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A NEW CASE OF UNIPARENTAL CHROMOSOME ELIMINATION IN AN INTERSPECIFIC HYBRID OF COTTON F_1 (*GOSSYPIUM HIRSUTUM* L. × *G. BARBADENSE* L.)

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SUMMARY

Cytogenetic and molecular genetic studies of the cotton haploid describe its morpho-biological features in comparison with the parental genotypes. This research aimed to study the cotton haploid (277_2) spontaneously developed through interspecific crossing of monosomic line Mo15 (*Gossypium hirsutum*) with Pima 3-79 (*G. barbadense*) to create the chromosome-substituted cotton lines. With species incompatibility, selective elimination of chromosomes took place in one of the parental genomes observed in interspecific hybrids. The haploid plant displayed characteristics of a thin and tall stem, dense foliage, shortened internodes, small three-lobed leaves, and complete sterility. In the metaphase I of meiosis, 26 univalents manifested random distribution in the pollen mother cells. The haploid stood out by the complete absence of bivalent formation and presence of unpaired chromosomes in the pollen mother cells. Molecular genetic analysis of the haploid using SSR markers revealed the alleles only from the species *G. hirsutum* in all 26 chromosomes of the haploid genome, which confirmed the selective elimination of chromosomes of the entire paternal genome. The promising results indicated the possibility of using haploid inbreeding by developing doubled haploids (DH).

Keywords: Cotton, *Gossypium hirsutum, G. barbadense,* monosomic line, haploid, selective elimination of chromosomes, SSR markers

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Key findings: Cytogenetic analysis of the interspecific F_1 hybrid (277_2) obtained through crossing of the monosomic line Mo15 (*G. hirsutum* L.) with disomic line, Pima 3-79 (*G. barbadense* L.) appeared with morpho-biological features and complete absence of chromosome pairing. The SSR markers confirmed the presence of alleles only from the species *G. hirsutum*, indicating selective elimination of chromosomes.

INTRODUCTION

Selective elimination of chromosomes in one of the parental genomes during interspecific hybridization of plants often leads to the formation of haploids, with the chromosomes of the one paternal genome eliminated due to species incompatibility. The barley haploids in hybrids (*H. vulgare* L. × *H. bulbosum* L.) were notable with the elimination of chromosomes of species *H. bulbosum* (Symko, 1969; Kasha and Kao, 1970; Lange, 1971). The factors causing the elimination of *H. bulbosum* chromosomes resulted from genes located on both arms of chromosome 2 and the short arm of chromosome 3 of the *H. vulgare* (Ho and Kasha, 1975).

Genomic hybridization in situ (GISH) studies of 6-13-day-old embryos obtained from crossing the barley line *H. vulgare* with *H. bulbosum* and in mitosis. It showed the chromatin of the only species, *H. bulbosum,* occupied decondensed territories within the nucleus, causing spatial separation and occupation of separate domains (Gernand *et al.,* 2006). Crosses of hexaploid wheat (*T. aestivum* L.) with barley (*H. bulbosum*) resulted in endosperm degeneration 14–18 days after pollination, and cytological analysis revealed a haploid karyotype in 57 out of 70 resulting plants (Barclay, 1975). The crosses between wheat and maize (*Z. mays* L.) displayed the elimination of one or more maize chromosomes in 70% of the analyzed zygotic mitosis (Laurie and Bennett, 1989).

Combined analysis of wheat and millet (*Pennisetum glaucum* L.) crosses revealed a complex stepwise process of chromosome elimination in millet by partitioning the parental interphase chromatin as a peripheral position of millet chromatin (Gernand *et al.,* 2005). The repeated study of wheat-millet crosses disclosed chromosome elimination with new features during embryogenesis, such as chromosomal rearrangements and micronuclei, which may arise due to breakage of chromosome bridges and non-disjunction of millet chromosomes (Ishii *et al.,* 2010). The crosses of wheat and wild species *Imperata cylindrica* L. demonstrated the elimination of chromosomes of the cogon grass resulting from non-disjunction of sister chromosomes to the division poles in anaphase. This eventually led to the formation of micronuclei and the removal of chromosomes during one division cycle (Komeda *et al.,* 2007).

In understanding the mechanism of chromosome elimination, the major breakthrough came about through the analysis of centromeric histone H3 (CENH3). It showed the inactivation of the species *H. bulbosum* chromosome centromeres by the loss of histone CENH3 triggers a mitosis-dependent process of uniparental chromosome elimination in unstable hybrids of *H. vulgare* × *H. bulbosum* (Sanie *et al.,* 2011).

In the tetraploid cotton species *G. hirsutum* L. (2n=52, AD_1), a concept of complete sterility existed in its haploids. Meanwhile, haploids of another tetraploid species, *G. barbadense* L. (2n=52, AD_2), showed characteristics of partial fertility and the presence of four seeds in one boll, and the seed set rate was only 1.25% (Endrizzi, 1966). In the species *G. barbadense*, the main source of different types of haploids incurred genetic control with semigamy, in which independent division of the nuclei of the egg and sperm was evident (Turcotte and Feaster, 1963; 1969). Further analysis of studies on haploidy suggested the location of the semigamy gene is on the short arm of chromosome 4 (Gwyn, 1995).

Several studies have examined semigamous cotton lines and reported they produce a significant number of small seeds, with the seed weight correlated with the percentage of haploidy (Zhang *et al.*, 1998).

However, other studies have emphasized the expression of semigamy as a sporophytic and gametophytic control of a single incompletely dominant gene, Se (Zhang and Stewart, 2004). A series of molecular genetic studies identified four primer pairs by comparative microarray analysis (Curtiss *et al.,* 2011) and six primer pairs by differential display (Curtiss *et al*., 2012a). These revealed polymorphisms that appeared to be unique to either the hemigametic or the nonhemigametic genotype. However, another study (Curtiss *et al*., 2012b) identified three molecular markers associated with the hemigametic genotype.

A study of histone H3, the loss of which causes centromere inactivity, identified 34 genes in the cotton plant *G. hirsutum* belonging to the H3 gene family for the first time, having divided into four subclasses: CENH3, H3.1, H3.3, and H3-like. All the genes' locations were on chromosomes 5, 6, 8, 10, and 13 of the A subgenome (Zhang *et al.,* 2020).

At the National University of Uzbekistan, the conduct of research progresses to obtain chromosome-substituted lines based on crossing monosomic lines (Mo) of Upland cotton (*G. hirsutum*) with Pima 3-79 line (*G. barbadense*) and five-fold backcrossing (Sanamyan *et al.,* 2014). In conducting these studies, obtaining interspecific F_1 hybrids (Mo × Pima 3-79) has reached 35 variants of crossing monosomic lines with identified univalent chromosomes 2, 4, 6, 7, and 12 of the A_t-subgenome and chromosomes 17, 18, 21, and 22 of the D_t-subgenome of cotton with the donor line Pima 3-79 (*G. barbadense*) (Sanamyan *et al.,* 2022). Additionally, new interspecific hybrids were successful outcomes from crossing monosomic lines with unidentified univalents with the same donor line in 24 crossing variants, among which a new haploid cotton plant succeeded its identification.

Therefore, the presented research aimed to carry out a comprehensive study of this new haploid cotton plant, spontaneously raised as a result of interspecific crossing of the monosomic line Mo15 (*G. hirsutum*) with the Pima 3-79 (*G. barbadense*) for the development of chromosome-substituted cotton lines. This research presents the results of the cytogenetic and molecular genetic study of the obtained cotton haploid. It also sought to describe its morpho-biological features in comparison with the parental genotypes.

MATERIALS AND METHODS

Plant material

In this study, the monosomic line Mo15 of the species *G. hirsutum* (2n=51), the line Pima 3-79 of the species *G. barbadense* (2n=52), and the interspecific F_1 hybrid (Mo15 × Pima 3-79) were the studied specimens. The parental genotypes of this interspecific hybrid included a monosomic line obtained based on primary monosomic Mo15, induced in the first generation. It was a result of the pollination of a gamma-irradiated pollen line, L-458, at a dose of 25 Gy, on the eve of castrated flowers of the same line. Monosomic line crossing served as a female parent with the line Pima 3-79 of the species *G. barbadense*, obtained based on dihaploid; therefore, it is highly homozygous and is a genetic standard for this species of cotton in the USA (Endrizzi *et al.,* 1985). A long length of high-quality fiber characterized the said line; thus, it served as a donor parent of the substituted chromosome for developing new chromosome-substituted cotton lines. Monosomic line Pima 3-79 and the F_1 hybrids (Mo15 × Pima 3-79) underwent growing in a film greenhouse at natural temperature and light during summer and under film cover at the temperature of 30 °C/15 °C during day/night in the autumn-winter period.

DNA-extraction genotyping

Genomic DNA isolation from young leaves of F_1 hybrid seedlings (Mo15 × Pima 3-79) began at the 4–5 true leaf stage using the CTAB method analysis, performing SSR analysis according to a previously published method (Sanamyan *et al.,* 2022). Primer pairs for codominant chromosome-specific SSR markers were synthesized in accordance with previously established genetic mapping studies (Liu *et al.,* 2000; Hoffman *et al.,* 2007; Gutie'rrez *et al.,*

2009; Saha *et al.,* 2015), as listed in Table 1. For each chromosome, selection of four loci that were polymorphic occurred between L-458 (*G. hirsutum*) and Pima 3-79 (*G. barbadense*). For SSR, the electropherogram results' estimation was a/b/h, where locus a corresponded to the recipient L-458, locus b to the donor line Pima 3-79, and the genotype h was the disomic F_1 hybrid. In the haploid cotton F_1 hybrid, the elimination of *G. barbadense* chromosomes succeeded by the absence of amplification of the chromosome-specific marker on the chromosomes of *G. barbadense* and the presence of only the allele-specific PCR products of *G. hirsutum* (Liu *et al.,* 2000).

Cytological tests

Cytological analysis proceeded according to the method described in our previous study (Sanamyan *et al.,* 2022). Statistical processing of the obtained data continued according to B.A. Dospekhov (1985).

RESULTS

Cytogenetic study of new hybrid combination F_1 (Mo × Pima 3-79) obtained by crossing 24 monosomic lines of the species *G. hirsutum* with deficiency of non-identification of univalent chromosomes, with donor line Pima 3-79 (*G. barbadense*) showed the decrease crossability (ranging from 8.33% to 81.82%), as well as reduced setting of hybrid seeds (ranging from 23.29% ± 4.95% to 82.14% ± 7.24%), with their germination (ranging from 18.06% to 89.47%) in some hybrid variants, as compared with the cotton line L-458 (66.67%, 71.69% ± 2.17%, and 84.62%, respectively). In particular, the monosomic line (Mo15), which served in the crosses, also had distinction by reduced crossability with the line Pima 3-79 (79.92%), as well as low setting of hybrid seeds (25.29% ± 2.36%) and their reduced germination (83.72%). In particular, the monosomic line (Mo15), which served in the crosses, also had distinction by reduced crossability with the line Pima 3-79 (79.92%), as well as low setting of hybrid seeds (25.29% ± 2.36%) and their reduced germination (83.72%).

Therefore, detection succeeded in this variant of crossing F_1 (Mo15 × Pima 3-79) among 14 hybrid plants of one highly morphologically modified tall plant (277_2) of a columnar shape with a thin, tall stem, dense foliage, and shortened internodes (Figure 1b). Similarly, it was an unexpected and unique phenomenon. In addition, this plant showed characteristics of small, three-lobed leaves with one nectary, small bracts with 10–12 teeth, small flowers, fewer ovules in the ovary (29–32), and the absence of boll setting. Yet, the original lines (Mo15 and Pima 3-79) did not differ in such characteristics. They express similar characteristics of high growth, more sympodial branches (Figure 1a, c), and large five-lobed shiny leaves (15–20 cm) with three nectaries at the Pima 3-79, and three- and five-lobed leaves of medium size (10–12 cm) in the monosomic line Mo15.

Additionally, both original lines significantly differed in flower morphology, since the line Mo15 emerged with small bracts (with 9–11 teeth), pale yellow color of petals and pollen, and numerous oval-shaped bolls with more ovules in the ovary (41–43); however, they had reduced seed set. The cotton line Pima 3-79 was notable with large bracts (with 10–14 teeth), large flowers of bright yellow color with an anthocyanin spot at the base of the petals, and bright yellow pollen color. It also had elongated ovoid bolls with a pointed beak and fewer ovules (22–31), as well as a high seed set (88.09% ± 2.11%).

Cytogenetic analysis of the hybrid plant (277_2) discovered an absence of chromosome pairing at the metaphase I stage of meiosis and the presence in all studied microspores of 26 univalents. These showed random distribution in meiocytes, as located only along the walls of the microspores, and led to the formation of microspores with different numbers of chromosomes, indicating its haploid nature (Figure 2).

The process of meiosis reached completion by the formation of various types of polyads (pentads, hexads, heptads, and oktads) in the overwhelming majority of cells and a low meiotic index (13.33±0.47) in the haploid. As compared with the lines Mo15 and Pima 3-79, they showed a high meiotic index.

Table 1. Microsatellite markers (SSR) used in the analysis of cotton hybrids obtained from crossings of the monosomic line Mo15 with line Pima 3-79.

Chromosome	SSR marker	Size of PCR products for each SSR marker (n.b.p*)		Chromosome	SSR marker	Size of PCR products for each SSR marker (n.b.p*)	
		G. hirsutum (L-458)	*G. barbadense* (Pima 3-79)			*G. hirsutum* (L-458)	*G. barbadense* (Pima 3-79)
1	BNL2440	177	183	13	BNL4061	168, 201	168, 180
	BNL3655	127	108		BNL3623	345	237
	BNL3090	211, 238a	222		TMB2108	158	-
	BNL1667	164a	174		HAU1577	212	-
2	BNL1434	245	262	14	Gh067	170	180
	BNL3292	110, 113a	110, 122		BNL3545	187a, 108, 116, 139, 178	214, 107, 114, 129, 216
	NAU0895	202	-		BNL3644	191a, 184, 190	185
	DPL0674	232	255		MUSS354	397	-
3	BNL3408	128a	133	15	BNL3902	192a	171
	BNL3463	230	270		BNL2920	134a	147
	NAU862	200	-		TMB0201	202, 226	201
	TMB0564	101, 196	159		MUSS523	287	-
4	BNL2572	248	234	16	BNL3008	131a	139
	BNL4047	155	161		JESPR297	150	-
	TMB0446	176, 185	183		TMB2068	150	123, 133
	Gh124	180	200		Gh295	95	75
5	NAU861	215	190, 195	18	BNL2544	219	207
	BNL3255	227	206		TMB0029	197, 203, 212	197–212
	NAU3245	230	-		Gh501	195,149, 198	205,146, 201
	CIR373	164,22	170,01		BNL0193	109, 116	109, 111
6	BNL1440	256	266	19	Gh171	205	215
	BNL3650	352	338		NAU2503	250	-
	TMB1277	251	263		TMB0131	200	-
	TMB1538	178, 208	196		DPL0247	160	147, 154
7	BNL580	198, 204a	202	20	BNL3993	202a	194
	BNL1604	101	110		BNL3792	229, 232	211, 213
	CIR141	194	179		TMB0043	173, 178	175, 182
	Gh548	120	140		TMB1630	228	217
8	BNL3257	207a	190	21	BNL1705	192	168
	BNL387	210a	220		BNL3171	224, 226, 228	228, 230, 234
	NAU0920	150	-		NAU5312	150	-
	CIR244	123	129		Gh132	165	-
9	BNL1707	142, 145, 153a, 155, 157	142, 145, 155	22	BNL448	213a	202
	BNL4028	95, 182	95, 139		Gh052	133	120
	DPL0679	146, 174	146, 186		CIR218	163, 174	167, 175, 177
	TMB1758	176	-		Gh641	90	94
10	BNL256	200a, 205a	179, 185	23	BNL3511	162, 169	162, 175a
	BNL1161	204, 216a	196, 204		BNL3383	189	175a
	NAU2082	170	-		BNL3858	192	190a
	Gh058	175	100		JESPR151	151	114
11	MUCS088	137	-	24	BNL2568	141	150
	BNL4094	179	171		GH171	205	215
	MUCS399	193	-		MUSS255	207	-
	TMB0043	173, 178	175, 182		TMB1182	199	-
12	BNL3261	203	195	25	BNL3806	173, 207a	173, 181
	BNL391	307	355		TMB0313	164, 199	164, 173
	NAU4047	400	-		Gh515	130	120
	TMB1660	118, 127, 198	190		Gh537	200	190
17	BNL2471	195	191	26	BNL3816	184, 200	184
26	STV033	180, 192	187		TMB0366	201, 206, 216	201, 216

* Note - n.b.p. – nucleotide base pairs. Literary source: Liu *et al.,* 2000; Hoffman *et al.,* 2007; Guo *et al.,* 2008; Gutie´rrez *et al.,* 2009; Roberts and Ulloa, 2010; Zhao *et al.,* 2012; Ulloa *et al.,* 2013; Arioli *et al.,* 2015; Saha *et al.,* 2015. https://www.cottongen.org/data/download/marker_origin

Figure 1. Plants of the original lines and a haploid cotton plant: a) monosomic line Mo15 *G. hirsutum*, b) haploid cotton plant F_1 (Mo15 × Pima 3-79) (277_2), and c) line Pima 3-79 *G. barbadense*.

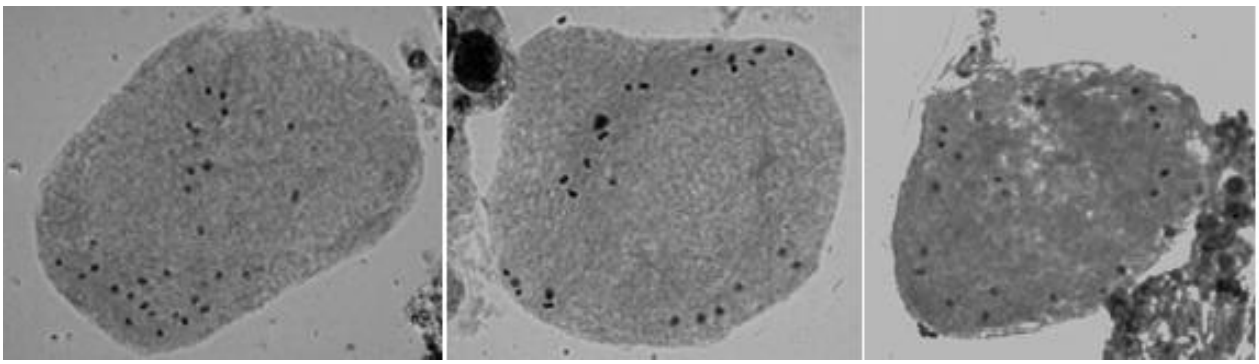

Figure 2. Metaphase I in meiosis of haploid cotton plant (277_2) obtained from crosses of monosomic line Mo15 species *Gossypium hirsutum* L. with the line Pima 3-70 species *G. barbadense* L.: 26 univalents.

All the studied types of sporades had the presence of an increased number of micronuclei (up to 5.44% ± 0.31%), versus the original genotypes, which indicated numerous eliminations of chromosomes and their non-inclusion in microspores.

Molecular genetic analysis of F_1 hybrids (Mo15 × Pima 3-79) revealed the presence of alleles only from the *G. hirsutum* and the absence of alleles from the *G. barbadense* in all 26 chromosomes of the haploid genome (Table 1, Figure 3). The results confirmed the selective elimination of chromosomes of the entire parental genome, probably due to cell cycle asynchrony and centromere dysfunction. However, at the same time, considering the number of hybrid seeds sown, the frequency of haploid induction was 7.14%.

DISCUSSION

For the development of chromosome-substituted cotton lines, crosses between the monosomic lines of *G. hirsutum* with the line Pima 3-79 of the species *G. barbadense* succeeded and proved of great interest for the introgression of alleles of useful traits. The 360 crosses involved monosomic lines with identified chromosomes, while over 250

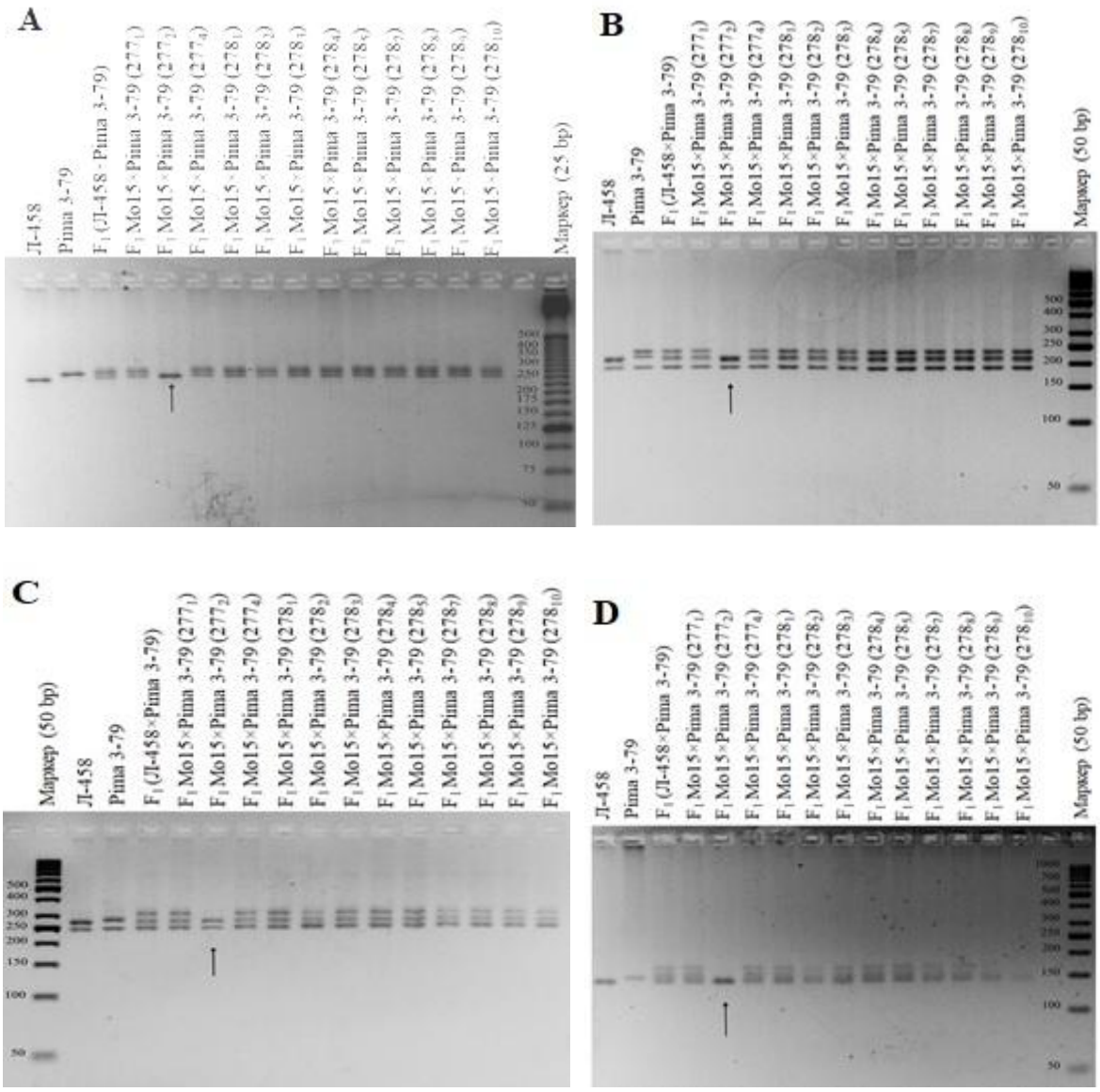

Figure 3. Electropherograms of the DNA amplicons of SSR markers in interspecific hybrids F_1 (Mo15 × Pima 3-79) chromosome-specific for the A_t-subgenomes: a) BNL1434 (2 Chr), b) NAU861 (5 Chr), c) BNL1440 (6 Chr), and d) MUCS0888 (11 Chr).

crosses were with monosomic lines with unidentified univalent chromosomes. However, out of these crosses, only one variant involving a monosomic line, Mo15, and line Pima 3-79 succeeded in identifying a haploid, which was a great surprise, indicating the greater rarity of such an event. According to our knowledge, this was the first case to detect a uniparental chromosome elimination in an interspecific cotton hybrid involving a monosomic line Mo15 (*G. hirsutum*) and a line Pima 3-79 (*G. barbadense*) (Ishii *et al.,* 2016; Dedukh and Krasikova, 2022).

Previous cytogenetic studies of cotton haploids confirmed the absence of normal bivalent chromosome pairing, and due to the presence in meiosis, numerous univalents and some number of paired chromosomes occurred (Barrow, 1971). Besides, six partially fertile haploids of cotton *G. hirsutum*, obtained in the

second generation after irradiation of seeds with X-rays, reached characterization by variations in the frequency of paired chromosomes and formation of triads, tetrads, and pentads (Mehetre and Thombre, 1981).

In our previous study, one induced haploid plant after fast-neutron seed irradiation appeared (Rakhmatullina and Sanamyan, 1992), while three appeared after pollination with irradiated pollen (Sanamyan, 2020). A comparative analysis of the previously obtained four haploids with the new haploid plant (277_2) revealed similarity between this haploid and the other two obtained after pollination with irradiated pollen and the absence of chromosome pairing.

Comparison of pairing in haploids of *G. barbadense* with pairing in diploid and triploid cotton hybrids that included A and D genomes indicated a low degree of pairing in haploids and proved inconsistent with the relatedness between these genomes (Kimber, 1960). According to their study, an explanation for this is the genetic regulation of meiosis, determining the bivalent pairing in tetraploid species of the *Gossypium* L. genus. Moreover, it limits the pairing of homologous chromosomes in meiosis in polyhaploids of these cotton species.

For identifying haploid plants, using SSR markers serves as a reliable tool for genotyping in various crops (Keles *et al.,* 2015). In this current study, the use of such molecular genetic markers confirmed the results of the cytogenetic analysis. It also indicated uniparental elimination of paternal chromosomes concerning the presence in the newly identified haploid (277_2) of alleles received only from the female parent and the absence of paternal alleles.

Factually, the phenomenon of elimination of chromosomes of one parental genome had a previous discovery in 74 hybrids involving monocotyledonous species and 35 hybrids involving dicotyledonous species (Ishii *et al.,* 2016). For the elimination of chromosomes of entire parental genomes in hybrids of different natures, various mechanisms attained proposals, with an artificial nutrient medium often used to save embryos. A previous study pointed out the potential use of haploid technology lines, as it is typical that the number of cultivars developed based on haploids was constantly increasing (Dyachuk *et al.,* 2019). The maize haploinducer production made it possible to use anthocyanin color genes to identify the hybrid embryos and haploid genotypes. Likewise, it helped synthesize a haploinducer line carrying a CRISPR/Cas construct in pollen grain sperms that simultaneously stimulate haploidy and edit the genome at a given DNA site (Ulyanov *et al.,* 2022).

Studies on the Upland cotton (*G. hirsutum*), devoted to obtaining haploids using androgenesis, have proven ineffective; however, in one tetraploid species (*G. barbadense*), a semigamous line emerged to produce haploids with a higher frequency (Endrizzi *et al.,* 1985). The use of a similar semigamous line of *G. barbadense* marked by the virescent gene (*Vsg*) allowed us to develop a new linkage map of tetraploid cotton (Zhang *et al.,* 2002). Applying an original approach to the model causes the induction of haploids in allopolyploid crops via an *in vitro* CenH3 PNKi and inhibition assay. As a result, a transgenic cotton line became an outcome using RNA interference of the histone protein CenH3 (Gao *et al.,* 2020).

The CRISPR-Cas9 technology made it possible to obtain mutant gossypol-free types and haplo-inducer lines of cotton (Long *et al.,* 2024). Thus, the results indicated the potential use of cotton haploids for developing the homozygous, transgenic, and haplo-inducer lines for the purpose of conducting new breeding and genomic studies, as well as editing the cotton genome.

CONCLUSIONS

This study analyzed the spontaneous emergence of a haploid cotton plant resulting from the selective chromosome elimination in one of the parental genomes (*G. barbadense*), discovered through interspecific hybridization. In this important industrial crop, the significance of this phenomenon appeared similar to that of other crop plants, such as the possible production of doubled haploids (DH),

which have the advantage of high homozygosity, enabling accelerated breeding research.

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