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Impact of Polyploidy on the Evolution and Diversity of Cotton

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Abstract Polyploidy, the condition of possessing more than two complete sets of chromosomes, has played a pivotal role in the evolution and diversification of cotton (*Gossypium* spp.). This study explores the impact of polyploidy on the genetic and phenotypic diversity of cotton species. By analyzing genomic data, historical breeding records, and evolutionary patterns, we elucidate how polyploidy has contributed to cotton's adaptability, stress resistance, and fiber quality. We discuss the mechanisms of polyploid formation, the evolutionary advantages conferred by polyploidy, and the role of polyploidy in the domestication and improvement of cotton varieties. Our findings highlight the significance of polyploidy in enhancing genetic diversity, which is crucial for future cotton breeding programs aimed at sustainability and resilience.

Keywords *Gossypium*; Polyploidy; Cotton evolution; Genetic diversity; Plant breeding

1 Introduction

Cotton (*Gossypium* spp.) is a significant crop not only for its economic value but also as a model organism for studying plant evolution and polyploidy. The genus *Gossypium* includes both diploid and polyploid species, with the latter playing a crucial role in the diversification and adaptation of cotton. The evolutionary history of cotton is marked by multiple polyploidization events, which have contributed to its genetic diversity and adaptability to various environmental conditions (Huang and Zhu, 2018; Chen et al., 2020b; Strygina et al., 2020).

Polyploidy, the condition of having more than two complete sets of chromosomes, is a common phenomenon in plant evolution. It is a significant driver of speciation and genetic diversity, providing plants with the ability to adapt to changing environments and stresses. In cotton, polyploidy has led to the development of allopolyploid species, which combine the genomes of different progenitor species. This genetic amalgamation has resulted in novel traits and increased resilience, making polyploid cotton species more adaptable and productive (Liu et al., 2019; Zhang et al., 2019; Dong et al., 2022; Heslop-Harrison et al., 2022).

This study aims to explore the impact of polyploidy on the evolution and diversity of cotton. By analyzing the genomic and phenotypic variations among different cotton species, this study seeks to understand how polyploidy has influenced cotton's adaptability, stress tolerance, and overall genetic diversity. The scope of this study includes a comprehensive review of the evolutionary history of cotton, the mechanisms of polyploidy, and the specific contributions of polyploidy to cotton's genetic and phenotypic traits. This study will also examine the implications of these findings for cotton breeding and crop improvement. To provide valuable insights that can inform future efforts in cotton breeding and genetic enhancement, ultimately contributing to the sustainability and productivity of this vital crop this research will delve into the evolutionary mechanisms and consequences of polyploidy in cotton.

2 Polyploidy in Cotton: An Overview

2.1 Definition and types of polyploidy

Polyploidy refers to the condition in which an organism possesses more than two complete sets of chromosomes. In plants, polyploidy is a common phenomenon and can be classified into two main types: autopolyploidy and allopolyploidy. Autopolyploidy arises from the duplication of chromosomes within a single species, leading to multiple sets of homologous chromosomes. In contrast, allopolyploidy results from hybridization between two different species, followed by chromosome doubling, which combines the distinct sets of chromosomes from each parent species (Huang and Zhu, 2018; Zhang et al., 2019).

2.2 Historical perspective on polyploidy in cotton

Polyploidy has played a significant role in the evolution and domestication of cotton (*Gossypium* spp.). The genus *Gossypium* includes both diploid and polyploid species, with the latter being of particular economic importance. The two most widely cultivated cotton species, *Gossypium hirsutum* (Upland cotton) and Pima cotton, are both allotetraploids, having originated from hybridization events between ancestral diploid species followed by chromosome doubling (Wang et al., 2018; Chen et al., 2020b). Historical evidence suggests that these polyploidization events were crucial for the development of cotton with superior fiber qualities, which have been selectively bred over time to meet human demands (Bao et al., 2019).

2.3 Mechanisms of polyploid formation

The formation of polyploids in cotton involves several mechanisms. Initially, hybridization between two distinct diploid species occurs, resulting in a hybrid with one set of chromosomes from each parent. This hybrid is typically sterile due to the inability of the different chromosome sets to pair correctly during meiosis. However, chromosome doubling can occur, either spontaneously or through induced mechanisms, leading to the formation of a fertile polyploid with homologous chromosome pairs (Cheng et al., 2018; Tossi et al., 2022). This process, known as allopolyploidization, has been a driving force in the diversification and adaptation of cotton species. Additionally, polyploidy can induce genetic and epigenetic changes, such as recombination suppression and altered gene expression, which contribute to the evolutionary success and domestication of polyploid cotton (Chen et al., 2020b; Heslop-Harrison et al., 2022).

By understanding the definition, historical context, and mechanisms of polyploidy in cotton, researchers can better appreciate its impact on the evolution and diversity of this important crop. The insights gained from studying polyploidy in cotton can also inform breeding programs aimed at improving fiber quality and stress tolerance in cultivated varieties.

3 Evolutionary Implications of Polyploidy in Cotton

3.1 Genetic and genomic changes post-polyploidy

Polyploidy, the condition of having more than two complete sets of chromosomes, has profound effects on the genetic and genomic architecture of cotton. Following polyploidization, cotton species exhibit significant genomic diversification, including subgenomic transposon exchanges that equilibrate genome size and evolutionary rate heterogeneities. These changes are accompanied by gene-family diversification and homoeolog expression divergence among polyploid lineages, which are crucial for the adaptation and evolution of cotton species. Additionally, polyploidy induces recombination suppression, which correlates with altered epigenetic landscapes. This suppression can be overcome by wild introgression, providing a mechanism for genetic recombination and crop improvement (Figure 1) (Chen et al., 2020b). The merger of two independent genomes during polyploidization leads to deep modifications in genome architecture, gene expression, and molecular interactions, which are essential for the phenotype and evolutionary trajectory of polyploid cotton (Blasio et al., 2022).

The research of Chen et al. (2020b) provides a detailed representation of the evolutionary history, genomic features, and syntenic relationships among five cotton allotetraploid species: Gh, Gb, Gt, Gd, and Gm. It elucidates the intricate evolutionary processes triggered by a key polyploidization event, merging distinct African and American genomes, leading to the emergence of five distinct cotton species. This research provides a detailed depiction of their unique genomic adaptations, observable through their diverse seed morphologies and genetic architectures. By mapping genome-wide syntenic relationships and pinpointing structural variations among the subgenomes, the research not only highlights the genomic resilience and adaptability of these species but also enhances understanding of polyploid speciation and adaptation.

3.2 Hybridization and speciation

Polyploidy plays a critical role in hybridization and speciation in cotton. Interspecific hybridization, followed by chromosome doubling, results in the formation of allopolyploids, which are common in cotton. This process generates novel genetic variants that are adaptable to different environments, thereby driving speciation (Blasio et al., 2022). The combination of hybridization and polyploidy enables the creation of new species with unique genetic and phenotypic traits, contributing to the diversification of cotton. The evolutionary history of many cultivated cotton species, such as Upland and Pima cottons, can be traced back to such hybridization events, highlighting the importance of polyploidy in their speciation (Huang and Zhu, 2018). Furthermore, polyploidy-related changes in gene expression and epigenetic modifications play a significant role in the adaptation and speciation of cotton (Anatskaya and Vinogradov, 2022).

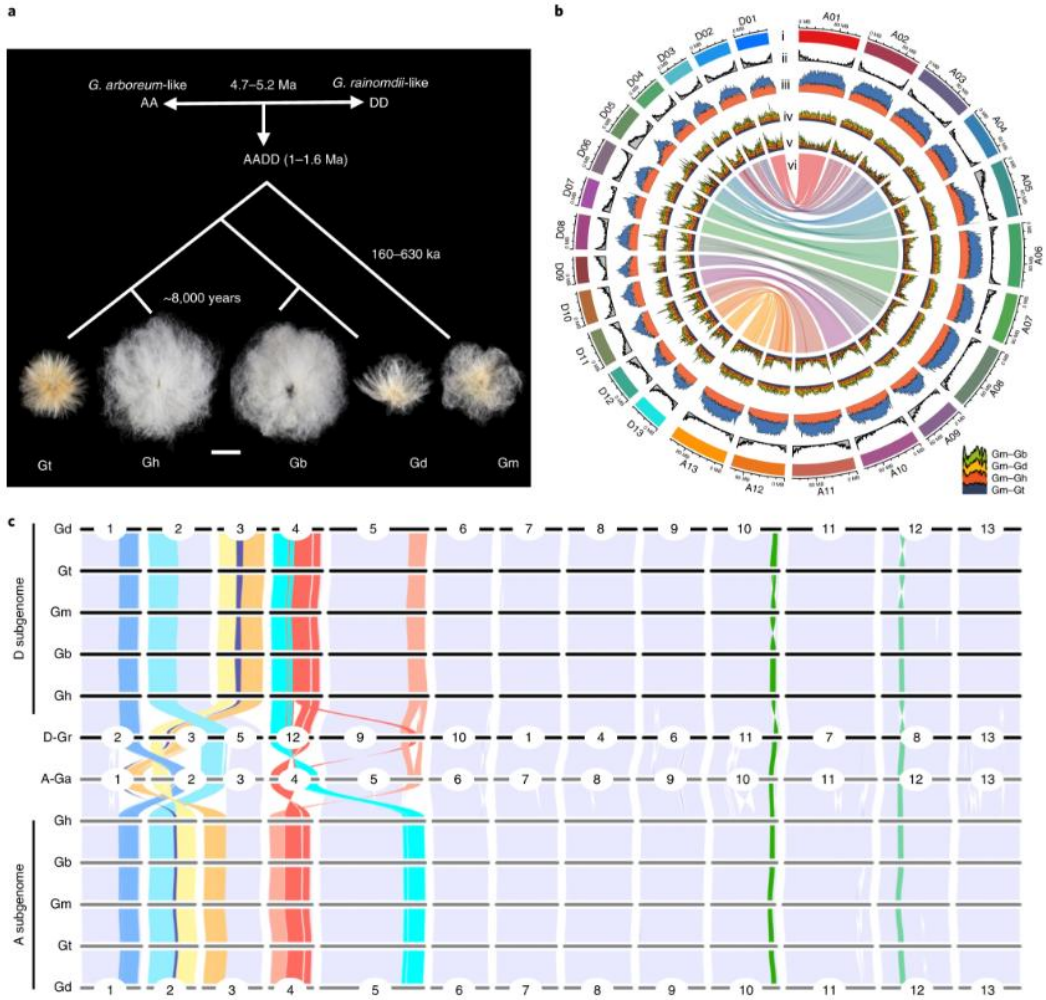


Figure 1 Sequencing features of five cotton allotetraploid species (Adopted from Chen et al., 2020b)

Image caption: a, Evolution and domestication of five polyploid lineages, Gh, Gb, Gt, Gd and Gm, after polyploidization between an A-genome African species (Ga-like) and a D-genome American species (Gr-like). Typical seeds from each species are shown. The divergence time estimates are based on 21,567 single orthologs among the 5 species by using the synonymous substitution rate (r) of 3.48×10^{-9} (Methods and Supplementary Note). Scale bar, 10 mm; ka, thousand years ago. b, Chromosomal features and synteny of the Gm genome. Notes in circos plots: (i) estimated lengths of 13 A and 13 D homoeologous pseudochromosomes; (ii) distribution of annotated genes; (iii) TE content (Gypsy, steel blue; Copia, grey; other repeats, orange); (iv,v) stacked SNP (iv) and indel (v) densities between Gm and Gb, Gd, Gh and Gt, respectively (see inset), and (vi) syntenic blocks between the homoeologous A and D chromosomes. The densities in plots in (ii) – (v) are represented in 1 Mb with overlapping 200-kb sliding windows. c, Genome-wide syntenic relationships among A and D subgenomes in five allotetraploids relative to the A-genome-like Ga (A2 genome) and D-genome-like Gr (D5 genome). Structural variations among syntenic blocks are marked with colored ribbons (Adopted from Chen et al., 2020b)

3.3 Adaptive evolution and environmental adaptation

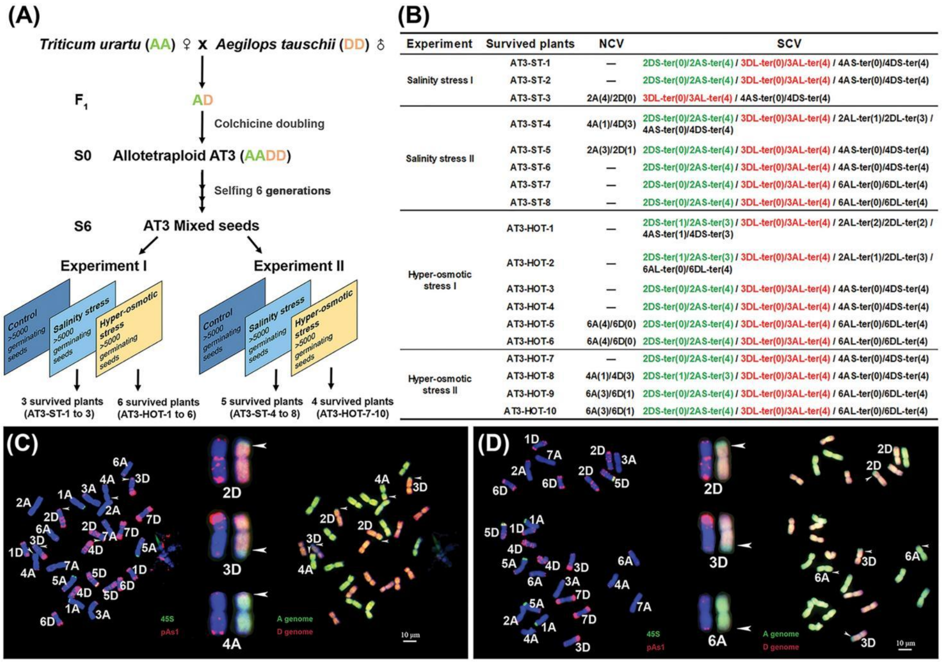
Polyploidy provides cotton species with an evolutionary advantage by enhancing their ability to adapt to various environmental conditions. Polyploid cottons often exhibit increased stress tolerance, which allows them to thrive in harsh or disturbed environments (Peer et al., 2020). The increased genetic diversity resulting from polyploidy enables rapid short-term evolutionary adaptation, fueling genomic diversity and the independent origins of polyploidy (Wei et al., 2019). Polyploidy-related increases in biological plasticity and stress resistance manifest in the evolution, development, and adaptation of cotton species (Anatskaya and Vinogradov, 2022). Additionally, polyploidy-induced changes in cell size and other functional traits contribute to the ecological divergence and adaptive evolution of cotton (Bomblies, 2020). These adaptive traits are crucial for the survival and success of polyploid cotton species in changing environmental conditions.

Polyploidy has significant evolutionary implications for cotton, driving genetic and genomic changes, hybridization and speciation, and adaptive evolution. These processes contribute to the diversity and resilience of cotton species, enabling them to thrive in various environments and under different stress conditions. The insights gained from studying polyploidy in cotton can inform efforts to improve crop resilience and productivity through targeted breeding and genetic modification strategies.

4 Polyploidy and Cotton Diversity

4.1 Genetic diversity in polyploid cotton species

Polyploidy has been instrumental in shaping the genetic diversity of cotton species. The allopolyploid cotton species, such as *Gossypium hirsutum* and *G. mustelinum*, exhibit a wide range of genetic variations due to the combination of different genomes (A and D genomes) from their diploid progenitors (Dong et al., 2019; Dong et al., 2022). This genetic diversity is further enhanced by mechanisms such as homoeologous exchange, which allows for rapid adaptation to environmental stresses (Figure 2) (Wang et al., 2022). Studies have shown that polyploid cotton species possess a higher level of genetic diversity compared to their diploid counterparts, which contributes to their ability to thrive in diverse and often stressful environments (Heslop-Harrison et al., 2022; Luque et al., 2022).



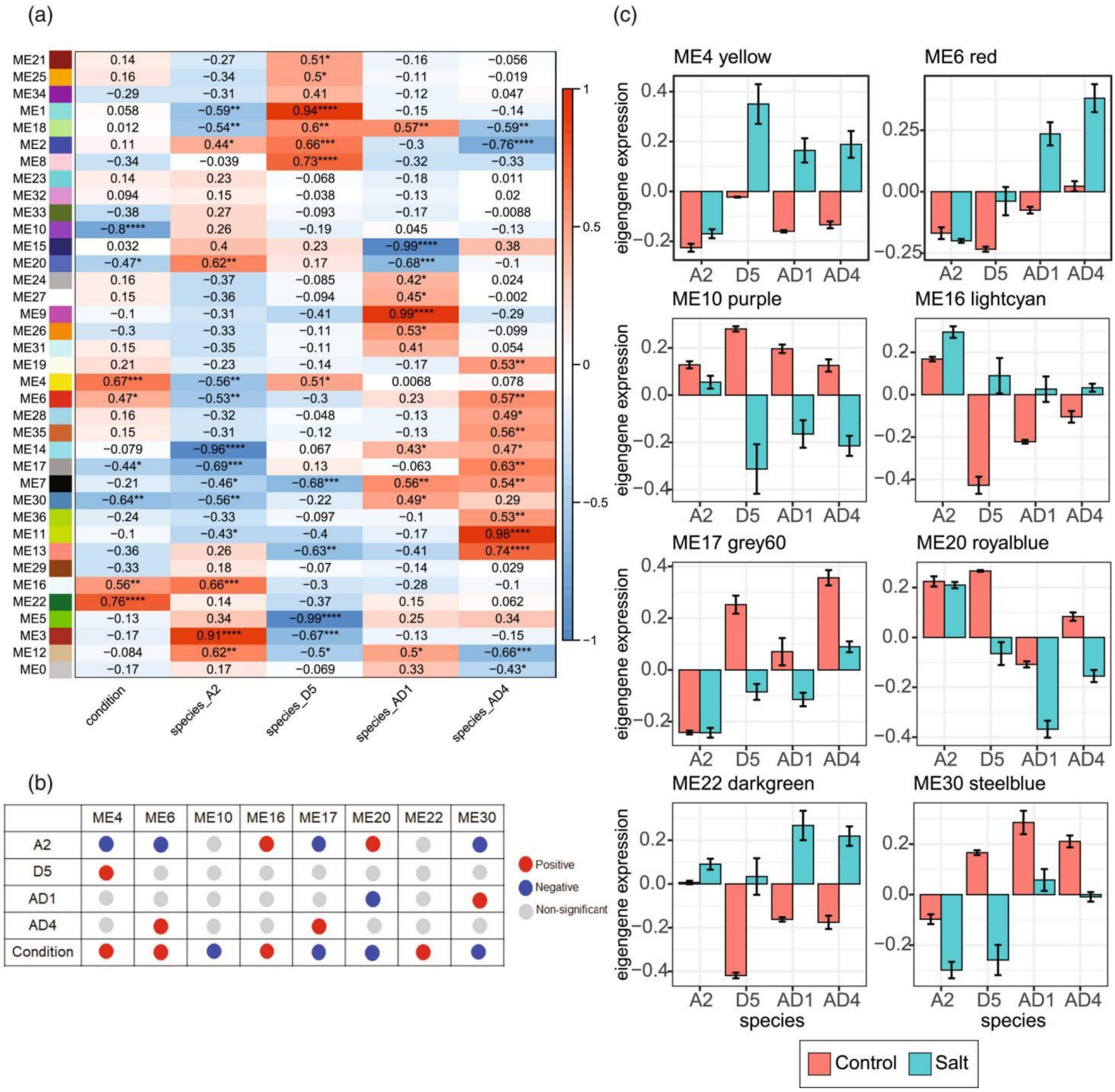
Experiment	Survived plants	NCV	SCV
Salinity stress I	AT3-ST-1	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-ST-2	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-ST-3	2A(4)/2D(0)	3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
Salinity stress II	AT3-ST-4	4A(1)/4D(3)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 2AL-ter(1)/2DL-ter(3) / 4AS-ter(0)/4DS-ter(4)
	AT3-ST-5	2A(3)/2D(1)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-ST-6	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-ST-7	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)
	AT3-ST-8	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)
Hyper-osmotic stress I	AT3-HOT-1	—	2DS-ter(1)/2AS-ter(3) / 3DL-ter(0)/3AL-ter(4) / 2AL-ter(2)/2DL-ter(2) / 4AS-ter(1)/4DS-ter(3)
	AT3-HOT-2	—	2DS-ter(1)/2AS-ter(3) / 3DL-ter(0)/3AL-ter(4) / 2AL-ter(1)/2DL-ter(3) / 6AL-ter(0)/6DL-ter(4)
	AT3-HOT-3	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-HOT-4	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-HOT-5	6A(4)/6D(0)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)
	AT3-HOT-6	6A(4)/6D(0)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)
Hyper-osmotic stress II	AT3-HOT-7	—	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-HOT-8	4A(1)/4D(3)	2DS-ter(1)/2AS-ter(3) / 3DL-ter(0)/3AL-ter(4) / 4AS-ter(0)/4DS-ter(4)
	AT3-HOT-9	6A(3)/6D(1)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)
	AT3-HOT-10	6A(3)/6D(1)	2DS-ter(0)/2AS-ter(4) / 3DL-ter(0)/3AL-ter(4) / 6AL-ter(0)/6DL-ter(4)

Figure 2 Selection of AT3-ST and AT3-HOT individuals and summary of their karyotypes (Adopted from Wang et al., 2022)

Image caption: (A) The workflow of selected salinity- and hyper-osmotic-tolerant individuals (dubbed as AT3-ST and AT3-HOT, respectively) from a population of AT3. Experiments I and II represent two parallel selections schemes. In each experiment, >5000 uniformly germinating seeds for each of the three lines (AT3 and its parents, TMU38 and TQ27) were kept under control, salinity (200 mM NaCl), and hyper-osmotic (20% PEG6000) stress conditions. (B) The summarized karyotypes of eight AT3-ST and 10 AT3-HOT survivors from experiments I and II. NCV=numerical chromosome variation; SCV=structural chromosome variation; S=short arm of chromosome; L=long arm of chromosome; ter=terminal of chromosome, and the numbers in parentheses represent the dosage of the chromosome. Green highlights the HEs that occur between chromosome 2DS and 2AS, whereas red highlights the HEs that occur between chromosome 3DL and 3AL. (C) Representative karyotypes of the survivors after salinity and hyper-osmotic stress, as revealed by FISH/GISH. Multiple restructured chromosomes due to HEs are illustrated. The white arrows denote the HEs position (Adopted from Wang et al., 2022)

4.3 Impact on disease resistance and stress tolerance

Polyploidy has a profound impact on the disease resistance and stress tolerance of cotton species. The increased genetic diversity and the presence of multiple gene copies in polyploid cotton provide a robust defense mechanism against various biotic and abiotic stresses. For example, polyploid cotton species have shown enhanced resistance to salinity stress, which is attributed to the complex regulatory networks and gene expression patterns that arise from polyploidization (Figure 3) (Ruiz et al., 2020; Dong et al., 2022). Furthermore, polyploidy can lead to the development of novel stress-responsive traits that are not present in diploid progenitors, thereby providing a broader range of adaptive responses to environmental challenges (Peer et al., 2020; Tossi et al., 2022).



	condition	species_A2	species_D5	species_AD1	species_AD4
ME21	0.14	−0.27	0.51*	−0.16	−0.056
ME25	0.16	−0.34	0.5*	−0.11	−0.019
ME34	−0.29	−0.31	0.41	−0.12	0.047
ME1	0.058	−0.59**	0.94****	−0.15	−0.14
ME18	0.012	−0.54**	0.6**	0.57**	−0.59**
ME2	0.11	0.44*	0.66***	−0.3	−0.76****
ME8	−0.34	−0.039	0.73****	−0.32	−0.33
ME23	0.14	0.23	−0.068	−0.18	0.011
ME32	0.094	0.15	−0.038	−0.13	0.02
ME33	−0.38	0.27	−0.093	−0.17	−0.0088
ME10	−0.8****	0.26	−0.19	0.045	−0.13
ME15	0.032	0.4	0.23	−0.99****	0.38
ME20	−0.47*	0.62**	0.17	−0.68***	−0.1
ME24	0.16	−0.37	−0.085	0.42*	0.024
ME27	0.15	−0.36	−0.094	0.45*	−0.002
ME9	−0.1	−0.31	−0.41	0.99****	−0.29
ME26	−0.3	−0.33	−0.11	0.53*	−0.099
ME31	0.15	−0.35	−0.11	0.41	0.054
ME19	0.21	−0.23	−0.14	−0.17	0.53**
ME4	0.67***	−0.56**	0.51*	0.0068	0.078
ME6	0.47*	−0.53**	−0.3	0.23	0.57**
ME28	0.16	−0.32	−0.048	−0.13	0.49*
ME35	0.15	−0.31	−0.12	−0.13	0.56**
ME14	−0.079	−0.96****	0.067	0.43*	0.47*
ME17	−0.44*	−0.69***	0.13	−0.063	0.63**
ME7	−0.21	−0.46*	−0.68***	0.56**	0.54**
ME30	−0.64**	−0.56**	−0.22	0.49*	0.29
ME36	−0.24	−0.33	−0.097	−0.1	0.53**
ME11	−0.1	−0.43*	−0.4	−0.17	0.98****
ME13	−0.36	0.26	−0.63**	−0.41	0.74****
ME29	−0.33	0.18	−0.07	−0.14	0.029
ME16	0.56**	0.66***	−0.3	−0.28	−0.1
ME22	0.76****	0.14	−0.37	0.15	0.062
ME5	−0.13	0.34	−0.99****	0.25	0.34
ME3	−0.17	0.91****	−0.67***	−0.13	−0.15
ME12	−0.084	0.62**	−0.5*	0.5*	−0.66***
ME0	−0.17	0.17	−0.069	0.33	−0.43*

	ME4	ME6	ME10	ME16	ME17	ME20	ME22	ME30
A2	🔵	🔵	⚪	🔴	🔵	🔴	⚪	🔵
D5	🔴	⚪	⚪	⚪	⚪	⚪	⚪	⚪
AD1	⚪	⚪	⚪	⚪	⚪	🔵	⚪	🔴
AD4	⚪	🔴	⚪	⚪	🔴	⚪	⚪	⚪
Condition	🔴	🔴	🔵	🔴	🔵	🔵	🔴	🔵

🔴 Positive
🔵 Negative
⚪ Non-significant

Figure 3 WGCNA of four cotton species in response to salt stress (Adopted from Dong et al., 2022)

Image caption: (a) Heatmap showing Pearson correlation between module eigengenes (by row) and categorical traits of ‘condition’ and ‘species’ (by column). The ‘condition’ trait is labeled 1 for the salt stress-treated samples and 0 for the untreated samples. The ‘species_A2’ trait, for example, is labeled 1 for A2 and 0 for the other samples. Each cell shows the correlation coefficient with significance as follows: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$. (b) Eight modules of interest with significant correlations. Red circles indicate positive correlations, blue circles indicate negative correlations, and gray circles indicate non-significant correlations. (c) Barplots of module eigengenes, with error bars denoting the standard deviation calculated from replicates (Adopted from Dong et al., 2022)

The research of Dong et al. (2022) presents a Weighted Gene Co-expression Network Analysis (WGCNA) of four cotton species in response to salt stress. By correlating module eigengenes with traits associated with salt stress and species differences, the study highlights significant genetic networks sensitive to salt exposure. The analysis reveals eight modules with distinct correlation patterns, indicating their potential roles in stress adaptation. These patterns are visually represented through heatmaps and color-coded correlation circles, emphasizing the differential gene expression under stress conditions. This analysis helps identify key gene networks associated with salt stress tolerance, offering insights into the molecular mechanisms underlying stress adaptation in cotton.

Polyploidy plays a crucial role in the evolution and diversity of cotton species. It enhances genetic and phenotypic diversity, improves agronomic traits, and increases resistance to diseases and environmental stresses. These attributes make polyploid cotton species highly valuable for both natural ecosystems and agricultural production.

5 Comparative Genomics of Polyploid and Diploid Cotton

5.1 Comparative genomic studies

Comparative genomic studies between polyploid and diploid cotton have revealed significant insights into the evolutionary processes and genetic mechanisms underlying cotton diversity and improvement. Polyploidy, the condition of having more than two sets of chromosomes, has played a crucial role in the evolution of cotton species. For instance, the genomic analysis of five allopolyploid cotton species, including Upland and Pima cottons, demonstrated that while these polyploid genomes are conserved in gene content and synteny, they have diversified through subgenomic transposon exchanges, which equilibrate genome size and evolutionary rates among homoeologs (Chen et al., 2020b). Additionally, the study of 3,248 tetraploid cotton genomes highlighted the role of extensive chromosome inversions in geographic differentiation and fiber improvement in cultivated Gossypium hirsutum (He et al., 2021).

5.2 Structural and functional genomic differences

Polyploidization induces significant structural and functional genomic changes in cotton. One notable structural change is the alteration in chromatin accessibility, which shows convergent evolution during polyploidization. This change is driven by the coordinated interplay among histone modifications, transposable elements, and cis-regulatory DNA elements (CREs) (Han et al., 2022). Functionally, polyploid cotton exhibits expression level dominance (ELD) bias toward the A genome, which is associated with the up-/downregulation of homologs from the D genome. This bias affects various biological processes, including fatty acid biosynthesis and microtubule procession, which are crucial for fiber development (Peng et al., 2020). Furthermore, polyploidy in cotton has been linked to recombination suppression, which correlates with altered epigenetic landscapes and can be overcome by wild introgression (Chen et al., 2020b).

5.3 Insights from transcriptomic and epigenomic analyses

Transcriptomic and epigenomic analyses provide deeper insights into the regulatory mechanisms influenced by polyploidy in cotton. For example, RNA-seq studies have shown that polyploid cotton exhibits differential gene expression patterns compared to its diploid progenitors, with significant expression asymmetry along chromosomes (Ramírez-González et al., 2018). These differences are often associated with epigenetic modifications, such as DNA methylation and histone modifications, which influence gene expression and contribute to the adaptive plasticity of polyploid cotton. Additionally, chromatin accessibility studies have revealed that polyploidization leads to dynamic changes in the regulatory landscape, which are essential for the coordinated expression of homoeologous genes and the overall phenotypic diversity observed in polyploid cotton (Han et al., 2022).

Comparative genomic studies between polyploid and diploid cotton have elucidated the structural and functional genomic differences induced by polyploidization. These differences, along with insights from transcriptomic and epigenomic analyses, highlight the complex interplay of genetic and epigenetic factors that drive the evolution and diversity of cotton species. The knowledge gained from these studies provides a valuable framework for future research and crop improvement efforts in cotton.

6 Polyploidy and Cotton Domestication

6.1 Role of polyploidy in cotton domestication

Polyploidy has played a crucial role in the domestication of cotton, particularly in the development of economically significant species such as Upland and Pima cottons. The process of polyploidization has led to the diversification of gene families and the divergence of homoeolog expression among polyploid lineages, which has been instrumental in the adaptation and improvement of cotton varieties. The occurrence of polyploidy has facilitated the retention and functional divergence of duplicated genes, contributing to the development of traits beneficial for domestication (Cheng et al., 2018; Zhang et al., 2019). Additionally, polyploidy has been associated with increased tolerance to abiotic and biotic stresses, which is advantageous for crop domestication and improvement (Tossi et al., 2022).

6.2 Comparative analysis of wild and cultivated cotton

Comparative studies between wild and domesticated cotton have revealed significant differences in gene expression and regulatory mechanisms. For instance, the fiber transcriptomes of wild and domesticated Gossypium hirsutum show genome-wide regulatory changes, with a high level of trans evolution enabled by genomic redundancy following polyploidy (Bao et al., 2019). These regulatory variations are linked to domestication traits and are often uncoupled between the two subgenomes of allotetraploid cotton. Furthermore, the domestication process has driven parallel gene expression similarities in the fibers of cultivated cottons, involving coexpression networks and RNA modifications (Chen et al., 2020b). These findings highlight the complexity of regulatory evolution and its impact on the domestication of cotton.

6.3 Domestication traits linked to polyploidy

Polyploidy has been linked to several key domestication traits in cotton. The process of polyploidization has induced recombination suppression, which correlates with altered epigenetic landscapes and can be overcome by wild introgression, thereby enhancing genetic diversity and adaptability (Chen et al., 2020b). Traits such as increased fiber quality and yield have been associated with polyploidy-induced gene retention and expression divergence (Cheng et al., 2018). Additionally, polyploidy has been shown to influence the development of traits related to stress tolerance, which are crucial for the successful domestication and cultivation of cotton in diverse environmental conditions (Tossi et al., 2022). The ability to manipulate genetic recombination and modify epigenetic landscapes through polyploidy provides valuable opportunities for crop improvement and the development of superior cotton varieties (Zhang et al., 2019).

Polyploidy has significantly impacted the evolution and domestication of cotton by driving gene diversification, regulatory changes, and the development of advantageous traits. These insights into the role of polyploidy in cotton domestication can inform future breeding programs and efforts to enhance cotton crop performance.

7 Implications for Cotton Breeding and Biotechnology

7.1 Breeding strategies utilizing polyploidy

Polyploidy has been a significant driver in the evolution and diversification of cotton species, providing unique opportunities for breeding strategies. The genomic diversification observed in allopolyploid cotton species, such as Upland and Pima cottons, has led to the development of traits beneficial for cotton improvement. These include increased fiber yield, enhanced stress tolerance, and improved fiber quality (Hu et al., 2019). The use of antimitotic agents to induce polyploidy has been a powerful strategy in plant breeding, resulting in increased biomass, yield, and stress tolerance (Chen et al., 2020a). Additionally, polyploidy can overcome the non-viability and infertility of interspecific hybrids, facilitating the development of new cotton cultivars with desirable traits (Trojak-Goluch et al., 2021; Yali, 2022).

7.2 Genetic engineering and genome editing approaches

Advancements in genetic engineering and genome editing technologies have opened new avenues for manipulating polyploid cotton genomes. The high level of trans regulatory evolution observed in polyploid cotton suggests that genomic redundancy following polyploidy enables significant regulatory changes, which can be harnessed for crop improvement (Bao et al., 2019). Techniques such as CRISPR/Cas9 can be employed to target specific genes and modify epigenetic landscapes, thereby enhancing desirable traits such as fiber quality and stress resilience. The integration of genomic insights from polyploid cotton species can empower efforts to manipulate genetic recombination and improve crop performance (Chen et al., 2020b).

7.3 Future prospects and challenges

The future of cotton breeding and biotechnology lies in the continued exploration and utilization of polyploidy. One of the main challenges is understanding the complex regulatory networks and epigenetic modifications that accompany polyploidization (Bao et al., 2019; Chen et al., 2020b). Further research is needed to elucidate the mechanisms underlying sub-genome dominance and gene expression divergence in polyploid cotton (Zhang et al., 2019). Additionally, the development of more efficient and precise genome editing tools will be crucial for overcoming the challenges associated with polyploid genome manipulation. The potential for polyploidy to generate novel traits and enhance species diversification under changing environmental conditions presents exciting opportunities for the future of cotton breeding (Peer et al., 2020; Heslop-Harrison et al., 2022). By leveraging the unique advantages of polyploidy, cotton breeders and biotechnologists can develop new strategies to improve cotton cultivars, ensuring their resilience and productivity in the face of global challenges.

8 Conclusions and Future Directions

Polyploidy has been identified as a significant evolutionary force in the diversification and domestication of cotton. The genomic analysis of allopolyploid cotton species, including Upland and Pima cottons, reveals that polyploid genomes, while conserved in gene content and synteny, have diversified through subgenomic transposon exchanges, gene-family diversification, and homoeolog expression divergence. Polyploidy has also been shown to induce recombination suppression, which can be overcome by wild introgression, thereby offering potential pathways for crop improvement. Additionally, polyploidization has been linked to increased tolerance to abiotic and biotic stresses, which is crucial for plant growth and productivity under adverse environmental conditions. The phenomenon of sub-genome dominance and the role of epigenetic modifications in genome evolution and gene expression have also been highlighted as critical aspects of polyploidy in cotton.

Despite the significant advancements in understanding the impact of polyploidy on cotton evolution and diversity, several gaps remain. Firstly, the precise mechanisms by which polyploidy induces recombination suppression and how this can be manipulated for crop improvement are not fully understood. Secondly, while the role of epigenetic modifications in sub-genome dominance has been acknowledged, the causal relationships between chromatin marks and gene expression require further elucidation. Additionally, the long-term evolutionary consequences of polyploidy on gene function innovation and species diversification need more comprehensive investigation. The specific pathways and genes involved in the increased stress tolerance of polyploids also warrant further study to fully harness these traits for crop improvement.

Future research should focus on several key areas to address the existing gaps in knowledge. Firstly, detailed studies on the mechanisms of recombination suppression and its manipulation through wild introgression could provide new avenues for genetic improvement in cotton. Secondly, advanced techniques such as high-resolution chromatin conformation capture and single-cell transcriptome sequencing should be employed to unravel the complexities of epigenetic modifications and their impact on gene expression and sub-genome dominance. Additionally, exploring the evolutionary trajectories of polyploid cotton species under different environmental conditions could offer insights into their adaptability and resilience. Finally, identifying and characterizing the specific genes and pathways involved in abiotic and biotic stress tolerance in polyploids will be crucial for developing more robust and high-yielding cotton varieties.

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Conflict of Interest Disclosure

The author affirms 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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