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Evolutionary Patterns of Chromosomal Inversion in Cotton

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Abstract Chromosomal inversions play a significant role in the evolutionary dynamics of plant genomes, including cotton. This study draws on recent genomic research to explore the evolutionary patterns of chromosomal inversions in cotton. Chromosomal inversions are widespread among various plant taxa and are often associated with locally favored traits and assortative mating, indicating their role in adaptation and speciation. In cotton, comparative genomic analyses reveal a complex evolutionary history, including an ancient polyploidy and extensive chromosomal rearrangements that have shaped the current genome structure. High-density genetic linkage maps have identified specific chromosomal inversions and translocations, further elucidating structural genomic changes within cotton. This study synthesizes current knowledge on the origin, frequency, and evolutionary significance of chromosomal inversions in cotton, providing insights into their contribution to genome evolution and adaptation.

Keywords Cotton, Chromosome inversion, Inversion, Adaptability, Genomics

1 Introduction

Chromosomal inversions are structural variations where a segment of a chromosome is reversed end to end. These inversions have long intrigued evolutionary biologists due to their ability to suppress recombination, thereby preserving co-adapted alleles and facilitating the maintenance of advantageous gene combinations. The role of chromosomal inversions extends beyond mere structural anomalies; they are pivotal in various eco-evolutionary processes, including mating systems, social organization, environmental adaptation, reproductive isolation, and speciation (Wellenreuther and Bernatchez, 2018). Recent studies have highlighted that inversions are taxonomically widespread, often ancient and large, and maintained by balancing selection, challenging the traditional view that balancing selection plays a minor role in maintaining genetic variation.

Cotton (*Gossypium* spp.) is a globally significant crop, both economically and agriculturally. Understanding the genetic mechanisms underlying its adaptation and evolution is crucial for improving cotton breeding programs. Chromosomal inversions in cotton can play a significant role in its adaptation to diverse environmental conditions and in the development of desirable agronomic traits.

By studying these inversions, researchers can gain insights into the evolutionary history of cotton, identify key genetic regions associated with important traits, and develop strategies to enhance cotton's resilience and productivity. Moreover, the study of chromosomal inversions in cotton can provide broader insights into the role of structural variations in plant evolution and adaptation (Schmidt et al., 2005).

The objective of this systematic review is to synthesize the current knowledge on the evolutionary patterns of chromosomal inversions in cotton. By reviewing the literature, we aim to elucidate the mechanisms by which inversions contribute to adaptation and speciation in cotton, identify the key traits associated with inversion polymorphisms, and explore the potential applications of this knowledge in cotton breeding and genetic improvement. This review will provide a comprehensive understanding of the role of chromosomal inversions in the evolution of cotton, highlighting their significance in shaping the genetic architecture and adaptive potential of this important crop species.

2 Chromosomal Inversions: Definitions and Mechanisms

2.1 Definition of chromosomal inversions

Chromosomal inversions are structural variations where a segment of a chromosome is reversed end to end. These inversions can suppress recombination within the inverted segment, which can protect co-adapted alleles and facilitate the maintenance of advantageous gene combinations. This suppression of recombination is a key feature that makes chromosomal inversions a significant focus in evolutionary biology (Wellenreuther and Bernatchez, 2018).

2.2 Mechanisms leading to chromosomal inversions

The formation of chromosomal inversions can occur through various mechanisms, including errors during DNA replication and repair, as well as through the action of transposable elements. These inversions can accumulate deleterious mutations, which can lead to overdominance and the maintenance of inversion polymorphisms. The dynamic nature of these inversions is highlighted by their ability to branch into multiple highly divergent haplotypes, which can halt fitness degradation and contribute to the long-term persistence of the inversion (Berdan et al., 2021).

2.3 Detection and characterization of inversions in plant genomes

Detecting and characterizing chromosomal inversions in plant genomes involves a combination of cytogenetic techniques, such as fluorescence in situ hybridization (FISH), and modern genomic approaches, including whole-genome sequencing and comparative genomics (Huang and Rieseberg, 2020). These methods allow researchers to identify inversion breakpoints, assess their size and age, and understand their evolutionary significance. The widespread occurrence and ecological importance of inversions underscore the need for integrating structural variation studies into the broader context of molecular adaptation and speciation research.

3 Evolutionary Significance of Chromosomal Inversions

3.1 Role in genetic diversity

Chromosomal inversions play a crucial role in maintaining and enhancing genetic diversity within populations. By suppressing recombination, inversions can preserve advantageous combinations of alleles, which might otherwise be broken up during meiosis. This preservation of co-adapted gene complexes can lead to increased genetic variation within populations, as different inversions can harbor distinct sets of alleles that contribute to various phenotypic traits. For instance, studies have shown that inversions are prevalent across a wide range of plant groups and are often associated with locally favored traits, suggesting their significant role in maintaining genetic diversity (Nosil et al., 2023).

3.2 Inversions as drivers of adaptation

Chromosomal inversions are pivotal in driving adaptation by facilitating the maintenance of beneficial allele combinations that enhance fitness in specific environments. The suppression of recombination within inversions allows for the retention of adaptive gene complexes, which can be crucial for survival and reproduction in changing environments. Research has documented that inversions are commonly linked to spectacular phenotypes and play a pervasive role in eco-evolutionary processes, including environmental adaptation (Berdan et al., 2021). In Drosophila, for example, inversion polymorphisms are associated with traits such as body size, which are subject to strong selection pressures and contribute to adaptive divergence (Hoffmann et al., 2004; Huang and Rieseberg, 2020).

3.3 Impact on reproductive isolation and speciation

Chromosomal inversions can significantly impact reproductive isolation and speciation by contributing to assortative mating and reducing gene flow between populations. Inversions can harbor traits that promote assortative mating, thereby enhancing reproductive isolation. This isolation can lead to the accumulation of genetic differences between populations, eventually resulting in speciation. Studies have shown that inversions are often associated with traits that contribute to assortative mating, suggesting their key role in speciation processes (Connallon and Olito, 2021). Additionally, the suppression of recombination within inversions can facilitate the maintenance of genetic differences between populations, further promoting reproductive isolation and speciation (Berdan et al., 2021).

4 Chromosomal Inversions in Cotton: A Historical Perspective

4.1 Early studies and discoveries

The study of chromosomal inversions in cotton has a rich history, dating back to the early 20th century when cytogenetic techniques first allowed scientists to visualize chromosomal structures. Early research primarily focused on identifying and cataloging inversions through microscopic examination of chromosomal spreads. These foundational studies laid the groundwork for understanding the role of inversions in genetic diversity and adaptation. For instance, early cytogenetic analyses revealed that chromosomal inversions could suppress recombination, thereby maintaining advantageous gene combinations and contributing to local adaptation and speciation (Wellenreuther and Bernatchez, 2018).

4.2 Advances with modern genomic tools

The advent of modern genomic tools has revolutionized the study of chromosomal inversions in cotton. High-throughput sequencing technologies and advanced bioinformatics have enabled researchers to map inversions with unprecedented precision. These tools have facilitated the identification of inversion breakpoints and the characterization of their genetic content. For example, recent studies have utilized multicolor banding and bacterial artificial chromosomes to achieve high-resolution mapping of inversion breakpoints, revealing complex molecular features such as gene destitution and co-localization with fragile sites (Schmidt et al., 2005). Additionally, genomic analyses have shown that inversions can capture locally adapted alleles and suppress recombination, thereby playing a crucial role in the evolutionary dynamics of cotton populations (Connallon and Olito, 2021).

4.3 Major findings and milestones

Several major findings and milestones have marked the study of chromosomal inversions in cotton. One significant discovery is the role of inversions in maintaining genetic diversity through balancing selection. Research has shown that inversions can harbor co-adapted alleles, which are protected from recombination, thus facilitating their maintenance in populations. Another important milestone is the understanding of the evolutionary dynamics of inversions, including the accumulation of deleterious mutations and the role of gene conversion in mitigating fitness decline (Berdan et al., 2021). Furthermore, studies have highlighted the taxonomic ubiquity of inversions and their pervasive role in eco-evolutionary processes, such as environmental adaptation and reproductive isolation.

5 Comparative Genomics of Wild and Cultivated Cotton Species

5.1 Overview of cotton genomics

Cotton (*Gossypium* spp.) has a complex genomic history characterized by polyploidization events and extensive chromosomal rearrangements. The reference genome sequence for cotton revealed a decaploid ancestor, indicating a 5× multiplication in the cotton lineage of an ancestral genome common to cotton and cacao (Wang et al., 2016). This complex evolutionary history is further supported by the presence of numerous chromosomal inversions and other structural variations that have played significant roles in the adaptation and speciation of cotton species (Huang and Rieseberg, 2020).

5.2 Identifying inversions in wild cotton species

Inversions are prevalent in wild cotton species and have been identified using advanced genomic technologies. For instance, the D genome assemblies of wild cotton species (Figure 1), built with long-read data, have unveiled numerous inversions that predominate among genome rearrangements. These inversions are often located in regions that are difficult to characterize using standard genome analysis methods, such as centromeres and repeat regions. The identification of these inversions has provided insights into the mechanisms of centromere evolution and stress tolerance divergence in wild cotton speciese (Yang et al., 2021)。

The study by Yang et al. (2021) showed the characteristics of genomic variation in the D genome in different *Gossypium* species. By comparing the D subgenomes of *G. barbadense*, *G. hirsutum*, *G. raimondii, G. davidsonii, G. thurberi* and *G. turneri*, the inversion regions in the genome were identified (orange and magenta marks). In particular, the figure shows a large inversion on chromosome 11 between *G. thurberi* and *G. davidsonii*, and the differences in chromatin interactions are revealed by Hi-C data heat maps. The A/B compartment characterization of chromosome 11 and the TAD heat map further depict the genomic structure around the inversion breakpoint. These findings provide important insights into the evolutionary significance of chromosome structural variation in wild cotton species and their possible adaptive functions.

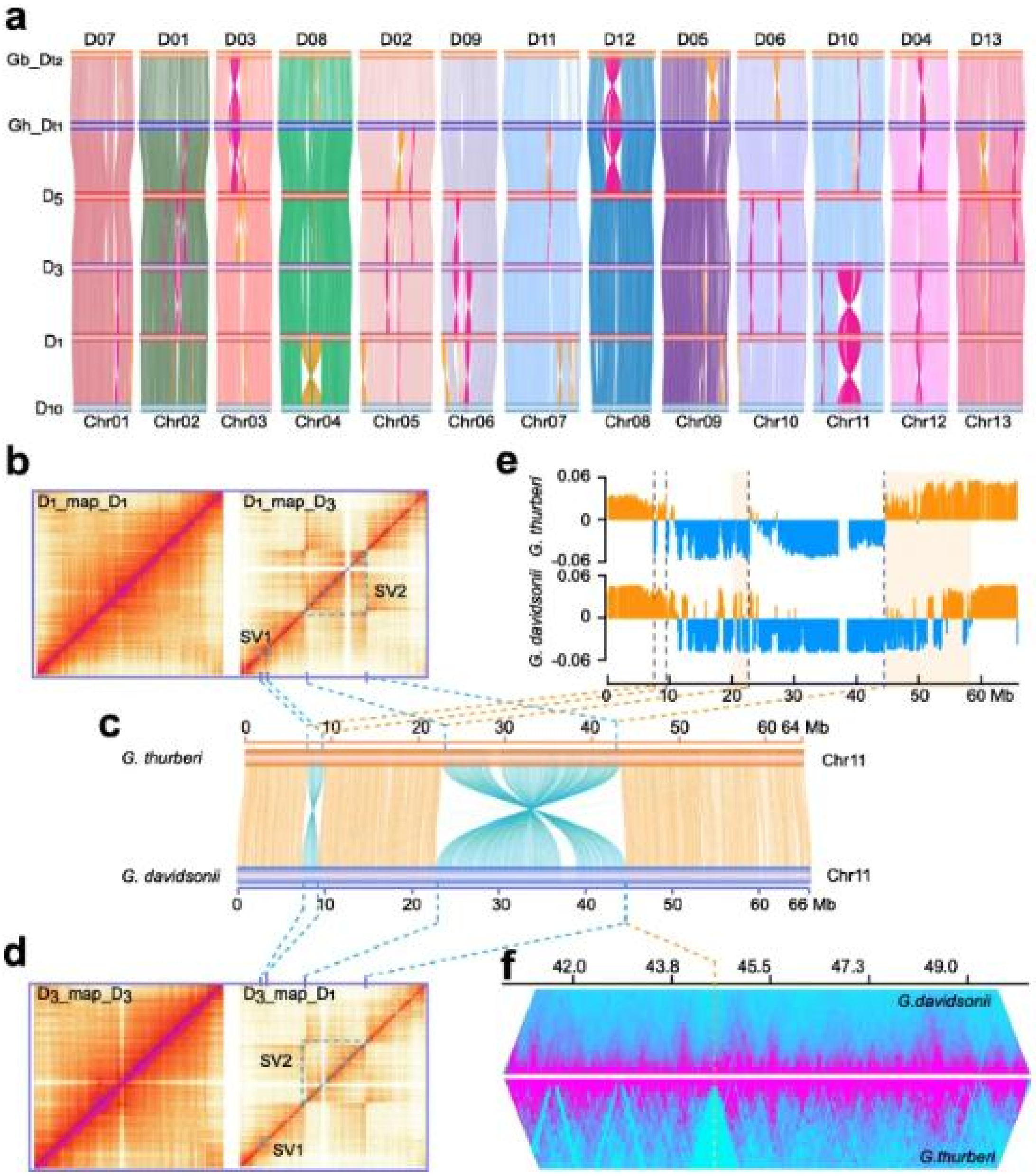

Figure 1 Characterization of genomic variation among different D genomes (Adopted from Yang et al., 2021)

Image caption: a Genome comparison of among *G. barbadense* (D subgenome, Gb_Dt2), *G. hirsutum* (D subgenome, Gh_Dt1), G. raimondii (D5), *G. davidsonii* (D3), *G. thurberi* (D1), and *G. turneri* (D10). b Identification of a large inversion on Chr11 between *G. thurberi* and *G. davidsonii*. d The panel shows chromatin interaction heat maps including *G. davidsonii* Hi-C data mapping *G. davidsonii* (D3_map_D3) and *G. thurberi* Hi-C data mapping *G. davidsonii* (D1_map_D3). e A/B compartments in Chr11; orange represents the A compartments and blue represents the B compartments. f TAD heatmap around the right breakpoint of the large inversion on Chr11 (Adopted from Yang et al., 2021)

5.3 Inversion patterns in cultivated cotton varieties

Cultivated cotton varieties also exhibit significant chromosomal inversions, which have been mapped using various genomic tools. A detailed restriction fragment length polymorphism (RFLP) map of *Gossypium hirsutum* and *Gossypium barbadense* revealed that most homoeologous chromosomal regions differ by inversions, reflecting the polyploidization events that have shaped the cotton genome (Dai et al., 2020). These inversions are associated with locally favored traits and contribute to the adaptation and speciation of cultivated cotton varieties (Huang and Rieseberg, 2020).

5.4 Comparative analysis between wild and cultivated species

Comparative genomic studies between wild and cultivated cotton species have highlighted the evolutionary significance of chromosomal inversions. In wild species, inversions are linked to stress tolerance traits, such as Verticillium and salt-stress tolerance, which can be exploited for crop improvement in cultivated varieties. In cultivated species, inversions are associated with traits that enhance fiber quality and yield, demonstrating their role in the domestication and improvement of cotton. The comparative analysis underscores the importance of structural variations, including inversions, in the evolutionary trajectories of both wild and cultivated cotton species, providing a framework for future genomic and breeding studies.

6 Case Studies: Specific Chromosomal Inversions in Cotton

6.1 Inversions linked to fiber quality

Chromosomal inversions have been shown to play a significant role in the fiber quality of cotton. A notable example is the Inv(A07)p1.09p2.23 inversion in dark-brown fiber cotton (*Gossypium hirsutum*). This inversion was identified through high-throughput resequencing and was found to induce micro-deletions, gene disruptions, and abnormal gene expression in the breakpoint regions. The inversion is significantly associated with fiber color and nine fiber traits, indicating its substantial impact on fiber quality (Wen et al., 2020). Additionally, comparative genomics analyses of *Gossypium hirsutum* and *Gossypium barbadense* have identified large paracentric and pericentric inversions in 14 chromosomes, which are linked to superior fiber quality traits. These inversions have been utilized to construct introgression lines, allowing the identification of 13 quantitative trait loci associated with improved fiber quality (Wang et al., 2018).

6.2 Inversions associated with stress tolerance

Chromosomal inversions also contribute to stress tolerance in cotton. Although specific inversions linked to stress tolerance in cotton are not detailed in the provided papers, the general role of inversions in environmental adaptation is well-documented. Inversions can capture locally adapted alleles and suppress recombination between them, thereby maintaining advantageous gene combinations that enhance stress tolerance (Connallon and Olito, 2021; Nosil et al., 2023). This mechanism is supported by studies in other plant species, where inversions are associated with traits that contribute to environmental adaptation and stress resilience.

6.3 Other notable inversions and their implications

Beyond fiber quality and stress tolerance, other notable chromosomal inversions in cotton have significant evolutionary and genetic implications. For instance, the study of chromosomal inversions in plants reveals that inversions are prevalent across a wide range of plant groups and are often associated with locally favored traits and assortative mating, suggesting their key role in adaptation and speciation (Huang and Rieseberg, 2020). Additionally, the dynamic nature of inversions, including the accumulation of deleterious mutations and the branching into multiple highly divergent haplotypes, highlights their complex evolutionary processes (Berdan et al., 2021). These findings underscore the importance of inversions in maintaining genetic variation and facilitating evolutionary resilience (Nosil et al., 2023).

7 Molecular Consequences of Chromosomal Inversions

7.1 Gene expression changes

Chromosomal inversions can significantly impact gene expression by altering the physical location of genes within the genome. This repositioning can bring genes into new regulatory environments, potentially leading to changes in their expression levels. For instance, inversions can place genes near different enhancers or silencers, thereby modifying their transcriptional activity (Crow et al., 2019). In cotton, such changes in gene expression could influence traits related to environmental adaptation and reproductive isolation, as inversions often protect co-adapted alleles from recombination, maintaining advantageous gene combinations.

7.2 Effects on Chromosomal Architecture

Inversions can also affect the overall architecture of chromosomes. By flipping a segment of the chromosome, inversions can disrupt the linear order of genes, which may interfere with normal chromosomal pairing during meiosis. This disruption can lead to reduced recombination rates within the inverted region, preserving specific allele combinations that might be beneficial for the plant's adaptation to its environment. In cotton, this could mean that inversions help maintain traits that are crucial for survival in specific ecological niches. Additionally, the structural changes brought about by inversions can lead to the formation of new chromosomal domains, which can further influence gene expression and chromosomal stability (Berdan et al., 2021)。

7.3 Implications for plant development and physiology

The molecular consequences of chromosomal inversions extend to plant development and physiology. By maintaining specific allele combinations, inversions can contribute to the development of traits that are advantageous under certain environmental conditions. For example, inversions in cotton may help preserve traits that enhance drought resistance or pest resistance, thereby improving the plant's overall fitness. Furthermore, the suppression of recombination within inversions can facilitate the maintenance of complex traits that involve multiple genes, which might be crucial for the plant's development and physiological processes (Nosil et al., 2023). The dynamic nature of inversions, including the potential for deleterious mutation accumulation and the branching into divergent haplotypes, underscores their significant role in shaping the evolutionary trajectory of cotton (Schmidt et al., 2019).

8 Evolutionary Dynamics of Chromosomal Inversions in Cotton

8.1 Phylogenetic analysis of inversion events

Chromosomal inversions have been extensively studied across various species, revealing their significant role in evolutionary processes. In cotton, phylogenetic analysis of inversion events can provide insights into the evolutionary history and relationships among different species. Studies have shown that inversions can be traced back to ancestral populations, indicating their long-standing presence and influence on genetic divergence (Nosil et al., 2023). For instance, in Drosophila species, fixed chromosomal inversions were found to predate species divergence, suggesting that these inversions were already present in the ancestral population before speciation occurred. Similarly, in *Arabidopsis thaliana*, the phylogenetic relationships inferred from inversion patterns revealed ancient introgression events and diverse haplotype patterns, highlighting the evolutionary significance of these inversions (Connallon and Olito, 2021). These findings underscore the importance of chromosomal inversions in shaping the phylogenetic landscape of cotton and other plant species.

8.2 Geographic distribution and adaptation

The geographic distribution of chromosomal inversions in cotton is closely linked to environmental adaptation. Inversions can protect co-adapted alleles by suppressing recombination, thereby facilitating local adaptation to diverse ecological conditions (Wellenreuther and Bernatchez, 2018). For example, in the malaria vector Anopheles funestus, chromosomal inversions were found to be strongly associated with ecological zones, suggesting a role in local adaptation (Ayala et al., 2008). Similarly, in *Arabidopsis thaliana*, the distribution of a specific inversion was linked to fecundity under drought conditions, indicating an adaptive advantage in certain environments (Fransz et al., 2016). In cotton, the study of inversion patterns across different geographic regions can reveal how these structural variations contribute to adaptation and ecological divergence. The presence of inversions in specific regions may indicate their role in conferring adaptive traits that enhance survival and reproduction in those environments.

8.3 Temporal patterns and evolutionary rates

The temporal dynamics and evolutionary rates of chromosomal inversions in cotton can provide insights into their role in long-term evolutionary processes. Inversions can accumulate deleterious mutations over time, leading to fitness decline in certain arrangements (Berdan et al., 2021). However, the branching of an arrangement into multiple highly divergent haplotypes can halt this fitness degradation, highlighting the dynamic nature of inversion evolution. In passerine birds, the fixation rates of inversions were found to vary across chromosomes, with higher rates observed on the Z chromosome compared to autosomes (Hooper and Price, 2017). This variation in fixation rates suggests that different selective pressures and evolutionary forces act on inversions over time. In cotton, studying the temporal patterns of inversion events can help elucidate the evolutionary rates and mechanisms driving the maintenance and divergence of these structural variations. Understanding the temporal dynamics of inversions can also shed light on their role in speciation and the formation of new species.

9 Future Directions and Research Prospects

9.1 Emerging technologies for studying chromosomal inversions

The study of chromosomal inversions in cotton has greatly benefited from advancements in genomic technologies. High-throughput sequencing and genome-wide association studies (GWAS) have enabled the identification and characterization of inversions across various species, including plants (Figure 2) (Mérot, 2020). Techniques such as CRISPR-Cas9 genome editing and optical mapping are emerging as powerful tools for precisely manipulating and visualizing chromosomal structures, respectively. These technologies can facilitate the detailed study of inversion breakpoints and their effects on gene function and expression (Wellenreuther and Bernatchez, 2018). Additionally, the integration of bioinformatics tools and machine learning algorithms can enhance the analysis of large genomic datasets, providing deeper insights into the evolutionary dynamics and functional consequences of inversions (Fragata et al., 2014).

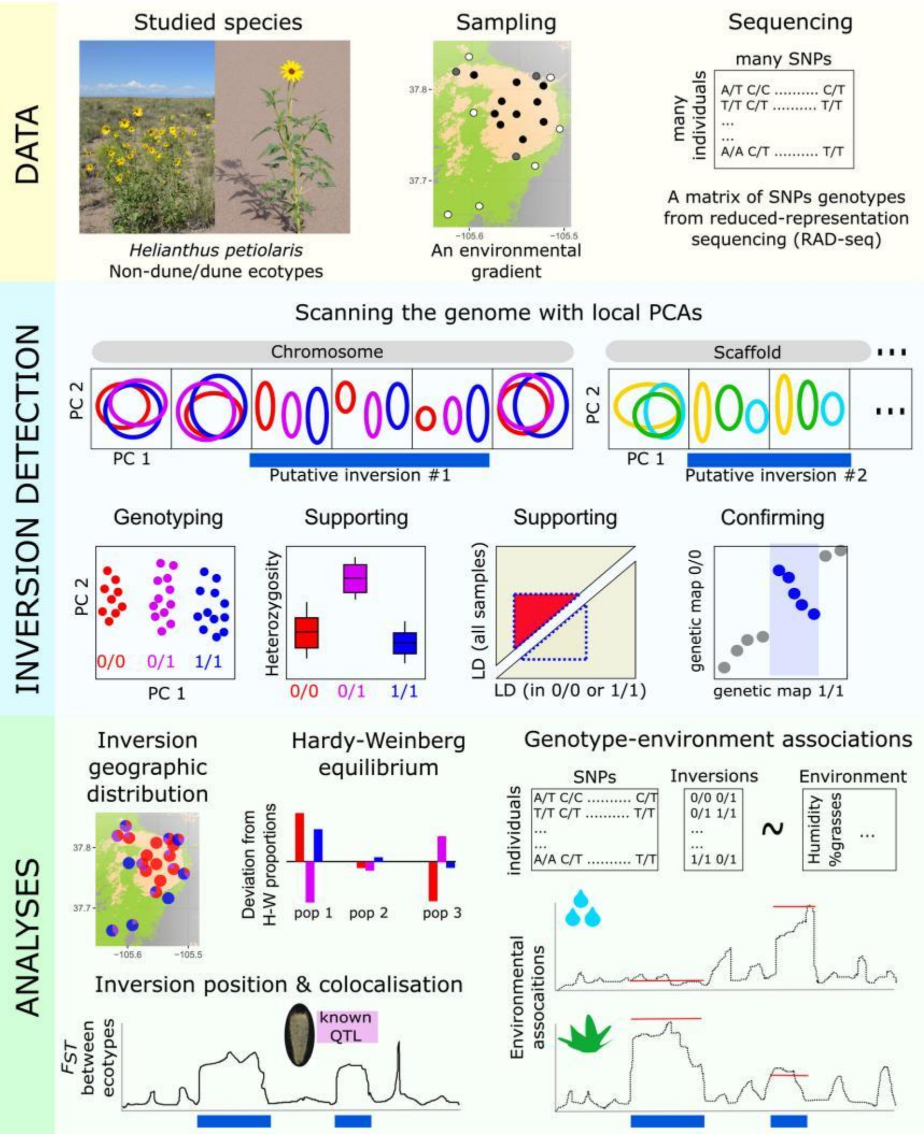

Figure 2 Detection of inversion in sunflower ecotypes and testing their role in adaptation to dune environments (Adopted from Mérot, 2020)

This infographic from Mérot et al. (2020) illustrates cutting-edge methods for detecting chromosomal inversions in population genetics, using Helianthus petiolaris as a model. The process begins with environmental sampling and SNP sequencing to create a genetic matrix. Local principal component analyses (PCAs) are then employed to scan for putative inversions across the genome. Once potential inversions are identified, further analyses confirm these findings through genotyping, Hardy-Weinberg equilibrium tests, and linkage disequilibrium studies. Geographic and environmental correlations are explored to understand the ecological significance of these inversions. This integrated approach enhances our ability to study structural variations across diverse populations and environments, offering insights into their evolutionary roles.

9.2 Potential applications in cotton breeding

Chromosomal inversions hold significant potential for cotton breeding programs. By reducing recombination between favorable alleles, inversions can help maintain advantageous gene combinations that contribute to traits such as disease resistance, drought tolerance, and fiber quality (Huang and Rieseberg, 2020; Nosil et al., 2023). The identification of inversions associated with locally adapted traits can inform the development of region-specific cotton varieties, enhancing crop performance under diverse environmental conditions (Korunes and Noor, 2018). Furthermore, understanding the role of inversions in reproductive isolation and speciation can aid in the creation of hybrid cotton lines with improved vigor and yield. The application of genomic selection methods that incorporate inversion data can accelerate the breeding process, leading to the rapid development of superior cotton cultivars.

9.3 Addressing knowledge gaps and challenges

Despite the progress made in understanding chromosomal inversions, several knowledge gaps and challenges remain. One major challenge is the accurate detection and characterization of inversions, particularly small and complex rearrangements that may be overlooked by current methods (Fragata et al., 2014; Connallon and Olito, 2021). Additionally, the functional impact of inversions on gene expression and phenotype is not fully understood, necessitating further research using functional genomics approaches (Nosil et al., 2015). The evolutionary mechanisms driving the maintenance and fixation of inversions in populations also require more investigation, particularly in the context of balancing selection and environmental adaptation (Pombi et al., 2008; Berdan et al., 2021). Addressing these challenges will require a multidisciplinary approach, combining genomics, evolutionary biology, and plant breeding to fully harness the potential of chromosomal inversions in cotton improvement.

10 Concluding Remarks

This systematic review has highlighted the significant role of chromosomal inversions in the evolutionary dynamics of cotton. Chromosomal inversions are structural variations that can suppress recombination, thereby maintaining co-adapted alleles and facilitating adaptation and speciation. The reviewed studies demonstrate that inversions are taxonomically widespread and often associated with locally favored traits, reproductive isolation, and environmental adaptation. Additionally, the accumulation of deleterious mutations within inversions and their impact on fitness and genetic variation were explored, revealing complex evolutionary processes that maintain these inversions over long periods.

The presence of chromosomal inversions in cotton suggests that these structural variations could play a crucial role in the plant's adaptation to diverse environmental conditions and in the development of locally adapted traits. This knowledge can be leveraged in breeding programs to enhance cotton's resilience and productivity. By identifying and utilizing inversions associated with beneficial traits, breeders can potentially improve cotton varieties through targeted selection and genetic engineering.

Chromosomal inversions are pivotal in shaping the evolutionary trajectory of cotton. Their ability to maintain genetic diversity and facilitate adaptation underscores their importance in both natural and artificial selection processes. Future research should focus on the detailed mapping of inversion breakpoints and the identification of causal variants within these regions to further elucidate their role in cotton evolution. Additionally, integrating genomic technologies and advanced breeding techniques will be essential in harnessing the full potential of chromosomal inversions for cotton improvement. Continued exploration of the evolutionary mechanisms underlying inversion maintenance and their ecological significance will provide deeper insights into the adaptive landscape of cotton and other plant species.

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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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