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DISTANT HYBRIDIZATION IN COTTON (*Gossypium* spp.): WILD GENETIC RESOURCES, BARRIERS, INTROGRESSION STRATEGIES AND BREEDING PROSPECTS

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ABSTRACT

Cotton (*Gossypium* spp.) is a globally important fibre and an oilseed crop, yet genetic improvement of modern cultivars is increasingly constrained by a narrow genetic base resulting from domestication and intensive selection. Wild and related *Gossypium* species harbour extensive genetic diversity for fibre quality, resistance to biotic stresses and tolerance to abiotic stresses such as drought and salinity. Distant hybridization, involving interspecific and intergenomic crosses, provides a powerful approach for introgression of such valuable alleles into cultivated cotton. Although, its application is limited by reproductive barriers, genomic incompatibility and hybrid sterility. This review synthesizes current knowledge on the origin and evolution of *Gossypium*, cotton germplasm resources and gene pool classification, biological barriers to distant hybridization and strategies developed to overcome these constraints. Emphasis is placed on well documented case studies demonstrating successful introgression using conventional backcrossing, chromosome substitution lines, somatic hybridization, QTL mapping and genomics assisted breeding. Integration of distant hybridization with advanced genomic and biotechnological tools is highlighted as a sustainable pathway for broadening the genetic base of cultivated cotton and achieving durable genetic gains.

Keywords : Cotton; *Gossypium*; distant hybridization; wild species; introgression breeding; fibre quality.

Introduction

Cotton (*Gossypium* spp.) is principal natural fibre crop of global importance, underpinning the agricultural and textile based economies of numerous countries. In addition to fibre production, cottonseed serves as a valuable source of edible oil and protein rich meal for livestock feed, thereby enhancing the overall economic significance of the crop. India occupies a distinctive position among cotton producing nations as it is the only country where all four cultivated species *Gossypium hirsutum*, *G. barbadense*, *G. arboreum* and *G. herbaceum* are grown commercially. Among these, *G. hirsutum* (upland cotton) accounts for the largest share of global production due to its high yield potential, wide adaptability and stable performance across diverse agro

climatic environments (Khadi *et al.*, 2010; Wendel and Cronn, 2003).

Substantial progress in cotton improvement has been achieved over past decades through conventional breeding, heterosis exploitation and large scale adoption of improved hybrids and varieties (May *et al.*, 1995). However, the rate of genetic gain has slowed in recent years. Molecular and pedigree based studies have revealed a narrow genetic base in modern cotton cultivars, largely resulting from repeated use of a limited number of elite parental lines and intensive directional selection (May *et al.*, 1995; Wendel and Cronn, 2003). This genetic uniformity has increased the vulnerability of cultivated cotton to emerging insect pests, evolving pathogens and climate associated abiotic stresses such as drought, salinity and heat,

raising concerns about the long term sustainability of current production systems (Shrestha *et al.*, 2025).

Wild relatives of cotton represent an extensive yet underutilized reservoir of genetic diversity. Numerous wild *Gossypium* species possess novel alleles conferring resistance to biotic stresses, tolerance to adverse environmental conditions and potential improvements in fibre quality and yield stability (Percival *et al.*, 1999). Effective utilization of this diversity is essential for broadening the genetic base of cultivated cotton and sustaining long term genetic progress. Distant hybridization between cultivated cotton and its wild relatives provides a direct approach for introgression of beneficial genes that are absent or rare in cultivated germplasm. Such interspecific and intergeneric hybridization has been integral to cotton evolution and continues to play a critical role in pre breeding and genetic enhancement programmes (Wendel and Cronn, 2003; Khadi *et al.*, 2010).

Unlike earlier reviews that primarily emphasized either classical wide hybridization or isolated genomic investigations, the present review offers an integrated perspective linking classical cytogenetics with modern genomics assisted introgression breeding in cotton. Dispersed case studies are consolidated into actionable breeding pathways, illustrating how wild *Gossypium* species have been successfully exploited using

chromosome substitution lines, QTL introgression and high resolution genomic tools. Particular emphasis is placed on pangenome resources and introgression dynamics that enable precise tracking of alien genomic segments. The review further highlights the strategic role of distant hybridization in enhancing climate resilience, including tolerance to heat, drought and salinity, thereby providing a forward looking framework for sustainable cotton improvement through systematic utilization of wild genetic resources.

Origin and Evolution of the Genus *Gossypium*

The genus *Gossypium* belongs to the family Malvaceae and comprises approximately fifty species distributed mainly across tropical and subtropical regions of the world (Wendel *et al.*, 2010). Phylogenetic, cytogenetic and molecular evidence indicates that *Gossypium* originated nearly 5–10 million years ago and subsequently diversified into multiple distinct genome groups (Wendel and Cronn, 2003). Diploid species are classified into eight genome groups designated A, B, C, D, E, F, G and K, which exhibit clear biogeographical structuring across Africa, Asia, Australia and the New World. This long term geographic isolation and independent evolutionary history have resulted in extensive morphological, physiological and genetic diversification within the genus (Wendel *et al.*, 2010).

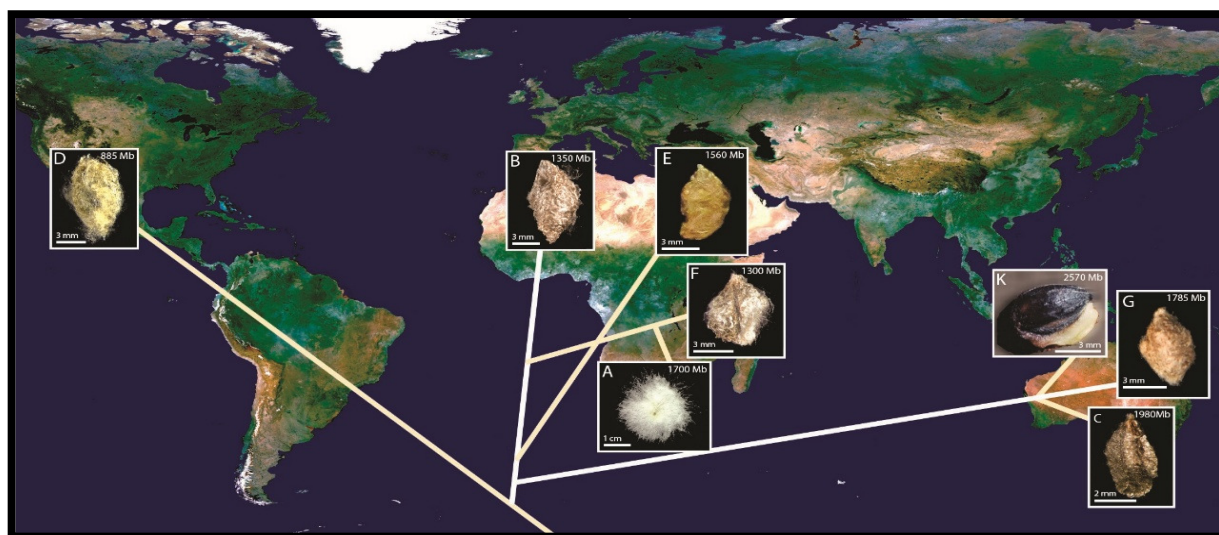


Fig. 1 : Evolutionary history of the genus *Gossypium* showing divergence into major diploid lineages including the New World clade (D genome), African-Asian clade (A, B, E and F genomes) and Australian clade (C, G and K genomes) approximately 5–10 million years ago. Adapted from Wendel *et al.* (2010).

Cultivated tetraploid cottons, *G. hirsutum* and *G. barbadense*, originated approximately 1–2 million years ago through an ancient allopolyploidization event involving hybridization between A-genome progenitor from the African-Asian region and D-genome

progenitor native to the New World, followed by chromosome doubling (Wendel and Cronn, 2003). Polyploidization played a central role in the evolution of spinnable fibres, enhanced environmental adaptability and agronomic superiority, ultimately

facilitating domestication and global dissemination of tetraploid cottons. Despite this evolutionary success, cultivated tetraploid species represent only a small fraction of the total genetic diversity present within the genus, emphasizing the importance of wild *Gossypium* species as valuable genetic resources for future cotton improvement (Wendel *et al.*, 2010).

Cotton Germplasm Resources and Gene Pool Classification

Cotton germplasm represents a wide spectrum of genetic resources including landraces, obsolete and

modern cultivars, advanced breeding lines, induced mutants, wild forms and wild *Gossypium* species (Percival *et al.*, 1999). For systematic and efficient utilization of this diversity in crop improvement, cotton germplasm is commonly categorized using a modified gene pool concept based on genetic relatedness and crossing ability (Harlan and de Wet, 1971). This classification framework has proven particularly useful for guiding pre breeding and introgression strategies in cotton improvement programmes.

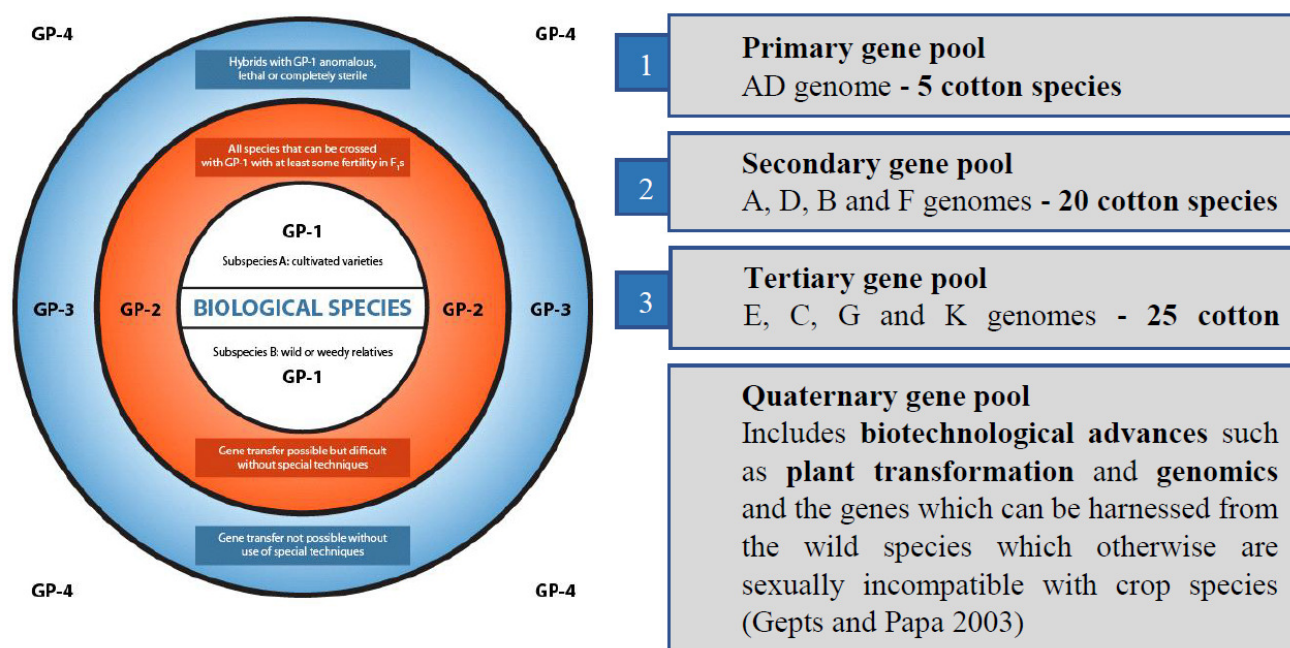


Fig. 2 : Gene pool classification of cotton germplasm and relative crossing ability of *Gossypium* species (Harlan and de Wet, 1971)

The primary gene pool comprises cultivated tetraploid cotton species and their intra specific variants, which are fully cross compatible and exhibit normal fertility (Harlan and de Wet, 1971). This gene pool forms the foundation of most commercial cotton breeding efforts due to ease of hybridization and reliable transfer of desirable agronomic traits (May *et al.*, 1995). The secondary gene pool includes closely related diploid species, primarily those belonging to the A and D genome groups. Although crosses between cultivated tetraploids and these diploids are possible, they often result in partial sterility and require cytogenetic manipulation for stabilization. Nevertheless, species in the secondary gene pool serve as important sources of resistance to insect pests and diseases, as well as tolerance to abiotic stresses.

The tertiary gene pool consists of more distantly related diploid species belonging to divergent genome

groups, where gene transfer is limited by strong reproductive barriers (Harlan and de Wet, 1971). Introgression from this pool typically necessitates specialized approaches such as bridge crossing, chromosome doubling, embryo rescue and development of chromosome substitution or introgression lines. Beyond conventional hybridization, the quaternary gene pool encompasses genetic variation accessible only through biotechnological interventions, including somatic hybridization, transgenic approaches and genome editing technologies. Strategic exploitation of secondary and tertiary gene pools through distant hybridization remains essential for broadening the genetic base of cultivated cotton and enhancing long term genetic gains (Khadi *et al.*, 2010).

Concept and Types of Distant Hybridization

Distant hybridization refers to the deliberate crossing of genetically diverse species or less commonly genera, with the objective of transferring useful traits that are absent or poorly represented in cultivated germplasm (Stebbins, 1958). In cotton improvement, distant hybridization is predominantly interspecific and involves crosses among different species within the genus *Gossypium*. This approach has been widely employed to introgress novel alleles for resistance to biotic and abiotic stresses, as well as for enhancement of fibre quality and adaptability (Khadi *et al.*, 2010).

Interspecific hybridization in cotton may involve crosses between species with the same ploidy level or between diploid and tetraploid species. Crosses involving different ploidy levels frequently result in reduced fertility, irregular chromosome pairing and meiotic abnormalities, thereby cytogenetic stabilization through chromosome doubling or other remedial techniques is required (Anwar *et al.*, 2022). Despite these challenges, such interploidy crosses have contributed significantly to the expansion of genetic variability in cultivated cotton.

Intergeneric hybridization within the family Malvaceae is rare and generally constrained by strong pre zygotic and post zygotic incompatibility barriers, limiting its practical utility in crop improvement. Consequently, interspecific hybridization remains the most feasible and widely adopted form of distant hybridization in cotton breeding programmes (Sargar *et al.*, 2023). Continued refinement of hybridization techniques and cytogenetic tools has enhanced the effectiveness of this strategy, reinforcing its importance in broadening the genetic base of cultivated cotton (Khadi *et al.*, 2010).

Barriers to Distant Hybridization in Cotton

Distant hybridization in cotton is limited by a series of biological constraints that operate at both pre fertilization and post fertilization stages (Stebbins, 1958). Pre fertilization barriers primarily involve disruptions in pollen–pistil interactions, including poor pollen germination, abnormal or arrested pollen tube growth and failure of pollen tubes to successfully reach the ovule. These incompatibilities are often intensified by differences in ploidy level, genome divergence and biochemical incongruence between pollen and pistil tissues, thereby reducing the likelihood of successful fertilization (Khadi *et al.*, 2010).

Post-fertilization barriers are generally more restrictive and represent the major impediment to wide hybrid formation in cotton. These include defective

endosperm development, premature embryo abortion, chromosome elimination, irregular chromosome pairing and cytoplasmic nuclear incompatibility (Daminova *et al.*, 2023). Such abnormalities frequently lead to hybrid inviability, reduced vigour or complete sterility, thereby limiting the direct use of interspecific or interploidy hybrids in breeding programmes (Stebbins, 1958). In cases where hybrids survive, genetic instability and breakdown in subsequent generations further constrain their utilization unless appropriate cytogenetic stabilization measures are employed (Pershina and Trubacheeva, 2017).

Strategies to Overcome Hybridization Barriers

A range of classical and modern strategies has been developed to overcome reproductive barriers associated with distant hybridization in cotton. Careful selection of parental genotypes and use of reciprocal crosses have been shown to enhance cross compatibility and improve hybrid recovery by minimizing pollen pistil incompatibility effects (Frankel and Hawkes, 1975; Khadi *et al.*, 2010). In cases involving ploidy differences, manipulation of chromosome number through induced chromosome doubling has been widely employed to restore meiotic stability and fertility in interspecific and interploidy hybrids (Stebbins, 1958).

Bridge crossing represents another effective approach, wherein an intermediate species compatible with both parental taxa is used to facilitate gene transfer between otherwise incompatible species. This method has enabled successful introgression of desirable traits from distantly related *Gossypium* species into cultivated backgrounds (Vroh *et al.*, 1999). In addition, in vitro culture techniques such as embryo rescue, ovule culture and ovary culture have been instrumental in recovering hybrid embryos that normally undergo abortion due to post fertilization barriers, thereby significantly increasing the efficiency of wide hybridization programmes (Murashige, 1974).

Biotechnological interventions further expand the scope of distant hybridization. Somatic hybridization through protoplast fusion circumvents sexual incompatibility barriers and allows direct combination of nuclear and cytoplasmic genomes from divergent species. This approach has proven useful for transferring novel traits where sexual hybridization is not feasible (Davey *et al.*, 2005). Moreover, the development of alien addition, substitution and introgression lines has facilitated stabilization, precise transfer and effective utilization of specific chromosomal segments from wild *Gossypium* species,

strengthening their role in cotton improvement programmes (Wang *et al.*, 2016).

Wild *Gossypium* Species and Their Breeding Potential

Wild *Gossypium* species represent a rich and diverse reservoir of genetic variation for numerous agronomically important traits that are largely absent in cultivated cotton. Extensive evaluation of wild and semi wild cotton germplasm has revealed their potential as sources of resistance to insect pests and diseases, tolerance to abiotic stresses and improvement of fibre quality and yield stability (Percival *et al.*, 1999).

Wild tetraploid species such as *G. tomentosum* and *G. darwinii* have been identified as valuable donors of alleles governing fibre strength, elongation and adaptation to drought and heat prone environments. Their genomic affinity with cultivated tetraploid cottons facilitates their utilization in

introgression breeding programmes. Diploid A genome species, including *G. arboreum* and *G. herbaceum*, are important sources of resistance to bacterial blight and tolerance to sucking insect pests and frequently serve as bridge species in interspecific hybridization (Xiao *et al.*, 2010).

Several D genome species contribute resistance to Verticillium wilt, bollworms, whitefly and salinity, while B, E and F genome species provide valuable traits such as cytoplasmic male sterility, cotton leaf curl virus resistance and nematode resistance. (Zhang *et al.*, 2008). Australian C-genome species further offer traits such as drought tolerance and glandless seeds, which are of increasing importance under climate change scenarios (Becerra Lopez-Lavalle *et al.*, 2011). Collectively, wild *Gossypium* species constitute indispensable genetic resources for broadening the genetic base of cultivated cotton and ensuring long term genetic improvement.





Fig. 3 : Representative wild and cultivated *Gossypium* species showing diversity in genome groups and morphological traits relevant for cotton improvement. Botanical illustrations reproduced from public domain sources (Watt, 1907).

Case Studies on Introgression Breeding in Cotton

Successful introgression breeding in cotton has been demonstrated through numerous independent and well documented studies spanning classical cytogenetics to modern genomics assisted approaches. These case studies collectively establish the practical feasibility of transferring valuable traits from wild and related *Gossypium* species into cultivated cotton and provide empirical evidence for the effectiveness of distant hybridization.

To further expand on this progress, the integration of diverse methodologies has addressed historical barriers to wide hybridization:

- Overcoming Biological Barriers:** The use of somatic hybridization and protoplast fusion has successfully overcome sexual incompatibility with wild species like *G. klotzschianum*, resulting in stable, abiotic stress tolerant hybrids.
- Genomic Mapping and Precision:** Modern QTL mapping and validation have allowed breeders to identify and introgress specific donor alleles for superior fiber traits from species such as *G. darwinii* and *G. tomentosum* without compromising the cultivated background's integrity.
- Bridge Breeding Strategies:** The application of hexaploid bridge hybrids has facilitated the transfer of critical disease resistance genes such as those for Cotton Leaf Curl Disease (CLCuD) from wild diploid species like *G. stocksii* into the tetraploid Upland genome.

- **Durable Resistance Confirmation:** Molecular marker validation now provides a framework for confirming that introgressed traits, particularly those for viral and bacterial blight resistance from donors like *G. arboreum*, are stably inherited and functionally active in advanced breeding lines.

Collectively, these case studies demonstrate that distant hybridization, when integrated with cytogenetic, molecular and genomic tools, has enabled successful introgression of diverse traits including fibre quality, disease resistance, insect resistance and abiotic stress tolerance into cultivated cotton.

Future Prospects

Future genetic improvement of cotton will increasingly rely on the strategic integration of distant hybridization with genomics assisted breeding approaches. Advances in high throughput genotyping, genome wide association studies, marker assisted selection and precise genome editing technologies have

created new opportunities to identify, track and deploy beneficial alleles from wild and related *Gossypium* species with high precision while minimizing linkage drag and undesirable background effects.

Comprehensive characterization of wild cotton germplasm through integrative multi omics approaches, including genomics, transcriptomics and phenomics, will be pivotal for uncovering novel genetic variation governing yield stability, fibre quality and resistance to biotic and abiotic stresses. The development of robust pre breeding populations, introgression lines and chromosome segment substitution lines will provide effective bridges between wild genetic resources and elite breeding materials. In the face of climate change and escalating production constraints, such integrated strategies will be essential for enhancing the resilience, adaptability and long term sustainability of global cotton production systems

Table 1 : Wild *Gossypium* species, genome groups and their breeding potent.

Species	Genome group	Key adaptive / agronomic traits	Breeding significance / utility
<i>G. hirsutum</i>	AD ₁	High yield, wide adaptability	Primary cultivated cotton; recurrent parent in introgression breeding
<i>G. barbadense</i>	AD ₂	Extra long staple fibre, superior fibre strength	Fibre quality improvement in upland cotton
<i>G. tomentosum</i>	AD ₃	Heat tolerance, nectariless trait, resistance to jassids and thrips	Donor for abiotic stress tolerance and insect resistance
<i>G. darwinii</i>	AD	Fine fibre quality, drought tolerance	Fibre improvement and stress tolerance
<i>G. arboreum</i>	A ₂	Resistance to bacterial blight, tolerance to sucking pests	Source of disease resistance; bridge species
<i>G. herbaceum</i>	A ₁	Abiotic stress tolerance, adaptability to marginal environments	Donor for stress tolerance and genetic diversification
<i>G. anomalum</i>	B ₁	Resistance to cotton wilt, angular leaf spot, aphids; CMS source	Important cytoplasmic male sterility (CMS) donor
<i>G. capitatis viridis</i>	B ₄	High fibre quality, resistance to Verticillium and Fusarium wilt	Fibre quality and disease resistance breeding
<i>G. triphyllum</i>	B ₂	Resistance to jassids, bollworms; bacterial blight resistance	Source of insect and disease resistance
<i>G. stocksii</i>	E ₁	Fibre strength, elongation, virus and drought resistance	Cotton leaf curl virus (CLCuV) resistance donor
<i>G. longicalyx</i>	F ₁	Probable CMS source; resistance to reniform nematode	Cytoplasmic male sterility and nematode resistance
<i>G. thurberi</i>	D ₁	Verticillium wilt resistance, frost tolerance	Disease resistance; D-genome introgression
<i>G. davidsonii</i>	D _{3-d}	Salinity tolerance	Donor for abiotic stress tolerance
<i>G. aridum</i>	D ₄	Resistance to reniform nematode; salinity tolerance	Nematode resistance and stress tolerance
<i>G. trilobum</i>	D ₈	Glabrous leaves; resistance to bollworm, pink bollworm, boll rot	Insect resistance breeding
<i>G. harknessii</i>	D ₂₋₂	CMS and fertility restoration	Hybrid cotton breeding programmes
<i>G. armourianum</i>	D ₂₋₁	Resistance to whitefly, bacterial blight, jassids; bridge species	Bridge species for distant hybridization
<i>G. sturtianum</i>	C ₁	Glandless seeds, photoperiod insensitivity	Oilseed quality improvement and breeding flexibility
<i>G. australe</i>	C ₃	Drought tolerance, glandless seeds	Abiotic stress tolerance; seed quality improvement

Table 2 : Different case studies of wide introgressions.

Donor species (Genome)	Recipient background	Target trait(s)	Breeding / analytical approach	Key outcome	Reference
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Drought and salt stress tolerance	Evaluation of introgression lines	Confirmed tolerance in new introgression lines.	Adams <i>et al.</i> (2011); Abdelraheem (2012); Zhang <i>et al.</i> (2012); Tiwari <i>et al.</i> (2013 ^a); Tiwari <i>et al.</i> (2013 ^b)
<i>G. arboreum</i> (A)	<i>G. hirsutum</i>	Cotton leaf curl virus (CLCuD) resistance	Introgression from Asiatic cotton	Transferred resistance genes into Upland cotton	Ahmad <i>et al.</i> (2011)
<i>G. anomalum</i> (B1)	<i>G. arboreum</i> (A2)	Fibre fineness	Backcross hybridization	Obtained fine quality cotton strains in cultivated coarse species	Apparthurai <i>et al.</i> (1964)
<i>G. thurberi</i> (D)	<i>G. hirsutum</i>	Higher fibre strength	Triple hybrid bridge: (<i>G. thurberi</i> × <i>G. arboreum</i>) × <i>G. hirsutum</i>	First use of wild species as a genetic source for high fibre strength	Beasley (1940)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Fiber quality (length, strength, elongation, micronaire)	Reciprocal backcross (S6 generation)	Significant Higher genotypic variance in <i>G. hirsutum</i> background; verified heritability of fiber traits	Chandnani <i>et al.</i> (2017)
<i>G. mustelinum</i> (AD)	<i>G. hirsutum</i>	Fiber quality, seed protein, and oil contents	Advanced backcross (BC3F1) and Whole genome re-sequencing	Identified 64 QTLs for 14 traits; <i>G. mustelinum</i> alleles increased fiber strength and improved seed pool contents	Chandnani <i>et al.</i> (2017); Zhu <i>et al.</i> (2020); Wang <i>et al.</i> (2017)
Wild <i>Gossypium</i> spp.	<i>G. hirsutum</i>	Disease resistance	Introgression + CRISPR validation	Functional confirmation of resistance genes	Chen <i>et al.</i> (2023)
<i>G. barbadense</i> (AD2)	<i>G. hirsutum</i> (AD1)	Kapas yield and superior fibre quality	Natural and planned interspecific crossing	Identified that wild/distant types contributed positively to fixable heterosis	Hutchinson (1959); Phillips (1974)
<i>G. barbadense</i> (AD)	<i>G. herbaceum</i> / <i>G. arboreum</i>	Fibre length, strength, and fineness	Interspecific hybridization	Isolated plants with 28 mm fibre length and 24 g/tex strength in diploids	Katageri <i>et al.</i> (2004)
<i>G. barbadense</i> (AD2)	<i>G. hirsutum</i> (AD1)	Fibre strength, fineness, and length	Interspecific hybridization	Evolved Varalaxmi, the first commercial hybrid with extra-long, fine, and strong fibre	Katarki (1971, 1981)
<i>G. anomalum</i> (B)	<i>G. arboreum</i>	Fibre length improvement	Wide hybridization and introgression	Developed variety AK 8401 with improved fibre length	Kulkarni <i>et al.</i> (2009)
<i>G. tomentosum</i> (AD)	<i>G. hirsutum</i>	Fibre elongation, strength, fineness	QTL mapping using introgression lines	Stable fibre quality QTLs expressed in cultivated background	Lacape <i>et al.</i> (2010)
<i>G. herbaceum</i> (A) / <i>G. australe</i>	<i>G. hirsutum</i>	"Glandless-seed and Glanded	Synthetic allotetraploid	Produced new synthetic	Liu <i>et al.</i> (2015)

(G)		plant" trait	bridge	allotetraploid (A ₁ A ₁ G ₂ G ₂) over a 9-year period	
<i>G. barbadense</i> (AD2)	<i>G. hirsutum</i> (AD1)	Yield and fibre traits	Multi-generational backcrossing (BC1 to BC4)	Found that fibre strength increased with additional backcrosses	McCarty <i>et al.</i> (1995)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Reniform nematode resistance	Interspecific crossing	Released three germplasm lines derived from Pima accession GB713.	McCarty <i>et al.</i> (2013)
<i>G. anomalum</i> (B)	Cultivated varieties	Fibre fineness and strength	Conventional and non-conventional blending	Recovered transgressive segregants with thinnest fibre and high cellulose deposition	Mehetre (2010)
<i>G. tomentosum</i> (AD3)	<i>G. hirsutum</i> (AD1)	Nectarilessness (insect resistance)	Introgressive gene transfer	Successfully transferred nectarilessness to Upland cotton (<i>e.g.</i> , DESTOM16)	Meyer and Meredith (1978); Meredith (1993)
<i>G. armourianum</i> (D)	<i>G. hirsutum</i>	Sucking pest (jassid) resistance	Male sterile triploid interspecific hybrids	Intermediate phenotypes produced; provides a source for introducing jassid resistance	Muthuraj <i>et al.</i> (2019)
<i>G. stocksii</i> (E)	<i>G. hirsutum</i>	Cotton leaf curl virus (CLCuD) resistance	Gene introgression	Transferred virus resistance genes and increased fiber strength	Nazeer <i>et al.</i> (2014)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Yield and fiber quality QTLs	Molecular markers and gene expression profiling	Identified QTLs and differentially expressed genes in introgression genotypes.	Pang <i>et al.</i> (2012 ^a); Pang <i>et al.</i> (2012 ^b); Fang <i>et al.</i> (2013 ^a); Fang <i>et al.</i> (2013b); Yu <i>et al.</i> (2012); Yu <i>et al.</i> (2013)
<i>G. aridum</i> (D)	<i>G. hirsutum</i>	Reniform nematode resistance	Bridging line introgression (Ren ari locus)	Successfully introgressed and located the resistance locus from <i>G. aridum</i> into Upland cotton	Romano <i>et al.</i> (2009)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i> (TM-1)	Various agronomic and fiber traits	Chromosome Substitution Lines (CSL)	Identified specific Pima chromosomes that improve fiber length and strength.	Saha <i>et al.</i> (2004); Saha <i>et al.</i> (2006 ^a); Jenkins <i>et al.</i> (2007 ^a); Jenkins <i>et al.</i> (2007 ^b)
<i>G. tomentosum</i> (AD)	<i>G. hirsutum</i>	Genomic mapping and marker localization	Monosomic and monotelodisomic substitution hybrids	Identified numerical and structural variations; offered germplasm for backcross substitution line development	Saha <i>et al.</i> (2006 ^b)
<i>G. anomalum</i> (B)	<i>G. hirsutum</i>	Fiber strength (QTLFS1)	F2, backcross, and RIL mapping populations	Identified a stable, large fiber strength QTL on chromosome 24 in the 'Suyuan 7235'	Shen <i>et al.</i> (2005); Zhang <i>et al.</i> (2003)

				line	
<i>G. klotzschianum</i> (D)	<i>G. hirsutum</i>	Abiotic stress tolerance	Somatic hybridization (protoplast fusion)	Overcome sexual incompatibility; stable stress tolerant somatic hybrids	Sun <i>et al.</i> (2004)
<i>G. barbadense</i> (AD2)	<i>G. hirsutum</i> (AD1)	Phenotypic and genetic diversity	RAPD markers and morphological traits	Identified genotypes genetically and phenotypically distinct from typical parent types	Tatineni <i>et al.</i> (1996)
<i>G. darwinii</i> (AD)	<i>G. hirsutum</i>	Root-knot nematode resistance	Interspecific crossing and screening	Identified natural variation as a tool to broaden the genetic base for nematode resistance	Turcotte <i>et al.</i> (1963)
<i>G. barbadense</i> (AD2)	<i>G. herbaceum</i> / <i>G. arboreum</i>	Yield, fibre length, and strength	Interspecific crossing and BC2 populations	Achieved recombinants with significantly higher fibre length (32.0 mm) and strength (27.4 g/tex)	Veeresh Gowda <i>et al.</i> 2004
<i>G. anomalum</i> (B1)	<i>G. hirsutum</i> (AD1)	Bacterial blight immunity and sucking pest tolerance	Interspecific hybridization	Developed variety Arogya for rainfed conditions with introgressed resistance	Vinitha and Phundhan Singh (2004)
<i>G. thurberi</i> (D) / <i>G. raimondii</i> (D) / <i>G. sturtianum</i> (C)	<i>G. hirsutum</i>	Glanded plant with low gossypol seeds	Trispecies bridge crosses & in vitro embryo culture	Developed germplasm with low gossypol seeds and normally glanded vegetative parts	Vroh <i>et al.</i> (1999)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Fusarium wilt resistance	Mendelian genetic analysis	Identified dominant resistance gene (Fov1) in Pima S-7	Wang and Roberts (2006)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Long staple fiber quality	Chromosome Segment Introgression Lines	Developed 174 CSIL representing 83% of the tetraploid genome	Wang <i>et al.</i> (2012 ^a)
<i>G. tomentosum</i> (AD)	<i>G. hirsutum</i>	Fibre uniformity, strength	Multi-environment QTL validation	Consistent fibre improvement across environments	Wang <i>et al.</i> (2012 ^b)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Glandless stem and bolls (Gl2e)	Interspecific crossing	Successful transfer of a dominant glandless gene allele	Yuan <i>et al.</i> (2000)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Fiber quality, sub-okra leaf, and heterosis	Interspecific crossing	Developed high-yielding lines with sub-okra leaf or high fiber quality	Zhang (1993 ^a)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Resistance to spider mites and Verticillium wilt	Interspecific crossing	Introduced resistance genes from Pima to Upland	Zhang (1993 ^b); Zhang (2011)
<i>G. anomalum</i> (B1)	<i>G. hirsutum</i> (AD1)	Fibre strength QTLs	SSR and RAPD marker identification	Identified nine molecular markers linked to major fibre strength QTLs	Zhang <i>et al.</i> (2003)
<i>G. davidsonii</i> (D)	<i>G. hirsutum</i>	Salinity tolerance, pest resistance	Wide hybridization + backcrossing	Fertile derivatives with introgressed resistance segments	Zhang <i>et al.</i> (2008)
<i>G. barbadense</i> (AD)	<i>G. hirsutum</i>	Thrips resistance	Interspecific crossing	Successful inheritance and transfer of resistance	Zhang <i>et al.</i> (2013)

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