum*

The genus *Gossypium* contains around 50 species, which are distributed in tropics and subtropics regions. Diploid *Gossypium* species are categorized into eight genome groups (A–G, K) based on chromosomal pairing affinities [8]. Despite the fact that numerous important diversification sites have been identified, these species collectively have a large distribution. A-genome species are found both in Africa and Asia; B- and F-genome species are mainly present in Africa; Arabia has E-genome species; C-, G-, and K-genome species can be found in Australia; whereas D-genome species can be found in Central and South America. The detailed grouping and geographical distribution of *Gossypium* species are summarized in Table 1. Although molecular phylogenetic investigations have established a phylogenetic framework for the genus and its many genome types, a thorough understanding of the evolutionary links between each species remains elusive [6]. *G. hirsutum* and *G. barbadense*, two domesticated species, plus *G. tomentosum* Nutt ex Seem, *G. darwinii* Watt, and *G. mustelinum* Miers ex G. Watt, are the five allotetraploid *Gossypium* species that have been extensively recognized in the past. *G. ekmanianum* Wittmack, a sixth species, was recently discovered, and a seventh was discovered (see below). Polyploid *Gossypium* has a broad geographic distribution that includes several seasonally dry subtropical and tropical parts of the North and South American continents, mainly near coasts, as well as numerous Caribbean and Pacific islands. As a result, these species are commonly referred to as New World cotton. The fact that *G. darwinii* (Galapagos Islands), *G. ekmanianum* (Hispaniola), and *G. tomentosum* (Hawaiian Islands) are all island endemics suggests that these species evolved after long-distance dispersion episodes [6,9]. The native Brazilian cotton (*Gossypium mustelinum*) has never been cultivated. It is tetraploid and may be crossed with cultivated cotton. *Gossypium mustelinum* is grown in semiarid region and expanded to the coastal area of northeast Brazil in 2018. It is cultivated in Paraiba and Pernambuco in Brazil [10]. *G. hirsutum* is native to Central America, whereas *G. barbadense* is native to South America, but their ranges overlap, notably in northwest South America and across the Caribbean. Two new species have just been added to the allopolyploid cotton group. Based on accessions obtained in the Dominican Republic, the species *G. ekmanianum* Wittm was recently revived [11,12]. A seventh species, *Gossypium stephensii* [13], has been recently discovered in the Wake Atoll in the Pacific Ocean (Wake, Peale, and Wilkes Islands) [13,14].

G. hirsutum, *G. tomentosum*, *G. ekmanianum*, and the newly found species form one clade; *G. barbadense* and *G. darwinii* form a second clade; and *G. mustelinum* remains the allopolyploid phylogeny's basal clade [6]. Because of their monophyletic origin, all seven polyploid species have two sets of 13 homoeologous chromosomes ($2n = 4x = 52$) and strict disomic chromosome pairing (Kimber 1961) A-genome cytoplasm. Polyploidization occurred about 1–2 million years ago by transoceanic migration of an Old World (A-genome) progenitor followed by hybridization with a native New World (D-genome) progenitor [6]. The At- and Dt-subgenomes of the tetraploids were provided by diploid progenitors that resemble *G. arboreum* or *G. herbaceum*, and *G. raimondii*, respectively, according to meiotic chromosomal pairing and comparative genome studies. The progenitors of these species separated from a common ancestor 5–7 million years ago, according to DNA sequence evidence [6,15]. Cotton's A- and D-genome progenitors have at least nine chromosomal rearrangements in common [16]. Furthermore, the A-genome contains around twice as much gametic DNA as the D-genome [17], with the increased genome size attributed mostly to the repetitive DNA fraction, as the quantity of single-copy DNA in both genomes is nearly equal [18]. Genetic mapping [19,20] identified the matching homoeologous chromosomes of the At- and Dt-subgenomes, which were recently confirmed by two draft genomes sequences [14]. In the At sub genome, direct comparisons of gene order and synteny between the two sub genomes revealed two reciprocal translocations between chromosomes 02/03 and 04/05, as well as multiple probable inversions [18,19]. The tetraploid chromosomes have also been aligned with those of their diploid progenitors, indicating that there has been more rearrangement since polyploid development [20,21]. Nonetheless, these findings suggest that gene collinearity between the two subgenomes is substantial, and that chromosomal structural rearrangement has been minimal after allopolyploid formation. A grouping of *Gossypium* species based on genomic diversity is shown in Table 1, and the evolution of *Gossypium* species, including tetraploid *Gossypium* species formation, is illustrated in Figure 1.

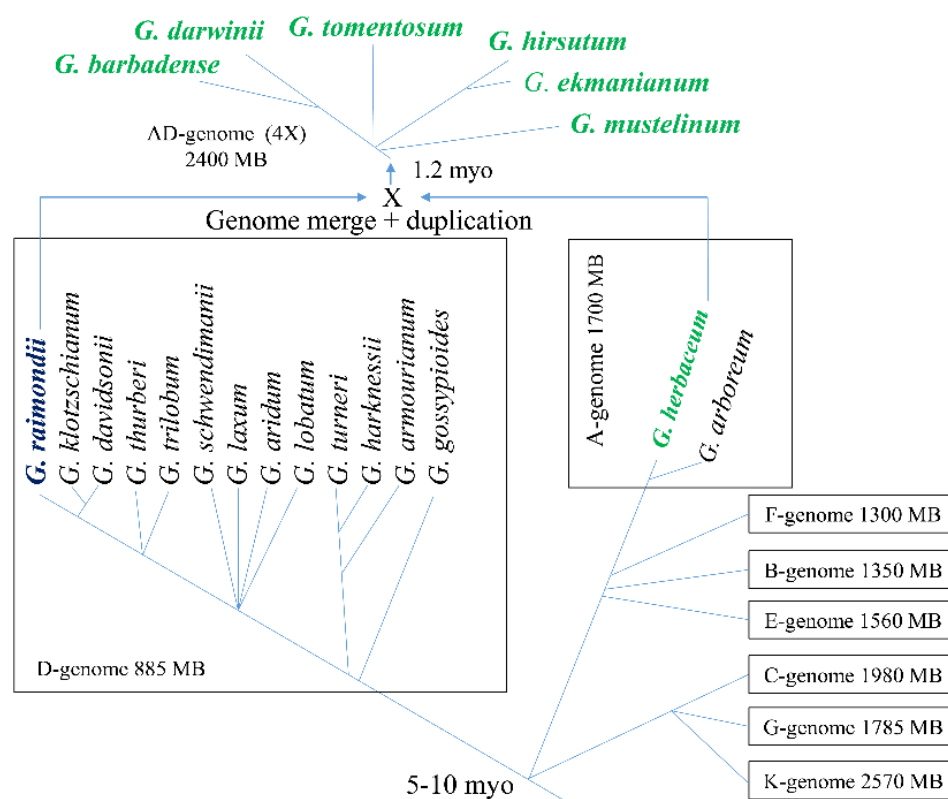


Figure 1. The evolution of *Gossypium* genus and the formation of tetraploid *Gossypium* species. MB show genome size of representative species.

Table 1. Grouping and geographical distribution of the genus *Gossypium* species based on genomic diversity validated by cytogenetic data and other means.

Genome Group	Ploidy (No. of Species)	Species Name	Geographical Distribution
A	2X (2)	<i>G. herbaceum</i> , <i>G. arboreum</i> ,	Asia, Africa
B	2X (3–4)	<i>G. anomalum</i> , <i>G. capitiviridis</i> , <i>G. triphyllum</i> , <i>G. trifurcatum</i>	Cape Verde Island, Africa
C	2X (2)	<i>G. robinsonii</i> , <i>G. sturtianum</i>	Australia
D	2X (13–14)	<i>G. armourianum</i> , <i>G. aridum</i> , <i>G. davidsonii</i> , <i>G. gossypoides</i> , <i>G. harknessii</i> , <i>G. klotzschianum</i> , <i>G. laxum</i> , <i>G. lobatum</i> , (<i>Gossypium</i> sp. Nov), <i>G. raimondii</i> , <i>G. schwendimannii</i> , <i>G. turneri</i> , <i>G. thurberi</i> , <i>G. trilobum</i>	Mexico, Peru, Arizona, Galapagos Islands
E	2X (5–9)	<i>G. areysianum</i> Deflers, (<i>G. benadirensis</i>), (<i>G. bricchettii</i>), <i>G. incanum</i> , <i>G. stocksii</i> , <i>G. somalense</i> , <i>G. trifurcatum</i> , (<i>G. trifurcatum</i>), (<i>G. vollesenii</i>)	Southwest Asia, Northeast Africa, Arabian Peninsula
F	2X (1)	<i>G. longicalyx</i>	East Africa
G	2X (3)	<i>G. australe</i> , <i>G. bickii</i> , <i>G. nelsonii</i>	Australia
K	2X (12)	<i>G. anapoides</i> , <i>G. cunninghamii</i> , <i>G. costulatum</i> , <i>G. exiguum</i> , <i>G. enthyle</i> , <i>G. londonderriense</i> , <i>G. nobile</i> , <i>G. marchantii</i> , <i>G. populifolium</i> , <i>G. pilosum</i> , <i>G. pulchellum</i> , <i>G. rotundifolium</i> .	Australia, Northern Territory, Cobourg Peninsula, Northwest Australia
AD	4X (7)	<i>G. barbadense</i> , <i>G. darwinii</i> , <i>G. ekmanianum</i> , <i>G. hirsutum</i> , <i>G. mustelinum</i> , <i>G. tomentosum</i> , <i>G. stephensii</i> .	New World tropics and subtropics, including Hawaii, Galapagos Islands and the Wake Atoll

3. Domestication of Upland Cotton

After polyploidization, *G. hirsutum* evolved to produce high-quality fiber and to best survive against adverse environments [7]. The domestication history of *G. hirsutum* is similar to that of the other three domesticated cotton species; indigenous peoples may have gathered and employed lint fibers for string and other textile items [7,20,21]. Domestication of cotton gave rise to long lint fiber, which has a flat convoluted ribbon shape that allows it to be spun into yarn [20,22]. Short ‘linters’ or fuzz stick to the seed coat tightly, whilst longer ‘lint’ fibers cling to the seed coat loosely. Fuzz fibers are an important source of raw material for paper and other industrial products. Cotton is the world’s most important fiber crop due to its longer, spinnable lint fibers, and these novel single-celled seed epidermal trichomes may have lured ancient peoples to the cotton plant in the first place. Four separate *Gossypium* species were domesticated independently by four civilizations on two continents, as previously stated: A-genome diploids *G. herbaceum* and *G. arboreum* were domesticated in Africa and Asia, and allopolyploids *G. hirsutum* and *G. barbadense* were domesticated in Central and South America [20,22,23]. Wild cotton feature short and coarse lint fibers that are very different from those seen in current cultivar cottonseed. Although the elongated seed trichomes may operate as a dispersion mechanism in some ecological circumstances and/or function in maintaining an adequate microbiological and hydration background for seed germination or early seedling development, the biological function of lint fiber has not been determined [24]. Early domesticators were likely drawn to primitive lint fiber, with current germplasm’s long lint fiber, resulting from the human selection of genotypes with enhanced fiber quality attributes, as well as higher lint output and other agronomic qualities [23,25]. Interestingly, the elongation of fiber cells during development is directly linked to the evolution of long spinnable lint fiber; particularly, developing fiber cells in domesticated diploid and tetraploid cotton all exhibit a protracted fiber-cell growth programmed. Only the F-genome/A-genome lineages developed this developmental novelty, which may

have aided the domestication of A-genome cotton [26,27]. When the A-genome joined the D-genome during polyploidization, this predisposition for extended lint fiber growth was passed on to allopolyploids [28]. *G. hirsutum* is said to have been domesticated in Mesoamerica's Yucatan Peninsula. According to Brubaker and [29], race 'punctatum' is the earliest domesticated form of *G. hirsutum*, having agronomic characteristics that are transitional between the really wild race 'yucatanense' and races with more advanced attributes such as latifolium and palmeri. Early attempts at domestication may have involved choosing a more appealing plant from the wild population to generate door-yard cultigens, which later evolved into large-scale field production as civilization grew and agriculture became more specialized. Increased lint output through choosing larger and more bolls per plant, lowering plant size from the shrubby/small treelike habit of wild cotton to a scale that people can utilize, and selecting for a more annual life cycle are all qualities that early agriculturalists may have preferred. Later decisions concentrated on finer, stronger, and consistently longer fibers to improve the fiber's quality. Other fiber qualities such as elongation and short fiber content have grown increasingly important as the textile industry has become more automated. As agriculture and agribusiness converge, the industrialization of production will continue to define aspects that increase production efficiency. For example, growing mechanization needed plant size selection, but monoculture's vulnerability to pests and diseases necessitated enhanced selection for resistance to these challenges. Ware [30] has published a thorough historical account of the history of *G. hirsutum* as Upland cotton cultivars from the time of European arrival to the middle of the twentieth century. The birth and development of Upland germplasm, the current cultivated form of *G. hirsutum*, occurred in the southern United States of America, despite the fact that the specific location of *G. hirsutum* domestication is unclear. The 'Cotton Belt' of the United States was the epicenter of upland cotton's genetic development. When a result, the cotton crop was brought to the eastern coastal areas of North America as Europeans departed. While all four domesticated *Gossypium* species were planted as crops in the United States from the start, the allotetraploids outperformed the A genome diploids. As the twentieth century progressed, a new categorization system based on geographic areas and industrial techniques emerged, which is still in use today: Acala type, Plains type, Delta type, and Eastern type [31]. Asiatic diploid species *G. arboreum* and *G. herbaceum*, with much shorter staple lengths than Upland or Sea Island cotton, were produced in cotton-producing nations such as India, China, and Russia prior to the establishment of the US cotton industry [32]. The new spinning methods available at the time could not handle the fiber produced by *G. arboreum* and *G. herbaceum*. While there has been some success in breeding for longer fiber length within the diploid species [33], more Upland germplasm was introduced to meet the need for new varieties with better fiber quality. By the 1920s, practically all worldwide breeding efforts had shifted to the allopolyploid *G. hirsutum*, a short-fiber Asiatic species [30].

4. Cotton Improvement

Since Niles and Feaster's report, the great majority of cotton breeding efforts have continued to use the same technique [9]. Cotton is mostly a self-pollinated plant; hence most cotton growers use a modified pedigree breeding approach to generate pure line cultivars. In general, parents with different attributes or traits of interest are chosen for cross hybridization, segregating populations are evaluated in the field to identify individual plants with the desired trait combinations, seed from the selected plants is evaluated in progeny rows, and inbred lines that outperform "check" cultivars are evaluated in replicated tests over multiple locations and years [34,35]. The procedures of cotton breeding programs have been nicely laid out in literature [36–38]. Current breeding operations make use of substantially more machinery, allowing them to handle a bigger number of progeny rows with fewer people and more sophisticated fertilization, plant growth control, and pest management. Although the relative significance of these features may have altered, the traits that are wanted in present cultivars are not significantly different from those in

earlier years of cotton cultivation [37]. In every commercial cotton breeding program, lint output remains the top objective [39–41]. Lint percent, which is a component of lint output, was probably one of the first qualities to be chosen throughout the domestication process and in early breeding, and is still the most desired character [23,42–46]. Environmental stability [47,48] and early maturity [49–51] are two more agronomic features that have risen in relevance [37]. Despite the fact that the advent of transgenic Bt cultivars has shifted the attention away from insect resistance, host-plant resistance remains significant for a variety of diseases and nematodes. Similarly, breeding efforts used to prioritize cotton genotypes with low vegetative growth and erect stature, but plant height and compact growth habits may now be readily regulated with plant growth regulators such as Mepiquat [52]. The second most significant aim in early breeding attempts was fiber quality, which is still the case in commercial cotton breeding projects [53–55]. The replacement of manual spinning methods with machine spinning and weaving technologies, which required adequate fiber length and strength to work properly, provided the motivation for this endeavor. Cotton fibers' quality is determined by their physical characteristics. Lint fiber is frequently spun into yarn, which is subsequently woven or knitted into a variety of textiles dependent on the quality and desired end-product characteristics. The collection of fiber characteristics that determine the efficiency of yarn spinning, weaving, and other fabric-making activities, as well as the quality of cotton textiles, is referred to as fiber quality. The key fiber factors that are substantially linked with spinning performance and end product quality are the length, strength, elongation, and fineness/maturity (measured in micronaire) of the fiber. The relevance of fiber characteristics and how they are quantified was nicely outlined by Chee et al. (2009) [56].

Lint production and fiber quality are both quantitatively inherited characteristics. For yield and fiber quality variables, Campbell et al. [57] reported the mean broad-sense and narrow-sense heritability. Although yield components and fiber quality attributes are both heritable and exhibit additive genetic variation and frequently exhibit a negative correlation, it is suggested that this is due to linkage rather than pleiotropy; however, Campbell et al. [58] found that the negative connection in Pee Dee germplasm maintains after over 80 years of breeding. As a result, improving yield and fiber quality simultaneously is the most difficult problem in cotton breeding.

Meredith and Bridge (1973) tested the performance of four cottons (*G. hirsutum* L.) cultivars under four environmental conditions and estimated seven yield components with seven fiber properties using nine different harvests. Results revealed that the lint index was lowest for early harvest and was highest for the middle harvests, while cultivars were the most important source of variations for fiber properties, indicating the importance of genetic variation for fiber quality traits improvements [59]. Later they used a modified recurrent selection method for improving lint percentage within a cotton (*G. hirsutum* L.) cultivar 'Deltapine 523,' through initially plant-based selection, followed by progeny-row basis selection and construction of S1, S2, and S3 selfed generations. They finally attained eight progenies in S3 with 2.5% higher span length [60], thereby significantly improving the cotton for lint yield, lint percentage, fiber length, lint index, and Micronaire in the S3 generation population compared to the S0 population [60]. Using *G. barbadense* as a donor parent, reciprocal backcross population of the S6 generation of *G. hirsutum* × *G. barbadense* crosses showed significant genotypic variations, and improvements in fiber-quality-related traits, including micronaire, fiber elongation, fiber strength, and upper half mean length showed significant higher genotypic variance in *G. hirsutum* background than *G. barbadense*, indicating cytoplasmic effects on the genetic variations and heredity [61]. The growing number of evidences has been reported to verifying the adoptive roles of alien introgression for different quality traits, especially fiber quality of *G. hirsutum* [62–68].

5. Development of Spinnable Fiber and Polyploidization

In terms of fiber quality improvement, it is worth noting that spinnable fiber appeared just once in *Gossypium*'s history, in an ancestor of the two domesticated diploid A-genome

species, after the F-genome lineage split. This feature was handed down to allopolyploid cotton when the A-genome fused with a D-genome from an ancestor that didn't make lint fibers in a shared nucleus [27,69]. As previously stated, the formation of long spinnable lint fiber is closely linked to a protracted elongation phase during fiber cell development.

Applequist, Cronn and Wendel [26] used accessions from the AD-genome allopolyploids *G. hirsutum* and *G. tomentosum*, as well as diploid species *G. herbaceum* (A-genome), *G. arboreum* (A-genome), *G. raimondii* (D-genome), *G. davidsonii* (D-genome), *G. anomalum* (B-genome), and *G. stur* (F-genome). Accessions from the AD-genome allopolyploids and the A-genome diploids have a much higher rate of fiber elongation than the other diploids, according to a comparison of growth curves across species. Hovav et al. [27] came to a similar result after comparing gene expression profiles over a developmental time-course of fiber from *G. herbaceum* and *G. longicalyx*. In domesticated A-genome *G. herbaceum*, their findings revealed significant changes in the expression of genes associated with stress responses and cell elongation, as well as a longer developmental profile. Thus, the evolution of lint fiber included a continuation of an ancient developmental program that developed prior to polyploidization in the ancestral A-genome. Polyploidization has another major meaning for the evolution of spinnable fiber, in addition to supporting the evolution of a protracted period of fiber elongation. The joining of the A- and D-genomes in a single nucleus may have allowed D-genome alleles (genes) to be recruited into fiber development, resulting in higher fiber quality and production in polyploid cotton. Because only A-genome diploid species generate spinnable fiber, the relevance of the D-genome in polyploid cotton fiber quality genetic determination has long been debated. Jiang et al. [70] presented the first evidence of the extent to which loci on the Dt-subgenome cause genetic variation in fiber quality attributes, showing that the majority of QTLs for fiber quality mapping to the Dt-subgenome. Numerous genetic mapping analyses, summarized by [56], have now supported the observation that the Dt-subgenome, from the ancestor that did not have spinnable fiber, plays a large role in the genetic control of polyploid cotton fiber growth and development. These findings show that Dt-subgenome genes have been recruited to the genetic regulation of fiber quality attributes, leading to polyploid cotton's transgressive fiber quality and yield compared to diploid progenitors. Many advantageous alleles at important loci for fiber qualities may have already been fixed as a result of natural selection, according to [70], because the At-subgenome has a significantly longer history of selection for fiber formation. On the other hand, fiber growth loci on the Dt-subgenome may not have been subjected to strong selection until after polyploidization, and hence, mutations that improved this feature may have only been advantageous after polyploidization. As a result, the Dt-subgenome may have had greater 'room for improvement' of fiber qualities when the artificial selection was recently enforced by domestication and breeding. Recruitment of Dt-subgenome loci may provide polyploid cotton more flexibility for artificial selection through breeding, explaining why polyploid cotton has better fiber characteristics than farmed A-genome diploids. The uneven pace of evolution in the polyploid AD-subgenome is a secondary consequence of polyploidization for spinnable fiber and a host of other characteristics that geneticists are only beginning to understand through genome sequence analysis. The majority, if not all, loci are duplicated in allopolyploid genomes by definition. Lynch and Conery [71] addressed the different outcomes of duplicated genes, claiming that most duplicated genes go through a brief period of relaxed selection before being silenced or pseudogenized. However, a tiny percentage of duplicated genes survive in duplicate and contribute to developing phenotypic complexity through natural selection. A null hypothesis is that homoeologous genes would develop independently and at comparable rates following polyploid formation in recent allopolyploids such as cotton, where the two subgenomes contain duplicated but somewhat divergent copies of most genes. Allopolyploid cotton have gone through bi-directional concerted evolution for some genes, resulting in differing directional biases in different sections of the genome. In situ hybridization revealed that distributed repetitive sequences that are A-genome specific at the diploid level had

expanded to the Dt-subgenome in allopolyploids, which provided the first clues to this occurrence [72,73]. Furthermore, multiple studies have found that the Dt-subgenome has much greater allelic diversity of homoeologous genes [74] and loci affecting quantitative features than the At-subgenome [18,75]. Non-reciprocal DNA conversion favors genes in the Dt-subgenome over genes in the At-subgenome, according to recent genome sequence comparisons [76]: for example, the sequences of around 40% of the At and Dt genes in an elite cotton cultivar change from their diploid ancestors. Most of these mutations are convergent, with at least one gene being changed to the Dt state at a rate more than double that of the reciprocal [9]. These findings show that polyploidization allowed D-genome genes to take on new tasks in the allopolyploid genome, potentially explaining why domesticated allopolyploid cotton outperforms its diploid offspring in terms of agronomic and fiber quality.

6. Gene Introgression and Inter-Specific Hybridization

Each phase in the domestication of cotton, from wild *G. hirsutum* to feral cultigens to the advent of Upland germplasm to current better cultivars, imposed severe genetic bottlenecks, limiting allelic diversity. Morphological [77], and molecular characterization have been used to record the amounts and patterns of genetic erosion involved with the formation of early cultigens, landraces, and current cultivars [78,79]. Too many genomic region and genes have reported to be introgressed from wild relative of upland cotton contributed to the improvements of upland cotton [8,65,80].

The average genetic distance across 378 Upland accessions from the United States examined with 120 SSR markers was only 0.195, demonstrating that Upland cotton germplasm is quite limited [79]. Lubbers and Chee [81] used 250 RFLPs to examine 320 Upland cultivars/germplasm from the United States National Plant Germplasm Collection and found cotton to have less genetic diversity than most important crops. When top germplasm from various geographical origins was assessed, the amount of genetic diversity did not improve. Indeed, the average number of alleles discovered per locus in a survey of 157 elite cultivars from China, the United States, Africa, the Former Soviet Union, and Australia utilizing 146 SSR loci was just 2.3 [82]. Surprisingly, these genetic limitations were followed by sustained improvements in several key cotton properties, particularly fiber quality. Given the low allelic diversity in the Upland cotton gene pool, it is reasonable to assume that the number of favorable alleles for fiber quality (such as fiber length and strength) that have yet to reach fixation is small, as these traits have been under intense selection pressure since the early stages of domestication. As a result, it is not unexpected that interspecific introgression has long been a topic of discussion in the Upland cotton community [83,84]. Upland cotton breeding has prioritized high production and adaptability, whereas domesticated strains of *G. barbadense*, often known as Pima, Egyptian, or Sea Island cotton, have prioritized improved fiber quality. As a result, farmed *G. barbadense* fiber is substantially longer, finer, and stronger than Upland cotton, which is more extensively grown. However, both Pima and Egyptian cotton have a restricted range of environmental adaptability in irrigated regions in dry zones of the Western United States and Lower Egypt, respectively, of the *G. barbadense* that are still in production. Nonetheless, this species' distinctive fiber qualities make it an attractive option for supplying additional genetic variety to increase Upland cotton fiber quality. It is no surprise, therefore, that studies of populations produced from interspecific hybridization between wild and domesticated strains of *G. barbadense* and Upland cotton have investigated the genetic basis and heritability of species fiber qualities [56,85]. Interspecies genome merge provides an opportunity to the introduce a foreign beneficial gene for crop improvements and genetic analysis. Saha et al. (2006) developed monosomic and monotelodisomic substitution hybrids between *G. hirsutum* and *G. tomentosum* and identified several types of numerical and structural variations and offered a valuable germplasm for localization of genomic markers and development of backcross substitution line for cotton cultivars' improvements [86]. Recently, Muthuraj et al. (2019) developed male sterile triploid interspecific hybrids between tetraploid *G. hirsutum*

and diploid *G. armourianum*, which showed intermediate phenotypes, and this germplasm is an important genetic source for introducing sucking cotton pest “jassid”-resistant genes into the cultivated cotton cultivars through conventional breeding schemes [87]. In order to barrier free wild gene introgression into cultivated cotton, a tri-species hybrid “(*G. arboreum* × *G. anomalum*) × *G. hirsutum*” was produced. The cytomorphological analysis of a tri-species hybrid and its backcross progenies to *G. hirsutum* showed the production of monovalent to hexavalent offspring and allo-syndetic chromosomes pairing, indicating the possibility of intergenomic genetic exchanges and yet a homoeologous relationship among these species [88]. As expected, the molecular marker data combined with cytogenetic findings determined the multi-genome background in monovalent to hexaploid progenies and provided an important intermediate material for introducing exotic genetic introgression [88]. Draye et al. (2005) used backcross-self-pollination population of a *G. hirsutum* and *G. barbadense* cross and identified 32 and 9 QTLs for fiber fineness and micronaire, respectively, and from nine micronaire QTLs, seven were also associated with fiber fineness; however, the majority of the members of the BC3F2 population showed inferior phenotypes, thus imposing hurdles to utilize *G. barbadense* in conventional planting breeding programs [89]. The breeding utilization of *G. barbadense*-introgressed line in *G. hirsutum* showed high mid-parent heterosis for yield, and F1 to F3 hybrids outcompeted the high-yielding commercial cultivar [90], indicating the suitability of introgressed lines for being outcompeting cultivars. Remarkable progress was made by Hulse-kemp et al. (2015) by developing CottonSNP63K, an Illumina Infinium array with 45,104 intraspecific and 17,954 interspecific putative SNP markers, and generating two high-density genetic maps, collectively providing new cotton resources for cotton breeders [91]. Later, Hinze et al. (2017) used this CottonSNP63K array and validated that it could distinctly separate *G. hirsutum* from other *Gossypium* species, distinguish the wild from cultivated types of *G. hirsutum*, and identify loci possibly linked to cotton seed protein contents [92]. As chromosome segment substitution (CSSLs) lines provide an ideal opportunity to map QTLs in interspecific hybrids, a CSSL derived by hybridizing and backcrossing *G. hirsutum* and *G. barbadense* genotyped by whole genome re-sequencing identified 64 QTLs for 14 agronomic traits, and many alleles of *G. barbadense* showed extremely high values for improving cotton seed pool contents [93]. Recombinant inbred line populations produced between the Chinese *G. barbadense* cultivar 5917 and the American Pima S-7 were tested for lint yield and fiber quality traits, followed by GBS sequencing, and there were 42 QTLs identified, including 24 QTLs on 12 linkage groups for fiber quality and 18 QTLs on 7 linkage groups for lint yield, thereby proving an initial material for fine mapping of QTLs, prediction of candidate genes, and development of molecular markers.

The majority of these genetic investigations have shown that fiber qualities are heritable [94–96], implying that interspecific introgression might increase specific Upland cotton fiber traits. In addition to fiber quality, wild and domesticated allotetraploid *Gossypium* is a significant source of disease and pest resistance genes that might be transferred into Upland cotton [65,97–99]. Pathogens, nematodes, and insects cause severe crop losses anywhere cotton is grown, and crop protection expenditures account for a large percentage of the high unit cost of cotton production, which is why transgenic pest-management cultivars are so appealing. According to Meredith Jr [100], breeding for disease resistance is more important than breeding for pest resistance in most breeding programs. This is especially true with the development of Bt cotton varieties, which are insect-resistant. Some wild species resistance characteristics are simply inherited, and breeders have taken advantage of these features since they are easy to select. However, many resistance qualities are quantitatively inherited, and using DNA markers to manipulate them has lately become considerably more successful. Disease resistance genes found in wild and domesticated allopolyploid *Gossypium* are summarized in Table 1. After polyploid development during the Mid-Pleistocene, around 1–2 Mya, *G. hirsutum*, *G. barbadense*, and the wild allopolyploid species separated from a common ancestor. When introduced into a diverse genetic background, mutations that have accumulated in various allopolyploid lineages may or may not interact positively

(Orr 1995). While allopolyploid species are sexually compatible, later-generation hybrids sometimes exhibit partial reproductive obstacles such as lower fertility, segregation distortion (non-Mendelian inheritance), and hybrid breakdown [101]. Jiang et al. [102] employed DNA markers to analyze the transmission genetics of an advanced back cross generation interspecific hybrid population between *G. hirsutum* and *G. barbadense*, demonstrating the effects of these barriers to gene introgression across allotetraploid cotton. Individual allele transmission patterns often promote the eradication of the donor genotype, maintaining the recurrent genotype's integrity. Segregation distortions were common, for example, and early generations of hybridization resulted in the full eradication of certain donor alleles as early as the BC3 generation due to under-representation of donor alleles. Interestingly, the segregating ratios at identical loci introgressed into different independently derived BC3 F2 families were highly variable, with some families favoring recurrent parent alleles while others favor donor parent alleles, implying that hybrid incompatibility is best explained by multi-locus epistatic interactions affecting gamete success and genotype fecundity. These findings illustrate the challenge of using interspecific populations to generate superior Upland cotton cultivars by pyramiding numerous beneficial alleles for quantitative features, including lint production, fiber length, fiber strength, and fiber fineness in a single genotype. Most attempts to directly mix Upland cotton with Sea Island (*G. barbadense*) varieties, as observed by Brown and Ware [103], revealed that while the F1 generation is beautiful, the F2 and F3 generations are regarded as “messy” and are nearly usually abandoned (Figure 2). While pedigree research revealed that several cultivars were created through interspecific hybridization, a molecular study using isozymes and DNA markers revealed that the Upland cotton gene pool is rather uniform. Rare alleles are found in just a few closely related cultivars within a germplasm group and are thought to have evolved by introgression [6,104]. Furthermore, none of these *G. barbadense*-introgressed alleles were discovered in current cotton cultivars, suggesting that the advantages of *G. barbadense* introgression in Upland cotton are still completely unmet. Conversely, the introduction of Upland cotton genes into Pima cotton, a cultivated variety of *G. barbadense*, has substantially aided the production and adaptability of current Pima cultivars [105,106].

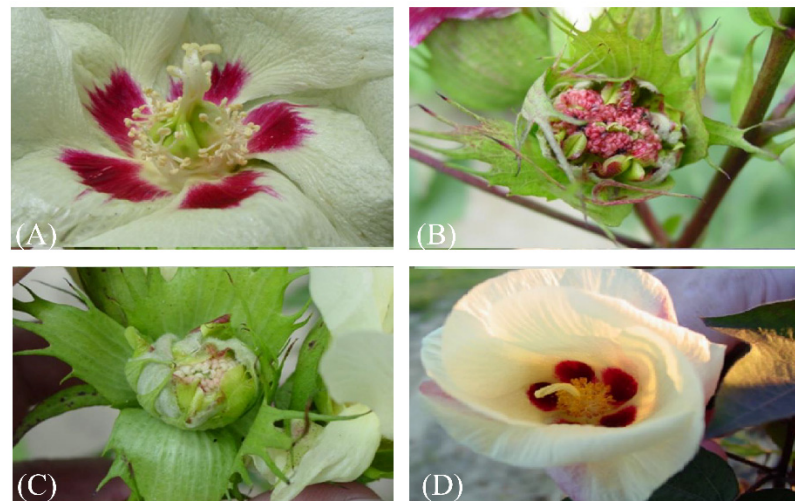


Figure 2. Floral abnormality in later generation hybrids between *Gossypium hirsutum* and *G. barbadense*: (A) abnormal style, stigma, and anther formation; (B,C) abnormal bud development; and (D) an abnormal flower of an F2 generation of *Gossypium hirsutum* × *G. barbadense*.

7. Introgressive Breeding

Interspecific populations derived from crossings between *G. hirsutum* and *G. barbadense* solved the classic problem of limited genetic diversity in Upland cotton genetic and QTL mapping in the early days. These two grown species are sought for somewhat different traits in addition to providing the DNA-level polymorphism required for genetic map

creation. As previously stated, *G. hirsutum* breeding has stressed maximal output and broad adaptability, whereas *G. barbadense* breeding has emphasized fiber quality. As a result, most genetic mapping [15,107] and molecular quantitative genetic studies of fiber properties have used populations derived from interspecific hybridization involving wild and domesticated forms of *G. barbadense* crossed with Upland cotton. QTLs for numerous fiber quality variables mapped in cotton were summarized by Chee and Campbell [57]. Some important QTLs for fiber length, strength, and fineness have now been found, and several have been verified [108,109]. This knowledge gives cotton growers greater options to improve certain fiber qualities in upland cotton by introducing genes from *G. barbadense* with minimal disruption to the favorable allelic combinations developed over a century of selective selection. Inbred backcross populations generated from crossing Upland varieties with the allotetraploid species *G. barbadense*, *G. tomentosum*, and *G. mustelinum* have been developed as part of a collaborative effort to minimize Upland cotton's genetic susceptibility [110]. Inbred backcrossing was used to reduce reproductive obstacles caused by interspecific introgression between these species [111,112]. One can examine very tiny pieces of introgressed DNA for agronomic or fiber quality performance and analyze them for QTLs by establishing a comprehensive set of Near Isogenic Introgression lines from the BC2 or BC3 families. Because recombination and segregation have split the donor genome into smaller components, the activity of specific genetic loci may be more clearly defined than in previous generations. Table 2 shows the number of QTLs detected in each of the inbred backcross groups. Rong, Feltus, Waghmare, Pierce, Chee, Draye, Saranga, Wright, Wilkins and May [18] reported the alignment of 432 fiber QTLs identified in 10 interspecific *G. hirsutum* by *G. barbadense* populations into a consensus map, providing further information on the genetic dissection of each of the fiber properties.

Table 2. Summary of QTL mapped in interspecific *Gossypium* species.

	<i>G. barbadense</i>				<i>G. tomentosum</i>			
	Gh	Gb	Total		Gh	Gt	Total	
Fiber length	17	11	28	[113]	4	0	4	[76]
Fiber strength	-	-	-		4	0	4	[76]
Micronaire	1	8	9	[89]	1	3	4	[76]
Fiber elongation	14	8	22	[114]	0	4	4	[76]

Favorable alleles: Gh = *G. hirsutum*; Gb = *G. barbadense*; Gt = *G. tomentosum*; Gm = *G. mustelinum* [90,114–116].

The QTL detection in reciprocal backcross populations of *G. hirsutum* × *G. barbadense* crosses [117] using BC4F1 and BC4F2 populations under three environmental conditions by SNP genotyping showed a small effect QTL made up 87% and 100% of QTL in *G. hirsutum* and *G. barbadense*, respectively; favorable alleles masked by unfavorable alleles, and there was higher potential for *G. hirsutum* improvement than *G. barbadense*. Three stable QTLs—two for fiber micronaire and fiber elongation in *G. hirsutum* and one for upper half mean length in *G. barbadense*—were observed, while four QTLs related to fiber quality exhibited opposite effects in reciprocal crosses, indicating the epistasis effects there [117]. Chandnani et al. (2017) studied the backcross population (BC3F1) of *G. hirsutum* × *G. mustelinum* using 216SR markers on 3202 plants, revealing allelic interactions, constraints on fixation, selection of donor alleles, and challenges in the retention of introgressed chromatin for crop improvement [118]. Waghmare et al. (2016) analyzed the introgression pattern/heredity into *G. hirsutum* from its sister *G. tomentosum* and found there were similar rates of introgression into two subgenomes of *G. hirsutum* (AtDt) and one unusual region for preferential introgression, and suggested genetic background profoundly preferential introgression, while the complex heredity of wild genetic material introgression imposed challenges to utilizing exotic genetic material crop improvements there. However, Wang et al. (2017) performed QTL mapping for fiber length in advanced backcross generations (BC₃F₂, BC₃F_{2:3} and BC₃F_{2:4}) of *G. hirsutum* × *G. mustelinum* and found the same

complexity in exotic introgression transmission but found the co-localization of many QRLs for upper half-mean length and the uniformity index of short fiber contents, indicating the co-selection potential of these QTLs for improvements [119]. The QTL mapping using the same population for fiber strength and fineness using SSR markers identified QTLs for fiber strength and 27 for micronaire and found that alleles from *G. mustelinum* increased fiber strength for 8 of the 15 QTLs and reduced micronaire length for 15 of 27 of the identified QTLs [120], supporting the notion that the fiber quality can be improved by utilizing genetic introgression from *G. mustelinum*. Transcriptome analysis for fiber strength in *G. hirsutum* line IL9 having introgression from *G. mustelinum* revealed there were 52 differentially expressed genes (DEGs) contributing to fiber strength relating to introgression from *G. mustelinum*, and two genes with known functions were identified within the fiber-strength quantitative trait loci (QTL) regions [121]. Wang et al. reported 15 stable QTLs for fiber quality and later used transcriptome analysis using same population; the integration of DEGs and QTL identified 31 genes in 9 QTLs, of which 25 probably related to fibers, suggesting candidate genes for fiber quality improvements [122]. Using a chromosome segment substitution line, Lu et al. (2021) identified six QTLs associated with fiber length and two QTLs associated with fiber strength, and through integrating transcriptome and qPCR data, they identified four promising candidate genes for fiber length associated with those QTLs [123]. A SLAF-Seq-based approach to construct high-density genetic map for Identifying fiber quality related QTL using RILs of with introgression from *G. barbadense* identified 104 QTLs, comprising 67 for fiber quality and 37 for yield-related traits, and identified six putative candidate genes for stable QTL, including *GhPEL6*, *GhCSLC6*, and *GhTBL5* for fiber length QTLs and *GhCOBL4*, *GhMYB4*, and *GhMYB85* for lint percentage QTLs [124].

The number of QTLs found for each fiber quality trait, their distributions in the genome, and the sources of favorable alleles from the respective polyploid progenitors have revealed a number of interesting findings about the genetic control of cotton fiber properties and the potential benefit of interspecific introgression. Introgressed alleles can improve Upland cotton fiber length, strength, elongation, and fineness; however, this also includes alleles from non-domesticated species with poor fiber quality as donor parents (Table 3). Nearly half of the QTLs were found in a small number of genomic regions known as ‘fiber QTL hotspots’, and the majority of the loci have predominantly additive gene action, confirming the long-held belief that polyploid *Gossypium* species are a source of valuable alleles for improving Upland cotton fiber quality. The high number of loci with minor effects, low level of consistency across loci discovered in various populations with the same pedigree, and absence of homoeologous linkage, however, underscore the overall difficulty of modifying these quantitatively inherited fiber properties. These findings show that lint fiber formation may be mediated by a complex gene network and that the evolution of spinnable fiber may have been mediated by coordinated changes in the expression of functionally different cotton genes. According to the enormous number of QTLs linked to the Dt-subgenome, which comes from an ancestor that does not generate spinnable fiber, it plays a substantial role in the genetic regulation of fiber growth and development. Despite the challenges of controlling alien alleles during introgressive breeding, a number of QTLs for fiber strength and length have now been successfully introgressed into Upland cotton, and their authenticity and improvement value has been confirmed using molecular markers: these QTLs are promising candidates for breeding using markers. Scientists from Nanjing Agricultural University in China, for example, have discovered a large fiber strength QTL (QTLFS1) on chromosome 24 in the germplasm line ‘Suyuan 7235,’ which is assumed to have been introgressed from the diploid species *G. anomalum* [115]. F₂, F₂:3, backcross, and recombinant inbred mapping populations resulting from the cross of line ‘Suyuan 7235’ ‘TM-1’ were used to find this QTL [115,116]. QTLFS1 was shown to be stable in four test locations in China and the United States over two growing seasons [125], indicating that it might be a promising option for increasing Upland cotton germplasm fiber strength. Kumar et al. [109] tested this idea by introgressing this QTL region into two

upland genotypes from the United States (‘Sealand 542’ and ‘Sealand 883’) with varied fiber strengths and found that segregating progenies bearing this QTL had enhanced fiber strength. This locus has now been independently demonstrated to possess at least three QTL clusters, with the allele from ‘Suyuan 7235’ imparting higher fiber strength, by utilizing a high marker density bordering the 10 cm gap inside the QTL region [109,126]. Shen et al. verified a fiber length QTL on Chromosome 1 (qFL-chr1) that was originally introgressed from *G. barbadense* using an inbred backcross technique [125]. The impacts of qFL-chr1 were identified in all three populations when planted in Nanjing, China, and Georgia in the United States over two years. The genetic effects of qFL-chr1 and QTLFS1 are small, with the donor alleles increasing fiber length and strength by just 1.45 mm [109] and 22.8 kN m kg⁻¹ [125], respectively. However, the acquired genetic resources and DNA marker toolkits represent two substantial contributions to Upland cotton fiber quality enhancement. First, QTL-carrying near-isogenic lines provide a novel genetic source for enhancing fiber length and strength in Upland germplasm. As previously stated, Upland cotton has a limited gene pool as a result of its evolutionary history, domestication, and current plant breeding procedures. Because farmed germplasm is so closely related, many beneficial genes, particularly those linked to production and fiber quality, may have become fixed in the top gene pool. While some transgressive segregation in fiber properties will continue to be discovered through crossing among elite parents, the use of interspecific gene combinations such as these QTLs provides an important source of new genetic variation to ensure continued genetic gain in Upland cotton fiber improvement.

Table 3. Resistant improvements against cotton’s disease and insect pests by introgressive breeding.

Disease/Pest	Causal Agents	Source ¹	Reference
Bacterial Blight	<i>Xanthomonas campestris pathovar malvacearum</i>	Ga, Gb	[127–130]
Fusarium Wilt	<i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i>	Gb	[97,131–134]
Leaf curl virus	<i>Begomoviruses</i>	Gh	[135–139]
Verticillium wilt root knot	<i>Verticillium dahliae</i>	Gb, Ga,	[140–143]
Nematodes	<i>Meloidogyne incognita</i> , <i>Rotylenchulus reniformis</i>	Gh, Gd, Gb	[144–149]
Blue Viral Disease	<i>Polerovirus</i>	Gh	[150]
Spider mites	<i>Tetranychus urticae</i>	Gb	[151–153]
Suckig pest	<i>Frankliniella occidentalis</i>	Gb, Gm Gd, Gt	[27,84,154,155]
Root rot	<i>Rhizoctonia bataticola</i>	Gh	[156–158]

¹ GB = *G. barbadense*, Gd = *G. darwinii*, Gh = *G. hirsutum*, Gm = *G. mustelinum*, Gt = *G. tomentosum*.

8. Conclusions

Polyploidization offered the tetraploid genome an advantage over its diploid forebears by allowing genes from the D-genome to be recruited to improve allopolyploid cotton fiber output and quality. Interspecific hybridization between an A-genome diploid species that produce spinnable lint fiber and a D-genome diploid species that does not produced allopolyploid cotton, which include the two species that provide the bulk of the world’s natural textile fiber. New genomic methods, such as whole genome sequencing and re-sequencing, have substantially aided our understanding of the *Gossypium* species’ origins, diversity, genome structure, and influence on human-directed evolution. More significantly, the genomic technologies combined with traditional cotton breeding will enable greater interspecific hybridization and gene introgression to offer the requisite usable genetic

variety for the genetically depleted Upland cotton gene pool to continue to develop. The use of interspecific gene combinations could help Upland cotton meet current and future cotton production challenges, such as those posed by environmental change, disease, and the need for yield stability and specific combinations of desirable fiber traits to compete favorably with synthetic textiles made from oil-based products.

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