

ANCIENT TO MODERN ORIGINS: THE EVOLUTIONARY JOURNEY OF *GOSSYPIUM* GENUS AND ITS IMPLICATIONS FOR COTTON BREEDING

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ABSTRACT

Approximately 10-15 million years ago, this genus experienced rapid global radiation, leading to the emergence of eight major genome groups (A through G and K) consisting of 13 chromosomes in each group. Moreover, over the past 1-2 million years, the transoceanic dispersal of an A-genome taxon to the New World and subsequent hybridization with a native D-genome diploid resulted in the rise of allopolyploid cotton. This evolutionary process led to the diversification of three modern lineages encompassing seven described species, including the economically significant *G. hirsutum* L. and *G. barbadense* L. A parallel evolution, driven by human intervention, unfolded as these two allopolyploids were domesticated. Simultaneously, the independent domestication of two A-genome diploids, *G. arboreum* L. and *G. herbaceum* L., originally from Africa-Asia occurred. Recent genomic investigations have unlocked its paleopolyploid history of diploid species and shed light on the surprisingly high frequency of natural interspecific hybridization within and between genome groups. Furthermore, these studies have elucidated the diverse molecular mechanisms underlying allopolyploid genome evolution and provided a more refined understanding of the evolutionary association among the gene pools of each of the four cultivated species. *Gossypium* is an exceptionally diverse group, encompassing variations in fiber morphology, stress tolerance, and other agronomic characteristics, and represents a vast resource for breeders striving to develop improved cotton varieties. This comprehensive understanding of *Gossypium* genome evolution and its implications for targeted breeding paves the way for advancements in sustainable cotton agriculture.

Keywords: Polyploidy, Domestication, *Gossypium*, Diversity, Evolution

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1. INTRODUCTION

The cotton genus, *Gossypium*, encompasses a diverse array of species that hold immense agricultural significance and serve as captivating examples of biodiversity evolution (Zhou et al., 2022). The thriving global industry of cotton fiber production, derived from the epidermal seed trichomes of cultivated species, contributed 72.46 billion US\$ to the economy for the year 2021/2022. This value has decreased to 63.24 billion US\$ for 2022/2023 (<https://icac.org/News/News?YearsId=2023>) (Viot, 2019). Within the cotton genus, four distinct species have been independently domesticated, each displaying varying ploidy levels, making them intriguing subjects for evolutionary research (Wendel et al., 1992). Extensive investigations in this domain have primarily focused on unraveling the intricate evolutionary relationships among different species of cotton, delving into the consequences of polyploidy, studying the process of domestication, and obtaining an inclusive comprehension of the distinct biological characteristics that bestow cotton with its immense agricultural value. Recent technological advancements have greatly accelerated our understanding of cotton's biology and evolution, paving the way for novel research directions and innovative methodologies (Jareczek et al., 2023; Kamburova et al., 2021). The

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historical account involves actively shaping and molding the naturally existing diversity that has evolved over millions of years through diversification (Vega et al., 2023). Today, we continue to harness this rich legacy by deliberately incorporating genetic material from diverse wild gene pools into cotton breeding programs. Recognizing and appreciating this legacy of species formation and diversification is of utmost importance, particularly considering the current challenges faced by global ecosystems (Kasso and Balakrishnan, 2013; Wendel and Grover, 2015). This review aims to comprehensively explore the evolutionary history and taxonomy of *Gossypium*, providing readers with a valuable resource to delve into the extensive literature on the subject. Deep understanding of cotton's evolution can place us in a position to better appreciate its remarkable diversity and recognize its crucial role in advancing agricultural practices. Moreover, by exploring cotton's evolutionary history and harnessing its diverse genetic resources, we can drive progress and enhance the cultivation of this vital crop.

2. THE GENESIS OF THE COTTON GENUS

Gossypium is a member of a small group called Gossypieae, which belongs to the Malvaceae family. What distinguishes Gossypieae from other family members are the unique punctae or lysigenous cavities called "gossypol glands." The Gossypieae tribe is monophyletic, indicating that it encompasses all the descendants of a shared common ancestor (Wendel et al., 2002). It consists of nine genera, comprising approximately 120 species in total (Phuphathanaphong, 2006). Despite the significant diversity in morphology and cytogenetics among cotton species and their wide geographical distribution, molecular phylogenetic studies have confirmed that the cotton genus originated from a common ancestor (Cronn et al., 2002). Furthermore, these investigations have unveiled that the cotton genus is closely related to the sister lineages *Kokia* and *Gossypioides*, which inhabit Hawaii and East Africa/Madagascar, respectively. Notably, these lineages exhibit a reduced chromosome number ($n=12$), distinguishing them from *Gossypium*, which consists of diploid species, as well as other members of the cotton tribe ($n=13$). Despite being geographically separated by vast stretches of open ocean, the striking affinity between these two genera hints at the possibility of transoceanic migration having played a role in the evolutionary history of either one or both of these genera. However, several local varieties have played a major role both in domestication and genetic conservation (Kamal et al., 2024; Zafar et al., 2024a; Zafar et al., 2024b). Several scientific studies have duly acknowledged the occurrence of long-distance salt-water dispersal within the tribe (Sun et al., 2024) (Fig. 1).

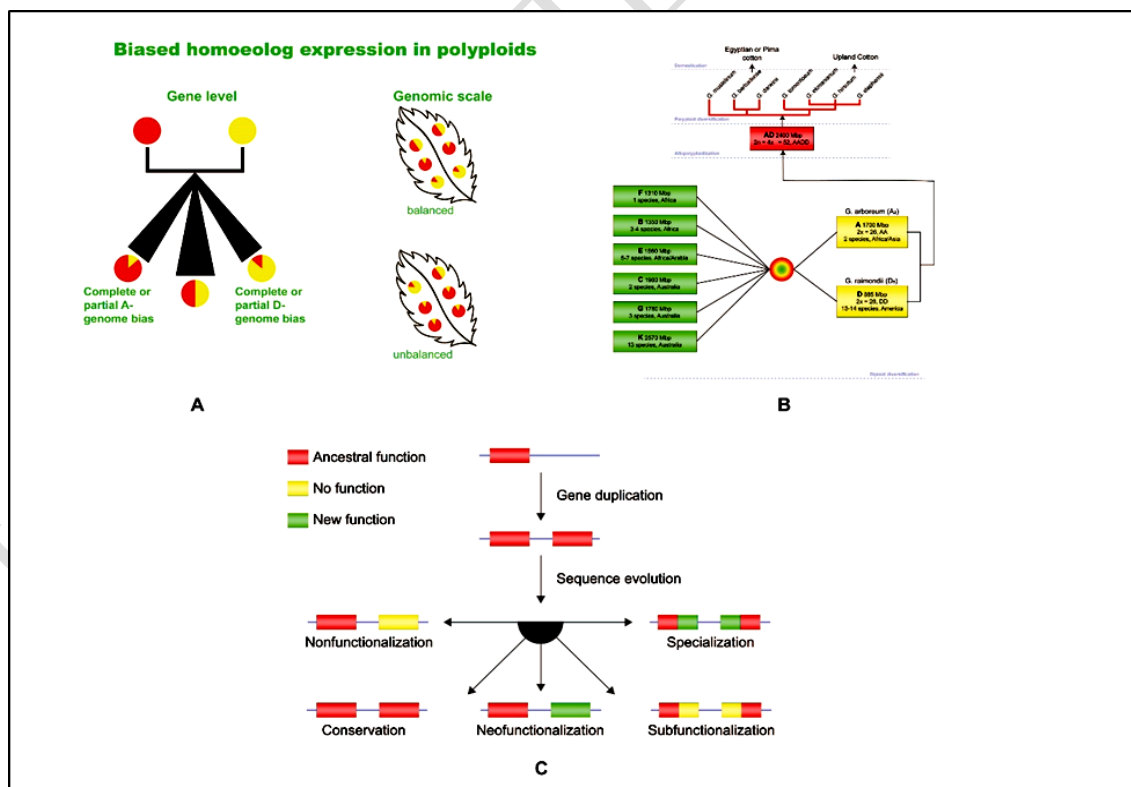


Fig. 1: (a): The evolutionary history of *Gossypium* involved rapid diversification of diploid species (b): The hypothesis elucidating the divergence of multi-copy genes subsequent to 1559 polyploidization 1560 (c): The phenomenon of preferential homoeolog expression in polyploids.

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3. THE DIVERGENCE, DEVELOPMENT, AND DIVERSIFICATION OF THE DIPLOID SPECIES OF *GOSSYPIMUM*

Diploid members of the *Gossypium* genus are categorized into eight genome groups (A through G and K) based on their observed meiotic pairing behavior during interspecific crosses. This classification system was established and documented (Beasley, 1940, 1942; Zhang and Endrizzi, 2015; Endrizzi et al., 1985). Over time, the classification within and among these groups has evolved through various approaches, including plant exploration, taxonomic studies, and evolutionary analysis (Watt, 1907; Hutchinson et al., 1947; Saunders, 1961; Wendel and Grover, 2015; Wang et al., 2018). Numerous molecular phylogenetic analyses have been conducted and have yielded valuable insights. These studies reported the genealogical lineages of *Gossypium* species to align with their genome classifications and geographic distributions. Each genome group corresponds to a unique and naturally occurring lineage, typically displaying geographical cohesion. Moreover, these genome groups are considered monophyletic, indicating their common ancestry. The diploid *Gossypium* species can be grouped into three major lineages based on continents: Australian subgenus *Sturtia* (C-, G-, K-genomes), American subgenus *Houzingenia* (D-genome) of the New World, and African/Asian subgenus *Gossypium* (A-, B-, E-, and F-genomes) of the Old World. Despite having the same $n=13$ diploid chromosomes, there is a remarkable over threefold variation in DNA content per cell among diploid species. This variation becomes evident when observing the gross morphology of chromosomes (Stephens, 1947; Katterman and Ergle, 1970; Abdul Kadir, 1976). However, further investigations utilizing high-quality genomes are required to comprehend gene evolution in diploid cotton fully (Page et al., 2013; Grover et al., 2019).

4. DISPERSAL EVENTS AND SPECIATION IN POLYPLOID COTTONS

The allopolyploids consist of two co-resident genomes, one originating from an African A-genome species and the other from a Mesoamerican D-genome species (Wendel and Cronn, 2003). The AD-genome allopolyploid species is believed to have originated in Mesoamerica through the remarkable transoceanic dispersal of an African A-genome species to the New World. The allopolyploid AD-genome cottons currently encompass seven recognized species. These species are *G. hirsutum* (AD)1, *G. barbadense* (AD)2, *G. tomentosum* (AD)3, *G. mustelinum* (AD)4, *G. darwinii* (AD)5, *G. ekmanianum* (AD)6, and *G. stephensii* (AD)7. Recent additions to this list include *G. ekmanianum* and *G. stephensii*, which were previously classified as variants of *G. hirsutum* and were not previously acknowledged but were found in germplasm collections (Krapovickas et al., 2008; Grover et al., 2015; Gallagher et al., 2017). The divergence led to the emergence of two primary clades: the *G. barbadense*-*G. darwinii* clade and the *G. hirsutum*-*G. tomentosum* complex. Recent discoveries have expanded the *G. hirsutum*-*G. tomentosum* complex with the inclusion of two newly identified species, *G. ekmanianum* and *G. stephensii*. It is noteworthy that the majority of these species are native to islands, with *G. barbadense* and *G. hirsutum* being the exceptions. The origins of these species can be traced back to transoceanic dispersal events that facilitated their colonization of distant locations (Zafar and Zhang, 2021). *G. stephensii* and *G. ekmanianum*, which exhibit a close relationship with *G. hirsutum*, have distinct geographical distributions. *G. stephensii* is exclusively found on Hispaniola, while *G. ekmanianum* is native to Wake Atoll (Grover et al., 2015; Gallagher et al., 2017). *G. darwinii* is indigenous to the Galápagos Islands, thriving in large and continuous populations in certain areas. In contrast, *G. tomentosum* is endemic to the Hawaiian Islands, with a scattered population structure consisting mainly of isolated individuals and small groups spread across multiple islands. Even the earliest diverging allopolyploid, *G. mustelinum*, has a distribution pattern reminiscent of an island, as it is a relatively uncommon species confined to a small region in northeast Brazil (Zafar and Zhang, 2021).

4.1. Polyploidy, Stress Tolerance, and Their Significance for Enhancing Crop Resilience in a Dynamic Environment

Polyploid plants often exhibit discernible physiological and morphological characteristics in comparison to their diploid predecessors. These distinct traits encompass enlarged roots, leaves, flowers, and seeds, widely recognized as the "gigas" phenomenon (Hu et al., 2021). Research findings consistently indicate that polyploid organisms often enjoy a competitive edge over their diploid counterparts in specific environments and temporal contexts, demonstrating a notable fitness advantage (Zafar et al., 2022a). Allopolyploid species are often found in coastal and insular regions (Fryxell, 1965), while diploid species are predominantly restricted to inland areas. This distribution pattern can be attributed to the ability of allopolyploid lineages to disperse salt-tolerant seeds across oceans. However, a recent study conducted using hydroponics examined the morphophysiological responses to salinity stress in a diverse array of diploid and allopolyploid cotton species (Dong et al., 2020). The findings of the study indicated that among the cotton species tested, the Brazilian allopolyploid *G. mustelinum* displayed the greatest level of salt tolerance. Nonetheless, the study revealed that there was no notable disparity in salt tolerance

between allopolyploid and diploid cottons, mainly due to significant variations observed within each group of genomes. These variations are associated with other environmental stressors like mineral nutrient deficiency and drought. Therefore, the hypothesis of increased salt tolerance in polyploid cotton cannot be entirely ruled out and warrants further investigation considering the complexities of natural conditions (Hu et al., 2021). Although significant progress has been made in understanding the molecular and physiological mechanisms underlying abiotic stress tolerance in cotton (Zafar et al., 2022b), the practical implementation of this knowledge to develop cotton cultivars with notable enhancements in high yield, stress tolerance, and superior fiber quality remains a challenging task (Manan et al., 2022).

4.2. Transposable Element Dynamics and Genome Modifications in Polyploid Species

When faced with changes, polyploid genomes often experience alterations in the composition of transposable elements (TEs) within the recently generated allopolyploid genome. Throughout hybridization and polyploidization, transposable elements (TEs), which are mobile DNA sequences, possess the potential to become activated. This activation can lead to a reduction in repression and/or an increase in transposition, resulting in alterations in gene expression and genome structure (Hu et al., 2021). Although these changes are frequently observed in polyploid species, certain polyploids may exhibit restricted transposable element (TE) activity following the process of polyploidization. The primary cause of genome size variation in diploid cotton species can be attributed to the presence of distinct families as well as classes of dispersed repetitive elements (Hu et al., 2021). Nevertheless, following allopolyploid formation, there is inadequate compelling data to suggest a noteworthy proliferation of transposable elements (TEs). Furthermore, the composition of transposable elements (TEs) inherited from the diploid progenitors remains predominantly preserved within the allopolyploid organisms (Hu et al., 2010; Zhang et al., 2015). Recent investigations involving various allopolyploid cotton species have revealed a distinct pattern: a reduction in the quantity of repetitive content within the A sub-genome in contrast to its progenitor, while the D sub-genome shows an increased abundance of repetitive elements compared to its diploid ancestor (Chen et al., 2020). These discoveries potentially suggest the presence of concealed changes in transposable element (TE) elements, involving preferential inter-sub genome TE transpositions in a specific direction and/or biased elimination of TE sequences from the genome. These changes may occur despite an overall reduction in genome size.

4.3. Evolution of Duplicate Gene Expression

In allopolyploids, homoeologous genes have the potential to display distinct expression patterns, known as "homoeolog expression bias," alongside sequence evolution (Yoo et al., 2014). Significant research has been undertaken in *Gossypium* to explore this phenomenon (Adams et al., 2003), unveiling the widespread occurrence, context specificity, and genome-wide bias of biased homoeolog expression. Furthermore, related phenomena, including expression-level dominance and the reconfiguration of co-expression networks, have been observed and extensively studied. Extensive studies conducted in cotton and other allopolyploid species have consistently revealed the widespread occurrence of homoeolog bias. Nevertheless, despite these notable findings, our comprehension of its physiological and evolutionary implications remains constrained and necessitates additional research to gain a deeper understanding (Hu et al., 2021). In the transcriptome analysis, a substantial portion of homoeologous gene pairs (ranging from 20% to 55%) display biased expression towards either the A or D subgenome across various tissues and developmental stages (Hovav et al., 2015; Yoo and Wendel, 2014; Zhang and Endrizzi, 2015). These findings align with previous observations regarding the specificity of homoeolog expression changes in different tissues and organs. Across various tissues, no clear overall dominance of either the A or D subgenome has been consistently observed in terms of biased homoeolog expression (Samuel Yang et al., 2006) in ovule development, a greater number of genes with A-biased expression were identified, while the reverse trend was seen in seeds. Additionally, in petal tissue, a combination of balanced and unbalanced expression patterns, with a slight preference towards the D subgenome, has been documented. It has extensively been investigated the phenomenon of homoeolog expression bias in *G. hirsutum*. The study uncovered a prevailing inclination towards the D sub-genome in 31 out of 35 tissue/stage samples, presenting compelling evidence for the widespread prevalence of this bias in the species (Zhang et al., 2015).

Research has revealed that a considerable portion of expression biases, which emerge during hybridization, persist throughout allopolyploid evolution, and in many cases, these initial biases become further accentuated over time. The presence of divergent cis-regulatory elements between parental genes is indicated by the distinct expression patterns of homoeologs observed during the hybridization of divergent diploid genomes. The significance of cis-regulatory differences becomes apparent as the equal expression of homoeologs would occur in the absence of any trans effects, emphasizing the absence of cis differences. In addition to examining homoeolog-

specific expression, researchers have investigated a range of expression patterns for homoeologous gene pairs. These patterns include non-additive and additive expression, expression-level dominance, and transgressive expression (Hu et al., 2021; Wittkopp et al., 2004).

4.4. Epigenetic Modifications

The process of polyploidization, particularly in allopolyploids arising from the hybridization of genetically distinct species, has the capacity to trigger epigenetic alterations, encompassing histone modifications, chromatin remodeling and modifications in DNA methylation. These modifications have been thoroughly examined in extensive reviews conducted by various researchers ((Ding and Chen, 2018; Song and Chen, 2015; Vicent and Casacuberta, 2017). Although our understanding of the precise epigenetic consequences of allopolyploidization in cotton remains incomplete, studies on DNA methylation patterns suggest a certain level of genomic stability within the allopolyploid cotton genome (Liu et al., 2001). In recent studies, a connection has been revealed between alterations in DNA methylation patterns and biased expression of genes in allopolyploid cotton, particularly among homoeologs, which are gene copies derived from distinct parental species (Song et al., 2016; Song et al., 2017). In addition, the loss of photoperiod sensitivity in cultivated cotton species has been associated with gene-specific demethylation, as observed in COL2D. These observations suggest that the evolutionary dynamics of allopolyploid cotton could be significantly influenced by epigenetic modifications (Song et al., 2017). Extensive research has established the significant influence of DNA methylation patterns on agronomic traits in allopolyploid cotton. Specifically, it has been found that demethylation is closely associated with increased susceptibility to verticillium stress in upland cotton (Guseinov et al., 1975).

5. INSIGHTS INTO DOMESTICATION THROUGH WHOLE GENOME RESEQUENCING AND GENOMICS OF FIBER DEVELOPMENT

The field of sequencing domesticated cotton genomes has witnessed remarkable advancements, primarily attributable to the crucial role played by the development of third-generation sequencing and next-generation sequencing (NGS) technologies. This is clearly demonstrated in various studies (Du et al., 2018; Li et al., 2015; Liu et al., 2015; Yuan et al., 2015; Zhang and Endrizzi, 2015). The latest sequencing techniques have been employed in these studies to deepen our comprehension of domesticated cotton genomes. Through these investigations, a valuable resource has been established, with broad applications in plant breeding, the discovery of genes and genomic research. Apart from the initial achievement of reference genome sequences, several studies utilizing whole-genome resequencing (WGR) have been carried out by various scientists (Du et al., 2018; Fang et al., 2017; Fang et al., 2017; Ma et al., 2018; Wang et al., 2017). Through exploring the evolutionary relationships, genomic variation structures, and diverse forms of variation, such as insertions/deletions (InDels) and single-nucleotide polymorphisms (SNPs), within populations, these investigations have yielded unprecedented insights. Consequently, our understanding of domesticated cotton genomes has been significantly enhanced, unveiling their immense potential across diverse fields of application (Page et al., 2016).

Resequencing was performed individually for diploid cotton accessions, involving 10 accessions, and for tetraploid cotton accessions, encompassing 34 accessions. The achieved average coverage per accession was approximately 37× for diploid cotton and 23× for tetraploid cotton. Remarkably, three notable datasets were released in the year 2017. A comprehensive sequencing effort was carried out by Fang et al. (2017), covering a total of 147 cotton accessions. Additionally, directed their attention towards 258 *G. hirsutum* cultivars (Fang et al., 2017), while Wang et al. (2017) performed sequencing on total 321 *G. hirsutum* cultivars (Wang et al., 2017). Furthermore, by 2018, a thorough sequencing had been conducted on a comprehensive dataset consisting of 419 accessions of core upland cotton. In another study, a significant contribution was to the field by conducting resequencing on 243 accessions of *G. arboreum* and *G. herbaceum* (Du et al., 2018). Cotton fiber development exhibits divergence among its various species for instance, *G. barbadense*, a specific cotton spp., produces longer and finer fibers owing to an extended elongation phase (Applequist et al., 2001; Tu et al., 2007). On the other hand, alterations in the developmental process of diploid cultivars lead to shorter, coarser, and weaker fibers, diminishing their commercial worth (Haigler et al., 2005). Current research indicates that the genetic and molecular mechanisms governing cotton fiber development are still not fully understood. However, it is suggested that hormones like ethylene and auxin, as well as sugar mediators, may play significant roles in this process (Gallagher et al., 2020). Historically, the polyploid nature of cotton and the challenges associated with regeneration after transformation have posed obstacles to both conventional breeding and genetic modification of the crop. These innovative tools offer promising opportunities to integrate molecular research into cotton breeding programs and expedite the development of genetically modified cotton varieties (Anwar et al., 2023; Kamal et al., 2019; Razzaq et al., 2021; Razzaq et al., 2022).

6. NATURAL AND ARTIFICIAL INTROGRESSION TO EXPLORE BREEDING TRAITS IN THE GENUS

As previously mentioned, domestication and improvement of cotton through selective breeding and crop enhancement have resulted in genetic bottlenecks, which have diminished the genetic diversity within cultivated cotton varieties and limited their capacity for further advancements (Zafar et al., 2022c). In contrast, wild progenitors and other related wild species of cotton exhibit a significantly higher level of genetic diversity, preserving important associated traits and genetic variants absent in the cultivated gene pool. These wild relatives act as a valuable reservoir of genetic diversity adapted to diverse environmental conditions, which could prove essential in developing new cotton varieties capable of withstanding the challenges posed by climate change and other abiotic factors (Zafar et al., 2023). By accessing the genetic reservoir of these wild relatives, researchers can open up novel possibilities for advancing the development of improved cotton varieties with heightened resilience and adaptability (Dempewolf et al., 2017; Mammadov et al., 2018; Zhang et al., 2017; Zafar et al., 2022d).

The presented instances showcase the successful integration of favorable traits from wild species skillfully incorporated into cultivated cotton through strategic breeding programs. By harnessing the characteristics of glanded plants and glandless seeds, breeding endeavors have resulted in the development of upland cotton cultivars. These cultivars enable the utilization of cotton seed proteins and oil content, while concurrently preserving resistance against an extensive array of pests and diseases (Zhu et al., 2005). *G. anomalum*, an African species, has been instrumental in developing cultivars with stronger and finer fibers (Mehetre, 2010) and enhancing resistance to cotton rust and bacterial blight (Endrizzi et al., 1985). Genetic material from *G. longicalyx* has been incorporated into cultivated cotton to introduce resistance to reniform nematodes (Robinson et al., 2007). Furthermore, *G. stocksii*, *G. australe*, *G. bickii*, *G. sturtianum*, and *G. thurberi* have been utilized to transfer resistance for diseases such as fusarium wilt, cotton leaf curl virus and verticillium wilt (Wang et al., 2012; Zhao et al., 2012; Liu et al., 2015).

Various species of the American D-genome have developed distinct strategies to withstand drought conditions. For instance, *G. turneri*, *G. armourianum*, and *G. harknessii* have evolved unique adaptations to cope with drought, including reduced leaves, dense cuticles, and a dual layer of palisade cells. These modifications effectively minimize water loss. Conversely, *G. laxum*, *G. aridum*, and *G. lobatum* demonstrate a dormancy mechanism during dry seasons, enabling them to evade arid conditions. Remarkably, *G. gossypioides* and *G. thurberi* have evolved robust root systems that facilitate their growth on steep rocky slopes, even in locations far from watercourses. Certain species like *G. davidsonii*, *G. klotzschianum*, and *G. aridum* have also demonstrated salt tolerance, and through transcriptomic analyses, various stress-related genes have been discovered (Fan et al., 2015; Zhang et al., 2016; Wei et al., 2017). However, it's important to note that traditional breeding programs of this nature can be time-consuming and demanding regarding resources (Zafar et al., 2020; Razzaq et al., 2023).

7. CONCLUSION

In conclusion, the vast evolutionary history and exceptional diversity exhibited by *Gossypium* offer a remarkable opportunity for the purposeful integration of valuable genes sourced from diverse wild germplasm. Wild cotton species' wide array of traits signifies a corresponding genetic wealth controlling crucial characteristics, including physiology, chemistry, disease resistance, and fiber properties. As a result, these wild species act as an extensive genetic reservoir that can be effectively utilized by cotton breeders. While the genetic potential of wild *Gossypium* remains predominantly untapped, successful instances of incorporating these species into breeding programs have been well-documented. Diploid species have been effectively employed to introduce genes associated with fiber strength, disease resistance, cytoplasmic male sterility, and fertility restoration. Furthermore, deliberate gene transfer from wild and feral tetraploids has been utilized to introduce disease resistance, nectar less traits, and glandless cotton characteristics. These genetic enhancements, achieved through classical breeding methods, involve purposeful crossbreeding among multiple allopolyploids and diploid *Gossypium* species. Looking towards the future, the exploration of wild *Gossypium* and genetically distant germplasm sources will continue to rely on a combination of traditional breeding techniques and genetic engineering approaches. The development of efficient transformation systems has facilitated the widespread cultivation of transgenic cotton varieties with traits such as herbicide tolerance, insect resistance, and modified fiber properties. These advancements have had a profound impact on the global cotton industry, with transgenic cultivars now comprising a significant portion of cotton crops. By leveraging the extensive genetic diversity present in *Gossypium*, ongoing research and utilization of wild species will propel further progress in cotton breeding, leading to the development of superior cotton varieties. This comprehensive understanding of *Gossypium*'s evolutionary trajectory holds immense potential for targeted breeding objectives, laying the foundation for continued advancements and innovation in sustainable cotton production in agriculture.

Conflict of Interest: The authors declare that they have no conflict of interest for the publication of the manuscript.

Data availability statement: The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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