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Chromosome Pairing Behaviour in Intra- and Inter-specific Hybrids of Tetraploid Cotton (*Gossypium* spp.)

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Abstract

Cotton (*Gossypium* spp.) is one of the most important fiber crops worldwide. However, its productivity and stability are increasingly constrained by climate-related factors such as drought, salinity, high temperatures, and the rising impact of pests. Although conventional breeding methods are effective for improving yield and fiber quality, their precision and efficiency remain limited when addressing polygenic traits and complex stress tolerance. This study presents the results of cytogenetic investigations conducted on intraspecific and interspecific F_1 hybrids of tetraploid cotton species (*Gossypium hirsutum* L. and *Gossypium barbadense* L.). The analysis focused on the chromosome pairing in pollen mother cells at the metaphase I stage of meiosis. The results showed that in some intraspecific hybrids, normal chromosome pairing with 26 bivalents was observed, indicating cytogenetic uniformity. In contrast, some intraspecific hybrids exhibited considerable frequencies of univalents and quadrivalents. The highest mean number of univalents was recorded in ssp. *punctatum* var. *gambia* × ssp. *punctatum* (10.70±0.51) and ssp. *punctatum* var. *gambia* × ssp. *mexicanum* var. *microcarpum palmerii* (9.36±0.43). Quadrivalents were observed at low frequencies in ssp. punctatum var. florida × ssp. *punctatum* var. *hopi* (0.21±0.11) and ssp. *glabrum* var. *mari galante* × ssp. *punctatum* (0.14±0.10). These cytogenetic abnormalities suggest the presence of structural chromosomal differences and partial de-synapsis. In interspecific hybrids, univalents (0.12-0.28) and quadrivalents (0.11 ± 0.07) were detected at low frequencies, indicating the presence of karyotypic heterogeneity. However, the formation of 26 bivalents in the majority of hybrids confirmed their high level of phylogenetic relatedness. The obtained results are important for understanding the evolutionary and systematic relationships between *G. hirsutum* and *G. barbadense*, and provide a scientific basis for the targeted use of genetic resources in cotton breeding programs.

Keywords: Cotton, Cytogenetics, Meiosis, Chromosome Pairing, Bivalents, Hybrids

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Introduction

The genus *Gossypium* L. is one of the most important industrial crops, with its tetraploid species, *Gossypium hirsutum* L. and *Gossypium barbadense* L., occupying a leading position in global cotton production. The origin, genome structure, and evolutionary development of these species have long been the focus of cytological and cytogenetic studies. To address complex fundamental problems related to the systematics, evolution, and phylogeny of the genus Gossypium, not only distant hybridization but also cytogenetic investigations are of great importance (1). In particular, determining the degree of phylogenetic relatedness among intraspecific forms of tetraploid species such as *G. hirsutum* L. and *G. barbadense* L. remains a key issue.

Molecular genetic analyses of DNA have demonstrated that tetraploid species originated approximately 1–2 million years ago through interspecific hybridization between an Old

World A-genome diploid taxon (2n=2×=26) and a New World D-genome diploid taxon (2n=2×=26). Following polyploidization, an AD-genome tetraploid (2n=4×=52) was formed, giving rise to seven extant tetraploid species, including *G. hirsutum* L. and *G. barbadense* L., which now dominate global cotton production (2-3). To date, the systematics and phylogenetic structure of the genus Gossypium have been extensively studied by researchers worldwide, with its classification being refined using modern molecular-genetic and phylogenomic approaches (1,4). In particular, the origin, genome composition, and evolutionary relationships of tetraploid cotton species and their intraspecific forms have been thoroughly analyzed (5-7).

Early studies on chromosome number and characteristics in cotton species established that diploid species possess 2n=26 chromosomes, whereas tetraploid species contain 2n=52 chromosomes (8). Subsequent investigations, based on chromosome size, morphology, and meiotic behavior, led to the classification of genome groups, and it is now recognized that the genus Gossypium includes several diploid genomes and one tetraploid genome complex (9-10). Cytogenetic studies have shown that tetraploid cotton species originated through interspecific hybridization between diploid species belonging to different genome groups, followed by polyploidization. In this process, meiotic chromosome pairing characteristics - such as the formation of bivalents, univalents, and quadrivalents - serve as key indicators for assessing the degree of homology between genomes (1,8).

Modern molecular-genetic research further confirms that the origin of tetraploid cotton species is associated with hybridization between A- and D-genome diploid species (2). Moreover, under conditions of climate change, ensuring stable productivity in cotton requires the integration of genomics, conventional breeding, and modern biotechnological approaches (10). For example, the development of synthetic polyploids based on wild diploid species and their genomic and cytogenetic analysis (11), as well as the study of molecular-genetic features of tetraploid cotton forms (6), provide an important scientific basis in this field. These approaches allow for the integration of cytogenetic results with molecular and breeding data. At the same time, chromosome pairing behavior, de-synapsis events, and karyotypic variations in intraspecific and interspecific hybrids have not been sufficiently studied. Available data are often fragmented and sometimes contradictory, necessitating a more comprehensive investigation of the systematics and phylogenetic relationships of cotton species. From this perspective, the aim of the present study is to investigate chromosome pairing at the metaphase I stage of meiosis in intraspecific and interspecific F_1 hybrids of *Gossypium hirsutum* L. and *Gossypium barbadense* L., in order to determine their karyotypic similarity and degree of phylogenetic relatedness. These investigations suggest that some intraspecific forms have evolved independently, indicating that their systematic status may require reconsideration. Although numerous studies have been conducted on the genus Gossypium, chromosome pairing behavior at metaphase I of meiosis in intra- and interspecific hybrids of *G. hirsutum* and *G. barbadense*, particularly the formation of bivalents, univalents, and quadrivalents, has not been sufficiently and systematically investigated. Therefore, the aim of the present study is to analyze chromosome pairing at metaphase-I of meiosis in F_1 intraspecific and interspecific hybrids of *G. hirsutum* L. and *G. barbadense* L.

The scientific novelty of this study lies in the comprehensive quantitative analysis of bivalents, univalents, and quadrivalents in these hybrids, providing new cytogenetic evidence for determining the degree of genomic affinity and phylogenetic relationships. These findings serve as an important scientific basis for revising the systematic status of the genus *Gossypium*. At the same time, cytogenetic evidence plays a crucial role in substantiating proposed classification revisions. Therefore, the present study aims to elucidate karyotypic and phylogenetic relationships among intraspecific and interspecific forms within the genus Gossypium, thereby emphasizing its scientific relevance. Among the numerous changes occurring during evolution, chromosomal rearrangements in cotton play a particularly significant role.

Materials and Methods

In the present study, cytogenetic characteristics of meiosis were investigated in intraspecific and interspecific F_1 hybrids of cotton. In particular, chromosome pairing at the metaphase-I (MI) stage of the first meiotic division was analyzed, and the formation patterns of univalent, bivalent, and multivalent (quadrivalent) chromosomes were evaluated. The study was conducted using both classical and modern cytogenetic methods (12-14), and chromosome pairing at the metaphase I stage of meiosis was assessed.

Overall, between 6 and 36 cells were microscopically analyzed for each combination. In each preparation, metaphase plates were selected randomly and chromosomes were counted. Based on the obtained data, the mean values (M) and standard errors (±SE) were calculated for each parameter. Differences among variants were evaluated using descriptive statistical methods.

Plant material consisted of flower buds collected from 9 intraspecific and 15 interspecific F_1 hybrid combinations. The cotton genotypes used in the study were cultivated in Wagner pots under controlled experimental conditions. Plant growth and development were maintained under optimal agronomic practices, including regular irrigation and mineral fertilization. Uniform conditions were ensured across all experimental variants, and morpho-biological traits of the plants were systematically observed and recorded (Figure 1). Flower buds were collected in the morning between 8:00 and 10:00 a.m., at a size of 2-4 mm, corresponding to the active stages of meiosis. The samples were fixed in an ethanol-acetic acid solution (3:7) and subsequently sorted according to their developmental stages. Flower buds at the metaphase-I and tetrad stages were selected for further analysis.

Pollen mother cells (PMCs) were stained using iron-acetocarmine, and temporary squash preparations were prepared. The prepared slides were analyzed using a Leica CM E light microscope equipped with a Leica EC3 digital

camera. For each hybrid combination, cells at the metaphase-I stage were selected, and chromosome pairing configurations - univalents, bivalents, and multivalents - were recorded. The number of analyzed pollen mother cells (PMCs) varied among the combinations, which can be explained by the asynchrony of flower bud development and the availability of cells at the metaphase I stage. Nevertheless, the number of cells analyzed for each combination was sufficient for cytogenetic evaluation and ensured the reliability of the obtained results.

Figure 1. General view of the cotton plants used in the study and their cultivation conditions.

Results

Analysis of chromosome pairing at the metaphase I stage of meiosis revealed a wide range of variation in cytogenetic parameters among the studied F_1 hybrid combinations. Based on the characteristics of chromosome pairing, the combinations were classified into different groups.

In combinations exhibiting stable chromosome pairing, complete formation of 26 bivalents (26.00 ± 0.00) was observed, with no univalents or multivalents detected. This pattern was mainly characteristic of genetically close intraspecific combinations and indicates a high degree of homology between homologous chromosomes as well as genomic stability (Tab. 1).

Overall, the chromosome pairing patterns observed among the studied hybrid combinations exhibited a certain degree of variation. The formation of 26 bivalents in most hybrids indicates a high level of chromosome homology and cytogenetic compatibility between the parental genomes. Conversely, the occurrence of univalents and occasional quadrivalents in several hybrid combinations suggests structural divergence and varying degrees of genomic differentiation. These findings are in agreement with recent studies demonstrating considerable genetic diversity and subspecific differentiation within *Gossypium hirsutum*, which provide a genetic basis for the cytogenetic variation observed among the studied hybrids (17).

In some combinations, the number of univalents ranged from 0 to 10.70 ± 0.51, accompanied by a corresponding decrease in the number of bivalents to 20.65 ± 0.26. The increase in univalents reflects incomplete chromosome pairing, i.e., de-synapsis, indicating the presence of structural differences between genomes. Such patterns were particularly evident in certain intraspecific combinations. Multivalents (quadrivalents) were observed at low frequencies (0.14 ± 0.10–0.21 ± 0.11), suggesting possible chromosomal rearrangements, including translocation events. These observations, detected in specific combinations, reflect complex interactions between genomes(Tab. 1).

In one of the interspecific hybrid combinations - *G. barbadense* ssp. *vitifolium f.brasiliense* × *G. hirsutum* ssp. *mexicanum* var. *nervosum* (Yucatan) - cytogenetic analysis revealed the formation of large quadrivalent chromosome associations at the metaphase-I stage, predominantly in ring configurations. These quadrivalents were recorded at an average frequency of 0.11 ± 0.07 per cell. The formation of such associations indicates the presence of chromosomal exchanges via translocation rings, suggesting structural differences in chromosome organization between the parental forms involved in this combination.

In two other interspecific combinations - *G. hirsutum* ssp. *mexicanum* var. *nervosum* × *G. barbadense* ssp. *ruderale f.ishan nigeria*, and *G. barbadense* ssp. *ruderale f.ishan nigeria* × *G. hirsutum* ssp. *punctatum* var. *hopi* - a small number of unpaired univalent chromosomes (0.12 ± 0.12 and 0.28 ± 0.28 per cell, respectively) were observed at the metaphase-I stage. Notably, in both cases, one of the parental forms was *G. barbadense* ssp. *ruderale f.ishan nigeria*. This suggests that this genotype may exhibit elements of karyotypic incompatibility when hybridized with other forms.

Overall, the occurrence of quadrivalent associations in some interspecific hybrids indicates karyological heterogeneity of the parental forms and the presence of latent structural chromosomal variation. At the same time, the detection of univalents in certain combinations can be explained by partial genomic incompatibility and disturbances in homoeologous chromosome pairing.

Thus, although chromosome pairing in interspecific hybrids is generally stable, the presence of quadrivalents and univalents in some combinations represents important cytogenetic indicators reflecting the degree of genomic divergence and structural rearrangements. This allows such hybrids to be considered valuable models for studying genomic interactions and evolutionary changes.

Discussion

In this study, chromosome pairing behavior in intraspecific and interspecific hybrids of tetraploid cotton (*Gossypium* spp.) was comprehensively evaluated using cytogenetic approaches. The predominance of 26 bivalents in most hybrid combinations indicates a high degree of homology between parental genomes and confirms the close evolutionary relationship between *G. hirsutum* and *G. barbadense*. These findings are consistent with previous studies (3, 15-16).

However, the presence of univalent and multivalent chromosomes in certain combinations indicates partial disruption of chromosome pairing. Such abnormalities are likely associated with structural differences between parental

Table. 1 Chromosome pairing at the metaphase I stage of meiosis in intra- and interspecific F_1 cotton hybrids (*G. hirsutum* L. and *G. barbadense* L.)

Samples	Cell count	Mean per Cell		
		Univalents	Bivalents	Quadrivalents
Intraspecific hybrids (*G. hirsutum* L.)				
ssp. *punctatum var. gambia* × ssp. *punctatum*	17	10.70±0.51	20.65±0.26	0
ssp. *punctatum* var. *gambia* × ssp. *mexicanum* var. *microcarpum palmerii*	19	9.36±0.43	21.32±0.21	0
ssp. *mexicanum* var. *microcarpum palmerii* × ssp. *mexicanum* var.*nervosum* (Yucatan)	18	0	26.00±0.00	0
ssp. *mexicanum* var. *microcarpum palmerii* ×ssp. *purpurascens* var.*el-salvador*	36	0	26.00±0.00	0
ssp. *mexicanum* var. *microcarpum palmerii* × ssp. *punctatum* var. *hopi*	15	0	26.00±0.00	0
ssp. *mexicanum* var. *microcarpum palmerii* × ssp. *punctatum* var.*java*	11	0	26.00±0.00	0
ssp. *punctatum* × ssp. *purpurascens*	10	0	26.00±0.00	0
ssp. *punctatum* var. *florida* × ssp. *punctatum* var. *hopi*	16	0	25.57±0.23	0.21±0.11
ssp. *glabrum* var.*m.galante* × ssp. *punctatum*	14	0	25.71±0.19	0.14±0.10
Interspecific hybrids (*G. hirsutum* L., *G. barbadense* L.)				
G. barbadense ssp. *darwinii* × *G. hirsutum* ssp. *mexicanum* var. *microcarpum palmeri*	16	0	26.00±0.00	0
G. hirsutum ssp. *mexicanum* var. *nervosum* (Yucatan) × *G. barbadense* ssp. *ruderale* f.*ishan nigeria*	15	0.12±0.12	25.93±0.07	0
G. barbadense ssp. *ruderale* f.*ishan nigeria* × *G. hirsutum* ssp. *mexicanum* var. *nervosum* (Yucatan)	36	0	26.00±0.00	0
G. hirsutum ssp. *mexicanum* var. *nervosum* (Victoria.) × *G. barbadense* ssp. *ruderale* f.*ishan nigeriya*	27	0	26.00±0.00	0
G. hirsutum ssp. *mexicanum* var. *nervosum* (Yucatan*)* × *G. barbadense* ssp. *ruderae* f.*ishan nigeria* (бур.вол)	13	0	26.00±0.00	0
G. barbadense ssp. *vitifolium* f.*brasiliense* (red.) × *G. hirsutum* ssp. *mexicanum* var. *nervosum* (Yucatan*)*	16	0	25.70±0.11	0.11±0.07
G. barbadense ssp. *ruderale* f.*ishan nigeria* × *G. hirsutum* ssp. *punctatum* var. *hopi*	14	0.28±0.28	25.86±0.14	0
G. hirsutum ssp. *paniculatum* × *G. barbadense* ssp. *ruderale* f.*parnat*	16	0	26.00±0.00	0
G. barbadense ssp. *eubarbadense* (variety Surkon-9) × *G. hirsutum* ssp. *punctatum*	16	0	26.00±0.00	0
G. barbadense ssp. (variety Surkon-9) × *G. hirsutum* ssp. *punctatum* var. *gambia*	12	0	26.00±0.00	0
G. barbadense ruderale f. *ishan nigeriya* × *G. hirsutum* ssp. *euhirsutum* (variety Kelajak)	6	0	26.00±0.00	0
G. barbadense ssp. *darwinii* × *G. hirsutum* ssp. *euhirsutum (*variety Kelajak*)*	11	0	26.00±0.00	0
G. hirsutum ssp. *euhirsutum* (variety Kelajak) × *G. barbadense* ssp. *ruderale* f.*pisco*	7	0	26.00±0.00	0
G. barbadense ssp. *eubarbadense* (variety Surkon-9) × *G. hirsutum* ssp. *euhirsutum* (variety Kelajak)	12	0	26.00±0.00	0

genomes, including chromosomal translocations and inversions. In particular, quadrivalent associations observed in some interspecific hybrids reflect chromosomal rearrangements, whereas univalents indicate incomplete pairing of homologous chromosomes (de-synapsis).These factors may negatively affect meiotic stability and fertility.

Competitive interactions between conspecific and heterospecific pollen grains have a negative impact on fertility whereby Angiosperms evolved multiple prezygotic and postzygotic barriers to minimize the effect of fitness reduction. Prezygotic barriers impede hybridization and include pre-pollination isolation and gametic selection (18). Hybrid sterility, caused either by gene incompatibilities or chromosome rearrangements, is a common form of postzygotic reproductive isolation in plants (19). Pre-pollination isolation prevents the anticipated arrival of competitive foreign pollen grains on a stigma. These barriers include adaptations such as flowering asynchrony either during the day or along the year, or divergence in floral traits conditioning the pollinator preference or the mechanical interaction between flower and pollinator during visits. Various forms of gametic isolation, including stigma incompatibility and suppression of pollen tube growth, counteract foreign pollen germination deposited on a stigma. Modifications of the structure or chemical composition of stigma as well as factors controlling pollen recognition and self-incompatibility may contribute to increase incompatibility with foreign pollen. Self-incompatibility and interspecific incompatibility show similarities in the molecular mechanisms controlling the pollen-pistil interactions, since pollen of self-compatible species deposited on stigma of self-incompatible relatives is rejected but not in the reciprocal hybridization (20). Pollen deposited on the stigma of a distantly related species usually fails to germinate, but this is not the case between closely related species. In such cases, divergence between species in pollen tube performance in the style may cause either a more disruptive development of the foreign pollen tube or mismatches in the size of both structures, which contribute to avoid interspecific hybridization (18). Interspecific hybridization may represent a source of phenotypic innovation (19). Although interspecific hybrids usually show a low fertility, the offspring obtained allows to extend hybridization to further generations, which may display transgressive trait variation, that is, a gain or a loss of valuable traits with respect to the parental species. On the other hand, recurrent backcrosses of the hybrids with one of the parental species give rise to introgression of alien genes in any of the parental species and represent a common way of gene flow between species in hybrid zones (19). Darlington (21) proposed an inverse relationship between the fertility of an interspecific hybrid and the fertility of the allopolyploid generated from the homoploid hybrid by doubling its chromosome number. He argued that homoploid hybrids between closely related species will show a high level of meiotic pairing and fertility, while the fertility of the corresponding allopolyploids will be reduced because of uneven segregation of chromosomes from multivalents involving both homologues (equivalent chromosomes from the same genome) and homoeologues (equivalent chromosomes from related genomes). In contrast, homoploid hybrids between distant species will be sterile due to chromosome pairing failure, but allopolyploids will be fertile due to preferential formation of homologous bivalents at meiosis. The observed cytogenetic variability among hybrid combinations suggests differing levels of genomic compatibility and highlights the importance of cytogenetic analysis in identifying stable and unstable combinations. Such data are essential for understanding genome evolution and for evaluating the biological efficiency of hybrids.

Conclusion

The results of this study demonstrate that chromosome pairing in intraspecific and interspecific hybrids of tetraploid cotton is generally stable. The formation of 26 bivalents in most combinations confirms a high degree of compatibility between parental genomes. At the same time, the presence of univalent and quadrivalent chromosomes in certain hybrids indicates structural differences and partial genomic divergence, which may affect meiotic stability. The obtained results contribute to a deeper understanding of genome organization and evolutionary relationships within the genus Gossypium, and provide an important scientific basis for selecting genetically compatible and stable combinations in cotton breeding programs.

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