

Research Insight

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The Role of Interspecific Introgression in the Adaptation of *Gossypium* Species

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Cotton Genomics and Genetics, 2024, Vol.15, No.2 doi: [10.5376/cgg.2024.15.0009](https://doi.org/10.5376/cgg.2024.15.0009)

Received: 15 Feb., 2024

Accepted: 21 Mar., 2024

Published: 02 Apr., 2024

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Preferred citation for this article:

Zhang X., and Wang S.J., 2024, The role of interspecific introgression in the adaptation of *Gossypium* species, Cotton Genomics and Genetics, 15(2): 93-102 (doi: [10.5376/cgg.2024.15.0009](https://doi.org/10.5376/cgg.2024.15.0009))

Abstract The role of interspecific introgression in the adaptation of *Gossypium* species is crucial. *Gossypium* species exhibit rich diversity and wide geographic distribution, with adaptability being key to their survival and development. Interspecific introgression, the process of gene flow between different species, has played a significant role in the adaptation and evolution of *Gossypium* species. This study reviews the applications and adaptive advantages of interspecific introgression in *Gossypium* species, including enhanced abiotic stress tolerance, improved biotic resistance, increased yield and fiber quality, and broadened genetic diversity. By analyzing the taxonomy, geographic distribution, and evolutionary history of *Gossypium* species, this study explores the genetic basis of introgression, mechanisms of gene flow, and methods for detecting and analyzing introgressed genes. Additionally, historical and modern cases are examined to illustrate hybridization events and their impacts. On the molecular and genomic front, the study employs genomic tools to identify key genes and pathways involved in the introgression process. Although interspecific introgression shows great promise in breeding programs and genetic engineering, its implementation faces challenges. This study aims to guide future research by leveraging interspecific introgression to promote the conservation of *Gossypium* species and sustainable agricultural development, offering potential solutions for climate change adaptation.

Keywords Interspecific introgression; *Gossypium* species; Adaptability; Gene flow; Molecular genomics

1 Introduction

Gossypium, commonly known as cotton, is a genus that includes several species of significant economic importance due to their fiber production. The genus is divided into diploid and polyploid species, with the latter including the two most widely cultivated species, *Gossypium hirsutum* and *Gossypium barbadense*. *G. hirsutum*, also known as upland cotton, accounts for the majority of global cotton production, while *G. barbadense*, known for its superior fiber quality, is cultivated in more specialized markets (Fraïsse et al., 2016; Fang et al., 2021; Wang et al., 2022). Adaptation is crucial for the survival and productivity of *Gossypium* species in diverse environmental conditions. The ability to adapt to various climates and resist biotic and abiotic stresses determines the success of cotton cultivation. Adaptation mechanisms include genetic diversity, phenotypic plasticity, and the ability to acquire beneficial traits through processes such as introgression. These adaptive traits are essential for improving yield, fiber quality, and resistance to pests and diseases (Han et al., 2015; Chhatre et al., 2018; Wang et al., 2022).

Interspecific introgression refers to the transfer of genetic material between species through hybridization and backcrossing. This process can introduce new genetic variations that are not present in the original species, potentially leading to the acquisition of advantageous traits. In *Gossypium*, introgression from *G. hirsutum* to *G. barbadense* has been shown to significantly enhance genetic diversity and contribute to the adaptation and improvement of agronomic traits (Fraïsse et al., 2016; Hamilton and Miller, 2016; Wang et al., 2022). The significance of interspecific introgression lies in its ability to facilitate rapid adaptation to changing environments and improve crop performance, making it a valuable tool in plant breeding and conservation (Hamilton and Miller, 2016; Chhatre et al., 2018; Fang et al., 2021).

By examining the genetic and phenotypic impacts of introgression on *Gossypium* species, identifying key introgressed traits that contribute to adaptation and agronomic improvement, and discussing the mechanisms and evolutionary significance of introgression in *Gossypium*, this study hopes to provide new insights into the

potential applications of introgression in cotton breeding programs. By synthesizing findings from recent studies, this study will provide a comprehensive understanding of how interspecific introgression drives adaptation and enhances the genetic potential of *Gossypium* species.

2 *Gossypium* Genus: Diversity and Evolution

2.1 Taxonomy and classification

The *Gossypium* genus, commonly known as cotton, comprises approximately 50 species, including both diploid and tetraploid species. The primary cultivated species are *Gossypium hirsutum* and *Gossypium barbadense*, both of which are tetraploid and originated in the Americas. These species are classified based on their genomic constitution, with *G. hirsutum* and *G. barbadense* sharing the AD genome, a result of an ancient hybridization event between an A-genome diploid and a D-genome diploid species (Nie et al, 2020; Fang et al., 2021; Wang et al., 2022).

2.2 Geographic distribution and habitat variability

Gossypium species are distributed globally, with a significant presence in tropical and subtropical regions. *G. hirsutum* is widely cultivated due to its high yield, while *G. barbadense* is valued for its superior fiber quality. The geographic distribution of these species has been influenced by human cultivation practices, leading to their presence in diverse habitats ranging from arid to semi-arid regions. The adaptability of these species to various environmental conditions is partly due to interspecific introgression, which has introduced beneficial traits from one species to another, enhancing their ability to thrive in different habitats (Nie et al, 2020; Fang et al., 2021; Wang et al., 2022).

2.3 Evolutionary history and phylogeny

The evolutionary history of the genus *Gossypium* is characterized by hybridization and polyploidization events. Tetraploid species, including *G. hirsutum* and *G. barbadense*, originated from a hybridization event between an A-genome species from Africa or Asia and a D-genome species from the Americas. This event led to the formation of the AD genome, which has been crucial for the diversification and adaptability of these species. Introgression between species has played a key role in the evolutionary dynamics of *Gossypium*, promoting genetic diversity and the development of agriculturally important traits. Studies have shown that introgression from *G. hirsutum* to *G. barbadense* significantly influenced the latter's genetic structure and phenotypic traits, enhancing its adaptation to various environments and improving fiber quality (Zhang et al., 2016; Nie et al., 2020; Fang et al., 2021; Wang et al., 2022). Interspecific introgression events between *G. barbadense* and *G. hirsutum* have primarily driven population differentiation and agronomic trait variation (Figure 1). These introgression events have significantly increased the genetic diversity and degree of differentiation in *G. barbadense*.

Figure 1 shows the geographical distribution of 93 ex-situ samples collected in 1967 in Morelos, Mexico, and 13 in-situ samples re-collected in 2017. These samples represent maize landraces from different municipalities, providing detailed geographical references and sample race information. The different colors and shapes of the points indicate the status of the samples in 2017 and the races they represent, such as Ancho, Chalqueño, Cónico, Pepitilla, and Elotes Cónicos. Through these geographical distributions and sample descriptions, the study reveals the genetic diversity and selective pressures in different regions. This figure illustrates that landraces exhibit significant genetic variation across different geographical areas, highlighting the importance of in-situ and ex-situ conservation strategies in maintaining and utilizing maize genetic diversity.

The *Gossypium* genus exhibits remarkable diversity and evolutionary complexity, driven by hybridization, polyploidization, and interspecific introgression. These processes have not only shaped the taxonomy and classification of the genus but also enabled its widespread geographic distribution and adaptation to diverse habitats. The evolutionary history and phylogeny of *Gossypium* highlight the importance of genetic exchange in the development of traits that are critical for the survival and cultivation of these economically important species.

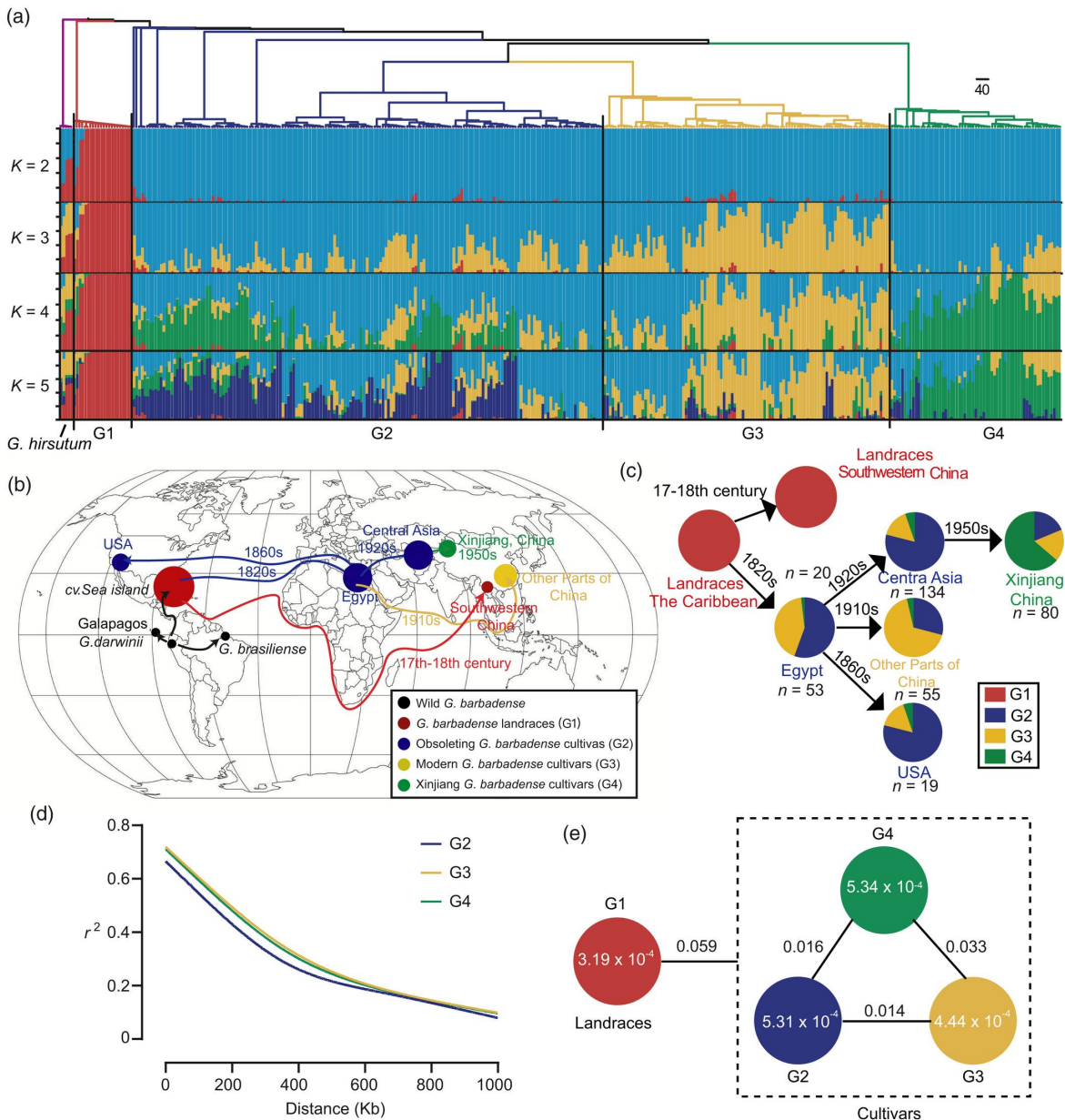


Figure 1 Genetic diversity and introduction history of *Gossypium barbadense* (Adopted from Wang et al., 2022)

Image caption: (a) The upper panel shows a neighbor-joining tree of 365 *G. barbadense* and five *Gossypium hirsutum* accessions constructed using 252 609 SNPs. (b) The left panel shows the dispersal route of *G. barbadense* among the major cultivation regions according to the literature. (c) The right panel indicates the genomic components of the four groups in the major cultivation regions. (d) Genome-wide averages of linkage disequilibrium (LD) decay in three cultivar groups. (e) Genetic diversity and population differentiation across four groups. Values in the circles represent the nucleotide diversity (π), and the values between the groups indicate population differentiation (F_{ST}). The cultivars shown include all the accessions in groups G2, G3, and G4 (Adopted from Wang et al., 2022)

3 Mechanisms of Interspecific Introgression

3.1 Genetic basis of introgression

Interspecific introgression in *Gossypium* species involves the transfer of genetic material from one species to another through hybridization and backcrossing. This process can significantly alter the genomic architecture of the recipient species, leading to increased genetic diversity and the introduction of beneficial traits. For instance, introgression from *G. hirsutum* to *G. barbadense* has been shown to reorganize the genomic structure of *G. barbadense*, contributing to population divergence and agronomic trait variation (Wang et al., 2022). Similarly, the introgression of chromatin from *G. tomentosum* into *G. hirsutum* has been studied to understand the

transmission genetics and the evolutionary consequences of such genetic exchanges. These introgressions often involve complex interactions between subgenomes, as seen in polyploid species like *G. hirsutum*, where multilocus interactions predominantly occur within the Dt subgenome (Waghmare et al., 2016).

3.2 Mechanisms facilitating gene flow

Several mechanisms facilitate gene flow between *Gossypium* species, including natural hybridization, human-mediated breeding programs, and the use of chromosome segment introgression lines (CSILs). Natural hybridization can occur in regions where different *Gossypium* species coexist, leading to spontaneous gene flow. Human-mediated breeding programs often involve controlled crosses and backcrosses to introduce desirable traits from one species into another. For example, the development of CSILs has been used to transfer long staple fiber quality traits from *G. barbadense* into the *G. hirsutum* background, utilizing molecular marker-assisted selection to track and select for introgressed segments (Wang et al., 2012). Additionally, the use of synthetic amphiploids has enabled the introgression of genes from diploid species like *G. arboreum* into tetraploid species like *G. hirsutum*, despite the challenges posed by species isolation and chromosomal structural variations (Feng et al., 2021).

3.3 Detection and analysis of introgressed genes

The detection and analysis of introgressed genes in *Gossypium* species involve various genomic and bioinformatic techniques. Genome-wide association studies (GWAS) and quantitative trait locus (QTL) mapping are commonly used to identify introgressed loci associated with specific traits. For instance, GWAS and QTL mapping have been employed to detect fiber-micronaire-related haplotype blocks in *G. barbadense*, one of which was introgressed from *G. hirsutum* (Wang et al., 2022). High-density genetic variation maps and specific locus amplified fragment sequencing (SLAF-seq) have also been utilized to identify introgression events and their effects on agronomic traits in both *G. hirsutum* and *G. barbadense* (Keerio et al., 2018; Nie et al., 2020). These methods allow researchers to pinpoint the genomic regions involved in introgression and assess their impact on phenotypic traits, thereby providing valuable insights for crop improvement and breeding programs.

4 Interspecific Introgression in *Gossypium* Species

4.1 Historical cases of introgression

Interspecific introgression has played a significant role in the evolution and adaptation of *Gossypium* species. Historical genetic introgression between *Gossypium hirsutum* and *Gossypium barbadense* has been documented, with evidence suggesting that these events have contributed to the improvement of agronomic traits in both species. For instance, a study on the genetic variation in cotton varieties developed in Xinjiang, China, identified several interspecific introgression events that were beneficial for fiber quality and yield traits in both *G. hirsutum* and *G. barbadense* (Nie et al., 2020). These introgressions have significantly enhanced fiber strength, length, and yield, while also improving the plants' adaptability to environmental stresses. Specifically, gene introgression events between *G. barbadense* and *G. hirsutum* have played a crucial role in enhancing agronomic traits in cotton (Figure 2).

Figure 2 from Nie et al. (2020) illustrates the impact of interspecific introgression, population differentiation, and gene flow between *Gossypium barbadense* and *Gossypium hirsutum*. The figure displays the genetic structure of different populations and the genomic distribution of introgression events, revealing how interspecific introgression reshapes the genomic architecture of cotton. The study indicates that these introgression events significantly affect fiber quality and agronomic traits in cotton. By selecting favorable haplotypes, it is possible to enhance cotton's adaptability and performance in various environments. These findings provide a scientific basis for further utilizing genetic diversity to improve cotton.

4.2 Modern examples and case studies

Recent studies have further elucidated the role of interspecific introgression in modern cotton breeding. For example, a comprehensive interspecific haplotype map revealed that six introgressions from *G. hirsutum* to *G. barbadense* were significantly associated with phenotypic performance, explaining a substantial portion of the variation in yield and fiber qualities (Fang et al., 2021). Another study focused on the breeding potential of

introgression lines (ILs) developed from interspecific crossing between Upland cotton and *G. barbadense*, highlighting the high heterotic vigor and improved yield and fiber quality in hybrids (Zhang et al., 2016). These findings underscore the potential of interspecific introgression in enhancing the genetic base and agronomic performance of cotton cultivars.

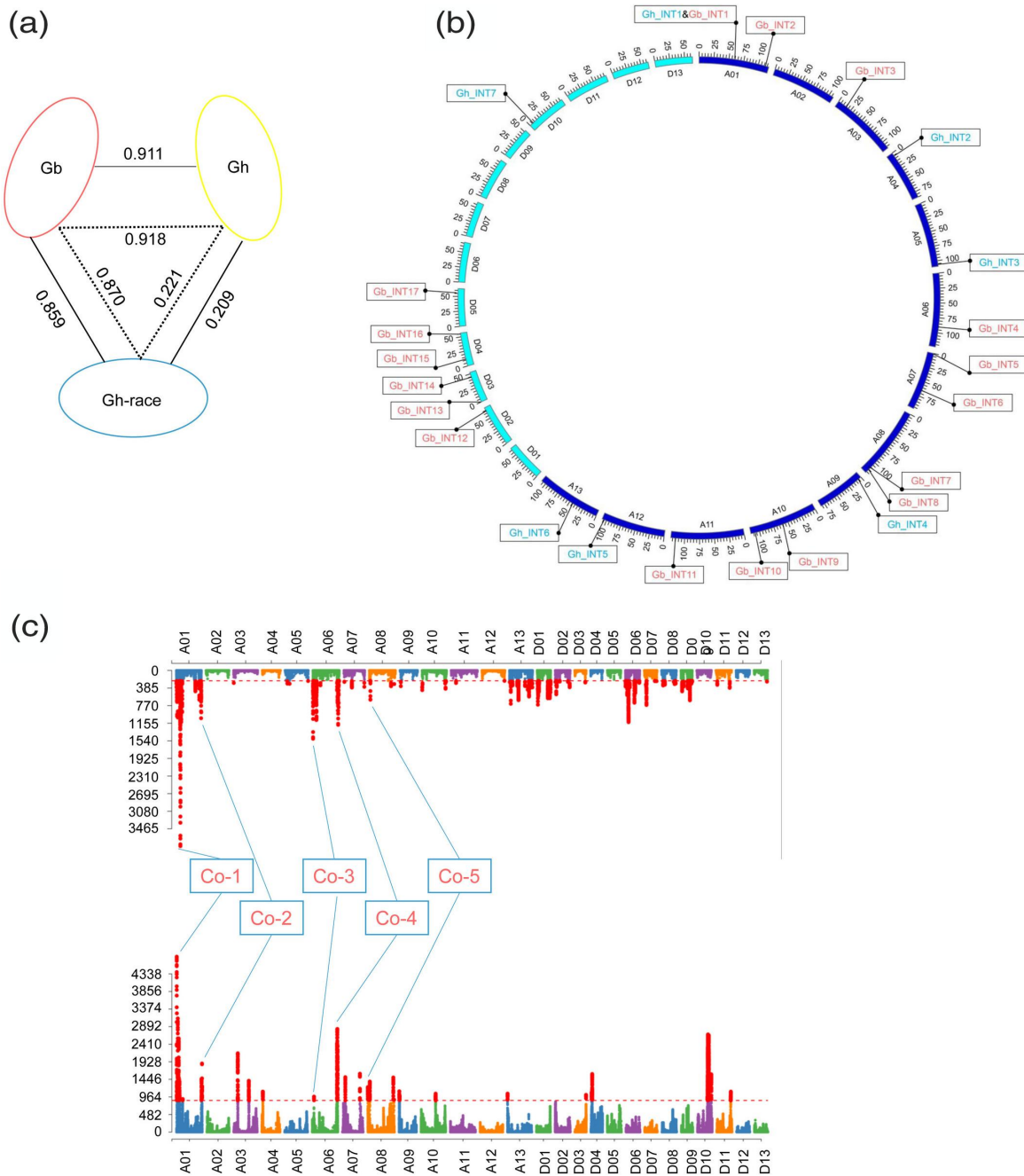


Figure 2 Population differentiation, introgression and selection (Adopted from Nie et al., 2020)

Image caption: (a) The population differentiation with and without introgression events among Gh, Gb and Gh-race groups; (b) Genetic introgressions in genome-wide scale. Gb-INT, introgression event from Gh to Gb; Gh-INT, introgression event from Gb to Gh; (c) Selective sweeps and co-selected loci in Gh and Gb panels (Adopted from Nie et al., 2020)

4.3 Hybridization events and their impact

Hybridization events between *Gossypium* species have had profound impacts on their genetic makeup and adaptation. Molecular evidence suggests that hybridization and introgression have been crucial in maintaining species integrity and cohesion in naturally isolated populations, such as those of inselberg bromeliads (Mota et al., 2018). In the context of *Gossypium*, hybridization has facilitated the transfer of adaptive alleles, contributing to

the divergent improvement of *G. hirsutum* and *G. barbadense* (Fang et al., 2021; Wang et al., 2022). Moreover, the introgression of adaptive genes has been shown to be environment-dependent, with specific alleles being favored under certain environmental conditions, thereby aiding in the adaptation to changing climates (Khodwekar and Gailing, 2017).

Interspecific introgression has been a pivotal mechanism in the adaptation and improvement of *Gossypium* species, with historical and modern examples demonstrating its significant impact on genetic diversity, agronomic traits, and environmental adaptation. The continued study and utilization of introgression in cotton breeding hold promise for further advancements in crop performance and resilience.

5 Adaptive Benefits of Interspecific Introgression

5.1 Enhanced abiotic stress tolerance

Interspecific introgression has been shown to significantly enhance abiotic stress tolerance in *Gossypium* species. For instance, introgression from *Gossypium hirsutum* into *Gossypium barbadense* has led to the identification of loci associated with adaptation to high-latitude environments, which are indicative of improved tolerance to abiotic stresses such as temperature extremes (Wang et al., 2022). Additionally, the introgression of genetic material from *G. arboreum* into *G. hirsutum* has revealed potential for improving traits related to abiotic stress resilience, such as boll number and fiber quality under varying environmental conditions (Feng et al., 2021).

5.2 Improved biotic resistance

Introgression also plays a crucial role in enhancing biotic resistance in *Gossypium* species. The transfer of genetic material from *G. barbadense* to *G. hirsutum* has been associated with improved resistance to pests and diseases, which is critical for maintaining crop health and productivity (Zhang et al., 2016). Moreover, the introgression of alleles from *G. tomentosum* into *G. hirsutum* has been shown to confer resistance to specific biotic stresses, further highlighting the importance of interspecific gene flow in developing resilient cotton varieties (Waghmare et al., 2016; Keerio et al., 2018).

5.3 Increased yield and fiber quality

One of the most significant benefits of interspecific introgression is the improvement in yield and fiber quality. Studies have demonstrated that introgression from *G. hirsutum* to *G. barbadense* has led to the identification of loci that significantly enhance fiber yield and quality traits (Nie et al., 2020). Similarly, the development of introgression lines (ILs) from *G. hirsutum* and *G. barbadense* has resulted in hybrids with high heterotic vigor, outperforming their parent cultivars in terms of yield and fiber quality across multiple generations (Zhang et al., 2016). Additionally, introgressed alleles from *G. barbadense* have been identified that contribute to superior fiber quality in *G. hirsutum*, without negatively impacting lint yield (Chen et al., 2018).

5.4 Broadened genetic diversity

Interspecific introgression is a powerful tool for broadening the genetic diversity of *Gossypium* species. The introgression of genetic material from *G. hirsutum* into *G. barbadense* has significantly increased the genetic diversity and divergence within *G. barbadense* populations, which is crucial for the long-term sustainability and adaptability of the species (Wang et al., 2022). Furthermore, the introgression of *G. arboreum* genes into *G. hirsutum* has introduced valuable genetic variation that was previously untapped due to species isolation, thereby enhancing the genetic base available for cotton breeding (Feng et al., 2021). This broadened genetic diversity is essential for developing new cultivars with improved agronomic traits and resilience to environmental changes (Hamilton and Miller, 2016).

6 Molecular and Genomic Insights

6.1 Genomic tools for studying introgression

The study of interspecific introgression in *Gossypium* species has been significantly advanced by the development and application of various genomic tools. High-throughput sequencing technologies, such as Specific Locus Amplified Fragment Sequencing (SLAF-seq), have enabled the identification of single nucleotide polymorphisms (SNPs) across the genome, facilitating the mapping of quantitative trait loci (QTLs) associated with fiber quality

and yield traits (Keerio et al., 2018). Additionally, genome-wide association studies (GWAS) have been employed to detect introgression events and selective sweep loci, providing insights into the genetic basis of agronomic traits in *Gossypium hirsutum* and *Gossypium barbadense* (Nie et al., 2020). Chromosome segment introgression lines (CSILs) have also been developed using molecular marker-assisted selection, allowing for the detailed analysis of introgressed segments and their effects on fiber quality traits (Wang et al., 2012).

6.2 Key genes and pathways involved

Introgression events have been shown to introduce key genes and pathways that contribute to the adaptation and improvement of *Gossypium* species. For instance, the introgression of haplotype blocks from *G. hirsutum* to *G. barbadense* has been linked to significant improvements in fiber micronaire and other agronomic traits (Wang et al., 2022). In *G. barbadense*, specific introgressed loci have been associated with enhanced fiber yield and quality, highlighting the role of these genetic elements in the species' adaptation to different environments (Nie et al., 2020). Furthermore, genes involved in stress response, digestive absorption, and secondary metabolite synthesis have been identified as having significant introgression signals, suggesting their importance in environmental adaptation and biocomponent metabolism (Jiang et al., 2022).

6.3 Functional genomics and transcriptomics

Functional genomics and transcriptomics approaches have provided deeper insights into the molecular mechanisms underlying introgression and its effects on *Gossypium* species. The use of high-density genetic variation maps has revealed the correlation between asymmetric interspecific introgressions and the improvement of agronomic traits in both *G. hirsutum* and *G. barbadense* (Nie et al., 2020). Transcriptomic analyses have identified key genes with pleiotropic effects that control multiple traits, such as growth period, plant architecture, and vegetative growth habit, further elucidating the complex genetic interactions resulting from introgression (Wang et al., 2022). Additionally, the integration of metabolomic data with genomic analyses has highlighted the role of specific genes, such as CYP512U6, in the biosynthesis of important secondary metabolites, demonstrating the functional impact of introgressed genes on the metabolic pathways of *Gossypium* species (Jiang et al., 2022).

7 Challenges and Controversies

7.1 Barriers to introgression

Despite the potential benefits, several barriers to successful introgression exist. One major challenge is the genetic incompatibility between species, which can hinder the transfer of desirable traits. For example, while interspecific introgression has been shown to improve certain traits in *G. barbadense*, it often comes with trade-offs, such as decreased fiber quality when yield is increased, and vice versa (Fang et al., 2021). Additionally, the narrow genetic base of *G. hirsutum* poses a significant barrier, limiting the effectiveness of introgression from *G. barbadense* (Zhang et al., 2016).

7.2 Potential negative consequences

The process of introgression is not without its potential drawbacks. One concern is the possibility of introducing deleterious alleles along with beneficial ones, which can negatively impact the overall fitness of the recipient species. For instance, while introgression has been shown to improve fiber yield in *G. barbadense*, it can also lead to a decrease in fiber quality (Nie et al., 2020; Fang et al., 2021). Moreover, the introduction of foreign genetic material can disrupt existing gene networks, leading to unforeseen phenotypic consequences.

7.3 Ethical and ecological considerations

The ethical and ecological implications of interspecific introgression must also be carefully considered. From an ethical standpoint, the manipulation of genetic material between species raises questions about the long-term impacts on biodiversity and the natural evolutionary processes. Ecologically, the introduction of new genetic material can have unpredictable effects on local ecosystems, potentially leading to the displacement of native species or the disruption of existing ecological balances (Hamilton and Miller, 2016). Conservation practitioners have traditionally been wary of hybridization due to these potential risks, although some argue that adaptive introgression could be a valuable tool for enhancing the evolutionary potential of species in the face of climate change (Hamilton and Miller, 2016).

8 Future Perspectives and Applications

8.1 Breeding programs and genetic engineering

Interspecific introgression has shown significant potential in enhancing the genetic diversity and agronomic traits of *Gossypium* species. The integration of genetic material from *Gossypium barbadense* into *Gossypium hirsutum* has been particularly beneficial in improving fiber quality and yield traits. Studies have demonstrated that introgression lines (ILs) developed from interspecific crosses exhibit high heterosis and combining ability, making them valuable for breeding programs aimed at yield and fiber quality improvement (Zhang et al., 2016; Keerio et al., 2018; Nie et al., 2020). Furthermore, the identification of quantitative trait loci (QTLs) associated with desirable traits in introgressed populations provides a roadmap for targeted genetic engineering efforts to enhance specific characteristics in cotton cultivars (Wang et al., 2012; Keerio et al., 2018).

8.2 Conservation and sustainable agriculture

Adaptive introgression is not only a tool for crop improvement but also holds promise for conservation and sustainable agriculture. The movement of genetic material between species can increase genetic diversity and resilience, which is crucial for maintaining evolutionary potential in changing environments (Hamilton and Miller, 2016; Burgarella et al., 2018; Suarez-Gonzalez et al., 2018). The conservation value of natural hybrid zones and the role of introgression in mediating extinction risk and enabling demographic recovery are increasingly recognized as important strategies for preserving biodiversity and ecosystem services (Hamilton and Miller, 2016; Miller and Hamilton; 2016). By leveraging the genetic diversity introduced through interspecific introgression, sustainable agricultural practices can be developed to ensure long-term productivity and environmental health.

8.3 Potential for climate change adaptation

Climate change poses significant challenges to agricultural systems, necessitating the development of crops that can withstand new environmental stresses. Interspecific introgression offers a mechanism for rapid adaptation by introducing alleles that confer resilience to changing climatic conditions. Studies have shown that introgressed alleles can enhance traits such as drought tolerance, heat resistance, and overall fitness in novel environments (Hamilton and Miller, 2016; Suarez-Gonzalez et al., 2018; Wang et al., 2022). The ability to harness adaptive introgression for climate change adaptation is particularly valuable, as it provides a means to quickly incorporate beneficial traits from wild relatives into cultivated species, thereby enhancing their ability to cope with environmental fluctuations (Miller and Hamilton; 2016; Burgarella et al., 2018).

9 Concluding Remarks

Interspecific introgression has played a significant role in the adaptation and improvement of *Gossypium* species, particularly *Gossypium hirsutum* and *Gossypium barbadense*. Studies have shown that introgressed haplotypes from *G. hirsutum* to *G. barbadense* have contributed to population divergence and increased genetic diversity, which are crucial for adaptation to different environments and improvement of agronomic traits. The introgression events have been associated with significant phenotypic variations, including yield and fiber quality, highlighting their potential in breeding programs. Additionally, the development of chromosome segment introgression lines (CSILs) has facilitated the transfer of desirable traits, such as long staple fiber quality, from *G. barbadense* to *G. hirsutum*, demonstrating the practical applications of introgression in cotton breeding.

Future research should focus on the detailed characterization of introgressed regions to identify specific genes and their functions in trait improvement. Advanced genomic tools and techniques, such as genome-wide association studies (GWAS) and molecular marker-assisted selection, should be employed to enhance the precision of introgression breeding. Additionally, exploring the potential of adaptive introgression in response to climate change could provide valuable insights into the conservation and management of genetic resources in cotton and other crops. Understanding the mechanisms underlying the stability and expression of introgressed traits across different environments will be crucial for developing resilient and high-performing cotton varieties.

Interspecific introgression has proven to be a powerful tool in the adaptation and improvement of *Gossypium* species. It has facilitated the transfer of beneficial traits, enhanced genetic diversity, and contributed to the development of superior cotton varieties with improved yield and fiber quality. As we face the challenges of

climate change and the need for sustainable agricultural practices, the role of introgression in breeding programs will become increasingly important. By leveraging the genetic potential of interspecific introgression, we can continue to enhance the adaptability and productivity of cotton, ensuring its viability as a critical crop for the future.

Acknowledgments

The authors extend sincere thanks to two anonymous peer reviewers for their feedback on the manuscript of this paper, whose evaluations and suggestions have greatly contributed to the improvement of the manuscript.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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