IRSTI: 62.33.29; 68.03.00; 68.35.37; 34.23.19 https://doi.org/10.26577/bb106120264

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PHENOTYPIC, CYTOGENETIC AND MOLECULAR ANALYSIS OF INTERSPECIFIC RAPESEED HYBRIDS

Rapeseed (*Brassica napus L.*) is a key oilseed crop, the value of which is determined by both yield and oil quality. In this study, doubled haploid (DH) interspecific hybrid lines of rapeseed × turnip (*B. napus* × *B. rapa*) was evaluated using an integrated approach including phenotypic analysis, cytogenetics, and molecular markers. Phenotypic evaluation revealed significant diversity in key quantitative traits, such as seed weight per plant, pod number, and thousand-seed weight, with heterosis evident in some lines. Early flowering of the hybrids compared to the parental forms indicates the influence of genomic interactions on plant development. Cytogenetic analysis using FISH and GISH confirmed the presence of chromosomes from both parents, revealing segments of introgression and signs of genomic stability after chromosome doubling. Molecular studies using SSR markers revealed high polymorphism and the presence of alleles introgressed from *B. rapa*, consistent with cytogenetic data. Analysis of the seed fatty acid composition revealed increased oleic acid content and low erucic acid levels, which meets modern oil quality requirements. These results demonstrate the effectiveness of combining interspecific hybridization and DH technology for identifying favorable allelic combinations that enhance the breeding value of lines. These lines may serve as promising material for improving the yield and quality of rapeseed oil.

Keywords: canola, doubled haploid, SSR markers, *B. napus, B. rapa*, tolerance.

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Тұраралық рапс будандарының фенотиптік, цитогенетикалық және молекулалық талдауы

Рапс (*Brassica napus L.*) өнімділігі мен май сапасына байланысты құндылығы жоғары негізгі майлы дақылдардың бірі. Осы зерттеуде рапс × қышабас (*Brassica rapa)* (*B. napus* × *B. rapa*) түр аралық гибридтерінен алынған қос гаплоидты (DH) желілер кешенді тәсіл арқылы бағаланды, оған фенотиптік талдау, цитогенетика және молекулалық маркерлер кірді.

Фенотиптік бағалау бір өсімдікке шаққандағы тұқым массасы, бұршаққын саны және мың тұқымның массасы сияқты негізгі сандық белгілер бойынша айтарлықтай әртүрлілікті көрсетті, кейбір желілерде гетерозис құбылысы байқалды. Гибридтердің ата-аналық формалармен салыстырғанда ерте гүлдеуі өсімдіктің дамуына геномдық өзара әрекеттесулердің әсерін көрсетеді.

FISH және GISH әдістерін қолданған цитогенетикалық талдау екі ата-ананың да хромосомаларының бар екенін растады, хромосомалардың екі еселенуінен кейін интрогрессия сегменттері мен геном тұрақтылығының белгілерін анықтады. SSR-маркерлер көмегімен жүргізілген молекулалық зерттеу жоғары полиморфизмді және Brassica rapa-дан интрогрессияланған аллельдердің болуын көрсетті, бұл цитогенетикалық деректермен сәйкес келеді.

Тұқымның май қышқылдары құрамын талдау олеин қышқылы мөлшерінің артқанын және эрук қышқылы деңгейінің төмен екенін көрсетті, бұл май сапасына қойылатын заманауи талаптарға сай келеді. Алынған нәтижелер қолайлы аллельдік комбинацияларды бекіту үшін түр аралық гибридизация мен DH-технологияны үйлестірудің тиімділігін дәлелдейді, бұл желілердің селекциялық құндылығын арттырады. Бұл желілер рапстың өнімділігі мен май сапасын жақсартуға арналған перспективалы материал бола алады.

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Фенотипический, цитогенетический и молекулярный анализ межвидовых гибридов рапса

Рапс (*Brassica napus L.*) является одной из ключевых масличных культур, ценность которой определяется как урожайностью, так и качеством масла. В настоящем исследовании оценивались двойные гаплоидные (DH) межвидовые гибридные линии рапса × репы (*B. napus* × *B. rapa*) с использованием комплексного подхода, включающего фенотипический анализ, цитогенетику и молекулярные маркеры. Фенотипическая оценка показала значительное разнообразие в ключевых количественных признаках, таких как масса семян на растение, количество стручков и масса тысячи семян, с проявлением гетерозиса в ряде линий. Раннее цветение гибридов по сравнению с родительскими формами указывает на влияние геномных взаимодействий на развитие растений. Цитогенетический анализ с использованием FISH и GISH подтвердил присутствие хромосом обоих родителей, выявив сегменты интрогрессии и признаки стабильности генома после удвоения хромосом. Молекулярное изучение с помощью SSR-маркеров выявило высокую полиморфность и наличие аллелей, интрогрессированных от *B. rapa*, что согласуется с данными цитогенетики. Анализ состава жирных кислот семян показал увеличение содержания олеиновой кислоты и низкий уровень эруковой кислоты, что соответствует современным требованиям качества масла. Полученные результаты демонстрируют эффективность сочетания межвидовой гибридизации и DH-технологии для фиксации благоприятных аллельных комбинаций, повышающих селекционную ценность линий. Эти линии могут служить перспективным материалом для улучшения урожайности и качества масла рапса.

Ключевые слова: канола, удвоенный гаплоид, SSR маркеры, *B. napus, B. rapa*, устойчивость.

Introduction

Rapeseed (*Brassica napus L.*) is one of the most important oilseed crops worldwide, ranking second after soybean in global vegetable oil production (Kalaida, 2021). Its economic value is determined not only by seed yield but also by oil quality, fatty acid composition, and adaptability to diverse agroclimatic environments. Modern breeding programs aim to improve both agronomic performance and oil quality parameters while maintaining environmental stability and resistance to abiotic and biotic stresses (Raboanatahiry et al., 2021).

Interspecific hybridization has long been recognized as a powerful strategy for broadening the genetic base of cultivated crops. In the genus *Brassica*, interspecific crosses between *B. napus* (AACC, 2n=38) and *B. rapa* (AA, 2n=20) allow the transfer of desirable alleles controlling yield components, flowering time, stress tolerance, and seed quality traits. However, genomic instability, segregation distortion, and complex recombination patterns often complicate the stabilization of such hybrids (Swarup et al., 2021).

Doubled haploid (DH) technology provides an effective approach for rapid fixation of recombinant genotypes and generation of completely homozygous lines within a single generation. The use of DH lines significantly accelerates breeding cycles and facilitates precise genetic and phenotypic evaluation. In interspecific Brassica breeding, DH technology has been successfully applied to stabilize novel genomic combinations and capture heterotic effects resulting from intergenomic recombination (Daurova et al., 2020).

Yield formation in rapeseed is a complex quantitative process involving multiple morphological and reproductive components, including plant height, branching pattern, number of siliques, seeds per silique, and thousand seed weight (Zhang et al., 2023). These traits are typically controlled by numerous quantitative trait loci (QTLs) distributed across A and C genomes. Understanding the phenotypic variation and genetic architecture underlying these traits is essential for effective marker-assisted selection and genomic improvement (Fujimoto et al., 2018).

Flowering time represents another key adaptive trait influencing yield stability and regional suitability (Xu et al., 2016). It is regulated by a complex network of genes associated with photoperiod, vernalization, and temperature response pathways. In interspecific hybrids, altered flowering dynamics may arise due to epistatic interactions between divergent parental genomes. Therefore, evaluating flowering behavior in DH interspecific lines pro-

vides insights into genomic stabilization and adaptive potential (Kim et al., 2015; Dezfouli et al., 2019).

At the chromosomal level, interspecific hybridization may lead to homoeologous exchanges, introgression of chromosomal segments, and structural rearrangements. Cytogenetic tools such as fluorescence in situ hybridization (FISH) and genomic in situ hybridization (GISH) allow precise identification of genome composition and detection of introgressed chromosomal regions (Amosova & Shirokovae, 2016). Such analyses are critical for confirming genomic constitution and understanding the cytological basis of phenotypic variation (Ma et al., 2006).

Molecular markers, particularly simple sequence repeats (SSRs), remain valuable tools for assessing genetic diversity, phylogenetic relationships, and allelic variation associated with agronomic traits (Guo et al., 2025). SSR markers provide high reproducibility and genome coverage, enabling detection of polymorphism among closely related genotypes. Integration of molecular marker analysis with phenotypic and cytogenetic data enhances the resolution of genetic structure and breeding potential assessment (Wolko et al., 2022).

The present study aimed to comprehensively evaluate doubled haploid interspecific hybrid lines between B. napus and B. rapa using an integrated approach combining phenotypic assessment, cytogenetic analysis, and molecular marker profiling. Specifically, we sought to (i) characterize variation in key quantitative traits, (ii) assess phenotypic diversity through multivariate statistical analysis, (iii) determine chromosomal composition using FISH/GISH, and (iv) evaluate genetic diversity using SSR markers. The obtained results contribute to understanding the breeding value and genomic stability of interspecific DH lines and provide a foundation for their utilization in rapeseed improvement programs.

Materials and methods

Plant Material

The study utilized doubled haploid (DH) lines of interspecific hybrids between rapeseed (*Brassica napus*) and turnip rape (*Brassica rapa*), designated as DHKZ and DHGY. These lines were previously developed using haploid technology followed by chromosome doubling, as described in our earlier work (Daurova et al., 2020).

Parental genotypes were used as controls and included two *B. napus* cultivars, ‘Kris’ and ‘Galant’ (All-Russia Research Institute of Agricultural Biotechnology), and two *B. rapa* cultivars, ‘Zolotistaya’ and ‘Yantarnaya’ (V.S. Pustovoit All-Russian Research Institute of Oil Crops).

Methods

Phenotypic Evaluation and Statistical Analysis

At physiological maturity, ten representative plants were randomly selected from each plot. The following morphological traits were recorded: plant height (cm), number of branches per plant, number of siliques per plant, silique length (cm), number of seeds per silique, thousand seed weight (g), and seed weight of the main inflorescence (g).

Chromosome Preparation and FISH/GISH Analysis

Mitotically active meristematic cells from root tips were used for cytogenetic analysis. Germinated seedlings were fixed and washed in SSC buffer (pH 4.6–4.8) for 20 minutes prior to enzymatic digestion. Root tips were treated with a digestion mixture containing 20% pectinase (Sigma-Aldrich) and 1% cellulase for 1.5–2.5 h at 37°C.

Following enzymatic maceration, root tips were rinsed in 45% acetic acid and squashed on glass slides. Preparations were dehydrated in absolute ethanol and air-dried according to standard cytogenetic protocols (Hasterok et al., 2005).

Chromosomal analysis was performed on 5–10 well-spread metaphase plates per sample. Each chromosome preparation originated from independent root tips, ensuring that each analyzed metaphase corresponded to an individual plant. Fluorescence in situ hybridization (FISH) and genomic in situ hybridization (GISH) were applied to detect genomic constitution and chromosomal introgression patterns.

DNA Isolation

Genomic DNA was extracted from young leaf tissue using the QIAGEN DNeasy Blood & Tissue Kit (Cat. No. 69504) following the manufacturer’s protocol. DNA integrity was assessed by agarose gel electrophoresis. DNA concentration and purity were measured using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA). Samples were diluted to a working concentration of 35 ng/μL for downstream molecular analyses.

SSR Marker Analysis and PCR Amplification

DNA concentration was additionally verified spectrophotometrically using a NanoDrop ND-1000 (Thermo Scientific, USA). PCR amplification was carried out in a total reaction volume of 20 μL containing: 1.5 μL 10× PCR buffer (10 mM Tris-HCl, pH 7.4; 50 mM KCl; 1.5 mM $MgCl_2$), 1 U Taq DNA polymerase (New England BioLabs), 10 mM

of each dNTP (Sigma), 10 mM of each primer, and 100–200 ng template DNA.

Amplification was performed in a T100 thermal cycler (Bio-Rad, USA) under the following conditions: initial denaturation at 95°C for 10 min; 35 cycles of denaturation at 95°C for 30 s, annealing at locus-specific temperatures (Table 3), extension at 72°C for 45 s; and a final extension at 72°C for 10 min (Zhu et al., 2021).

PCR products were separated using 2.7% agarose gels and 0.8% polyacrylamide gels (PAGE). Gels were stained with ethidium bromide (EtBr) and visualized under UV illumination.

Statistical analysis

Analysis of variance (ANOVA) was performed to determine statistical significance among genotypes. Duncan's multiple range test (DMRT) applied for post-hoc comparison at $p \leq 0.05$. All statistical analyses were cross validated using IBM SPSS Statistics v.23.

Results and discussion

Phenotypic variation

In interspecific hybrids *B. napus* × *B. rapa* (turnip rape), both fertile and sterile plants were observed among the DH progeny and subsequent generations. This segregation is typical for such crosses and is associated with genetic instability, including cytoplasmic male sterility (CMS) and/or nuclear sterility factors introduced from the parental species.

Phenotypically, fertile hybrids exhibited normal flowering with fully developed bright yellow flowers, well-formed stamens and anthers containing viable pollen, as well as the formation of normal siliques with seeds (Figure 1 A1-A3). In contrast, sterile plants were characterized by reduced floral organs (smaller petals, shortened stamens, degenerated anthers lacking pollen), diminished inflorescences, and often empty or poorly filled siliques, resulting in a significantly lower total number of siliques per plant seeds (Figure 1 B1-B3).

Cytological analysis confirmed these differences at the meiotic level. In fertile plants, meiosis proceeded normally: pollen mother cells (PMCs) completed all stages of meiosis I and II, forming regular tetrads, followed by the dissolution of the callose wall and the development of round, uniformly stained viable microspores/pollen grains with distinct exine (Figure A4). In sterile hybrids, meiosis was severely disrupted. Instead of normal meiotic division, sterile PMCs formed so-called "microspore analogues" (Figure B4) directly from the mother cells without completing meiosis (Fengqun & Tingdon, 1990). Subsequently, the cytoplasm of these analogues underwent nearly complete degradation, leaving only empty shells or collapsed cell walls . Notably, no dyads or tetrads were observed in sterile plants across all examined bud sizes (Zhou, 2003).

These meiotic abnormalities indicate a type of male sterility associated with disruption of early meiotic stages (meiosis abnormality-type male sterility), frequently linked to cytoplasmic factors (e.g., Ogura CMS or similar systems transferred during interspecific hybridization *B. napus* × *B. rapa*) and/or nuclear male sterility genes (Liu et al., 2020). The presence of both fertile and sterile individuals in the hybrid population reflects segregation of fertility restorer genes (Rf genes) and provides opportunities for selection of stable fertile lines for further breeding, as well as utilization of sterile forms in hybrid seed production systems, provided effective fertility restoration is achieved (Gaborieau & Brown, 2016).

Figure 1

Morphological characteristics of hybrid plants and assessment of pollen fertility

A1-A3 – Plants are well developed, with normally formed inflorescences and flowers, indicating preserved reproductive capacity; A4 – Pollen grains (acetocarmine staining) are predominantly spherical and uniformly stained, demonstrating high pollen viability; B1-B3 – Morphology of plants and flowers of the second line, showing normal floral structure and development; B4 – Pollen grains are largely deformed, irregular in shape, and weakly or unevenly stained, indicating pollen sterility. Scale bars: 40 μm.

Structural analysis and Fatty acid composition

Interspecific hybrid lines previously obtained using doubled haploid (DH) technology (Daurova et al., 2020) were selected and evaluated for key quantitative traits (Figure A-E). Structural and phenotypic analyses of the doubled haploid interspecific hybrids of *B. napus* × *B. rapa* (DHih) are presented in Figure 2.

The interspecific hybrid lines demonstrated superior performance in several yield-related traits compared with the parental controls. In particular, significant increases were observed in seed weight per plant and thousand seed weight (TSW). The highest TSW values were recorded in the hybrid combinations DHGY, where all analyzed DH lines exceeded the parental forms. Additionally, several lines derived from the DHKZ combination showed increased number of siliques per plant and higher seed weight per plant relative to the respective parents.

These results suggest the presence of heterotic effects in the interspecific hybrid lines. Heterosis for yield components such as silique number and seed weight has been widely reported in *Brassica* species, particularly in interspecific and inter-subspecific crosses (Pradhan et al., 1993; Snowdon&Iniguez, 2012). Increased thousand seed weight in DH-derived lines may reflect favorable allelic recombination and fixation of advantageous loci during doubled haploid production, as previously described for oilseed rape breeding programs (Friedt & Snowdon,2009).

The hybrid lines also exhibited variation in flowering time after planting. Flowering in hybrids ranged from 35 to 39 days, whereas the parental genotypes flowered later: *Brassica napus* cultivars Kris and Galant at 40 and 41 days, respectively, and *B. rapa* cultivars Zolotistaya and Yantarnaya at 37 and 39 days. Most hybrid lines initiated flowering around day 36 of the vegetative period. Earlier flowering in hybrids may indicate genomic interactions affecting developmental pathways, possibly involving vernalization and photoperiod-responsive loci. Similar shifts in flowering time have been observed in interspecific *Brassica* hybrids and are often associated with introgression of regulatory genes controlling floral transition (Xu et al., 2016; Xu et al., 2023).

Cytological analysis (described below) revealed the presence of C-genome chromosomes derived from *B. napus* in the hybrid lines, suggesting partial genome stabilization following interspecific hybridization. Chromosomal introgression between A and C genomes is a well-documented phenomenon in *Brassica* hybrids and may contribute to both phenotypic variation and heterosis (Xiong & Pires, 2011; Mason & Batley, 2015). The retention of C-genome chromosomal segments in DH lines indicates successful genomic recombination and stabilization during haploid induction and chromosome doubling.

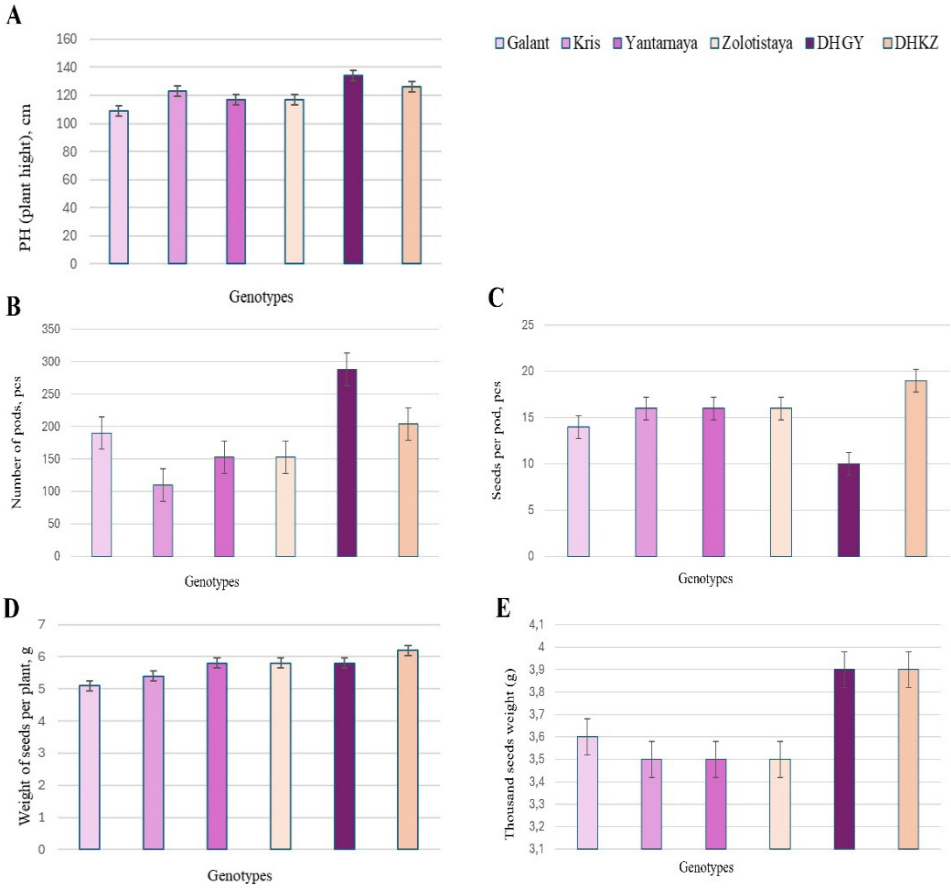
Overall, the interspecific DH lines combined early flowering with improved yield components, particularly thousand seed weight and seed mass per plant. The observed phenotypic superiority likely reflects both heterotic effects and genomic introgression, supporting the effectiveness of doubled haploid technology for fixation of favorable allele combinations in *Brassica* breeding programs.

One of the key indicators of breeding value in rapeseed is the fatty acid composition of seed oil. For food-grade rapeseed, the most important quality criterion is the absence or extremely low content of erucic acid (C22:1), which determines its suitability for human consumption and compliance with international canola standards.

Figure 3 presents the results of fatty acid composition analysis of all fertile mutant doubled haploid interspecific lines of *B. napus* × *B. rapa* (DHih). Gas chromatographic analysis revealed a significant increase in oleic acid (C18:1) content in several hybrid lines compared with parental genotypes. In the DHGY combination, oleic acid concentration increased by 6.7%, rising from 71.6% in the parental form to 74.5% in the hybrid lines. Similarly, lines derived from DHKZ exhibited an increase of 5.6%, from 71.4% to 73.5%.

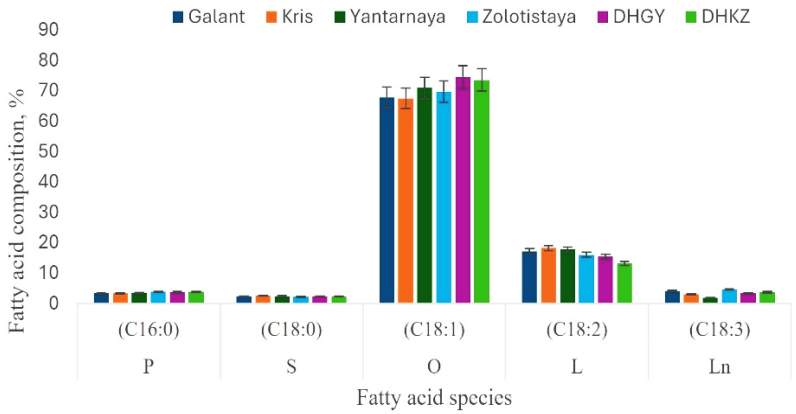
In addition to elevated oleic acid levels, most interspecific hybrid lines demonstrated a favorable fatty acid profile characterized by low concentrations of saturated fatty acids (palmitic acid, C16:0, and stearic acid, C18:0) and a high proportion of unsaturated fatty acids, including oleic, linoleic (C18:2), and linolenic acids (C18:3). Such a composition corresponds to modern nutritional requirements and improves oxidative stability of the oil.

Figure 2
Structural and phenotypic analyses of the doubled haploid interspecific hybrids and parental cultivars



A – Comparison of plant height; B – number of pods per plant; C – seeds per pod; D – seed weight per plant; E – thousand-seed weight. Values are means ± SE. $p < 0.01$

Figure 3
Seed oil fatty acid profiles (%) in parental rapeseed cultivars and interspecific DH hybrid lines with turnip rape



Fatty acids: C16:0 (palmitic, P), C18:0 (stearic, S), C18:1 (oleic, O), C18:2 (linoleic, L), C18:3 (linolenic, Ln). Genotypes: Galant, Kris, Yantarnaya, Zolotistaya — B. napus and B.rapa parents; DHGY, DHKZ — DH hybrids

Recent genomic and metabolic studies have confirmed that oleic acid content in *B. napus* is primarily controlled by allelic variation in the FAD2 gene family, which regulates the conversion of oleic acid to linoleic acid (Shaheen et al., 2023). Mutations or downregulation of FAD2 increase oleic acid accumulation, which has become a major target in rapeseed quality breeding programs. Furthermore, integrated genomic analyses have demonstrated that oil quality traits, including fatty acid composition, are influenced by multiple QTLs distributed across A and C genomes (Yusuf et al., 2022).

The absence of elevated erucic acid levels in the analyzed lines confirms the maintenance of canola-quality standards. Modern breeding strategies emphasize the development of low-erucic, high-oleic cultivars with improved oxidative stability and nutritional value (Zhao et al., 2022). The observed increase in oleic acid content in the DH lines therefore represents not only a quantitative improvement but also a significant enhancement of oil quality.

Overall, the fatty acid composition analysis indicates that the mutant doubled haploid interspecific lines combine agronomically valuable traits with improved oil quality parameters. The increase in oleic acid content, together with reduced saturated fatty acid levels, suggests successful fixation of favorable allelic combinations and highlights the potential of interspecific hybridization combined with DH technology for the development of high-quality rapeseed cultivars.

Chromosomal and Molecular marker analysis

The number of somatic chromosomes in the examined lines was determined using conventional cytological analysis (Figure 4A), while the genomic origin of chromosomes and segments was assessed by combined FISH&GISH (Figure 4B, C).

In metaphase spreads of the hybrids, the parental genomes were clearly distinguishable (Figure 4B). The maternal *B. napus* genome (AACC, 2n = 38) produced intense red, fluorescent signals, predominantly in centromeric and pericentromeric regions, with weaker extension into telomeric areas on some chromosomes. This pattern is characteristic of allotetraploid *B. napus*, where both A (*B. rapa*) and C (*B. oleracea*) subgenomes contribute to signal intensity when using total genomic DNA as a probe with appropriate blocking. In contrast, the paternal *B. rapa* genome (AA, 2n = 20) was labeled with distinct green signals covering entire chromosomes or large segments. On average, 10-15 green-labeled chromosomes or chromosome segments were observed per cell, consistent with an approximate AAC genomic composition (2n ≈ 29), typical of F□ triploid hybrids between *B. napus* and *B. rapa*.

Considerable inter-cellular variability was noted: some metaphases displayed only 7-9 green chromosomes (approaching the full A-genome contribution from *B. rapa*), while others showed fragmented or recombined signals (mixed red-green regions), indicative of homoeologous recombination between the A subgenomes of the two parents. In approximately 20% of metaphases analyzed, weak green signals appeared on predominantly red-labeled chromosomes, likely resulting from translocation events or incomplete blocking during hybridization.

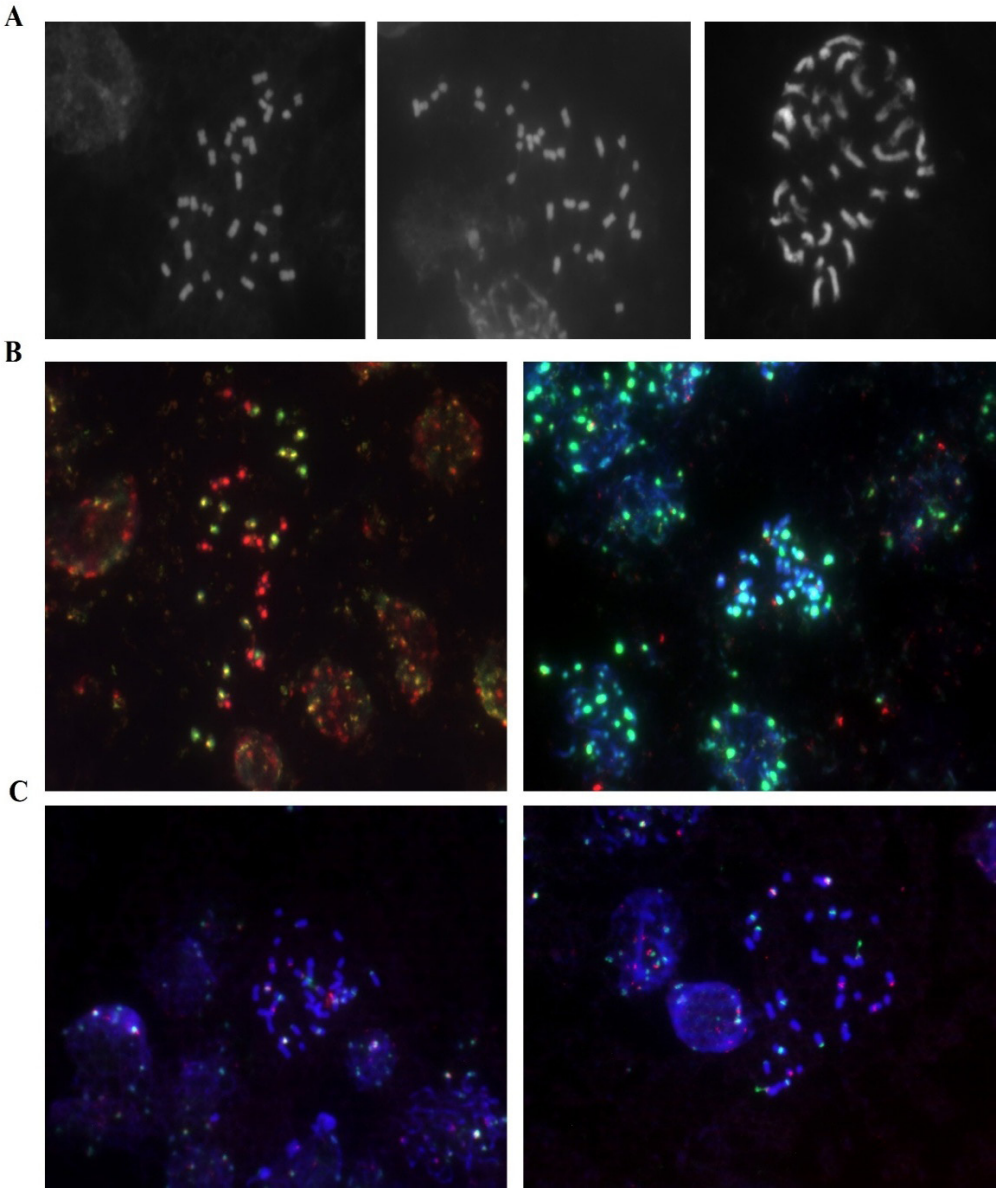
GISH preparations confirmed the presence of genomic material from both parental species in the analyzed plants (Figure 4C). Red and green hybridization signals were detected within the same cells, indicating the coexistence of both genomes and reflecting the genomic interactions typical of early-generation interspecific *Brassica* hybrids. Overall, the GISH results confirmed the hybrid origin of the plants and successful introgression of *B. rapa* genomic material into the *B. napus* background.

To further characterize chromosomal architecture and detect potential polymorphisms in ribosomal DNA (rDNA) loci, fluorescence in situ hybridization (FISH) was performed using specific probes for 25S rDNA and 5S rDNA (green); chromosomal context was provided by DAPI counterstaining (Figure 4C).

The 5S rDNA signals (green) were more numerous and dispersed, averaging 10.4 ± 1.6 sites per cell (range 9–14), often clustered in pericentromeric regions. This distribution reflects the additive contribution of the A subgenome from both parents and aligns with the known high multiplicity of 5S loci in the *Brassica* A genome. Co-localization of 5S and 25S signals (yellow overlays) was observed on certain chromosomes, a feature commonly reported for A-genome chromosomes (e.g., A1 and A3) in *Brassica*.

The 25S rDNA signals (red), were fewer, averaging 5.3 ± 1.1 per cell (range 5–9), and predominantly telomeric or sub-telomeric. Compared to stable *B. napus* lines (typically 6–8 sites), this number is reduced, likely due to partial elimination of the C-genome chromosomes and/or nucleolar dominance. Polymorphism was evident: in approximately 30% of cells, the intensity of one or more 25S sites was markedly reduced or absent.

Figure 4
Cytogenetic characterization of rapeseed parental lines and interspecific DH



A – Conventional chromosome spreads showing somatic chromosome number.
B, C – Combined FISH/GISH revealing genomic origins and chromosome segments (DAPI counterstain in blue; hybridization signals in red, green, and other colors)

A comparison of rDNA locus numbers in the parental species, stable *B. napus* lines, and the investigated DH hybrids is presented in Table 1. Table 1 demonstrates that the hybrids exhibit higher mean numbers of 5S rDNA loci compared to the parental forms, whereas variation in 25S rDNA loci suggests genomic restructuring following hybridization. Notably, the DHKZ genotype showed the highest average values for both 5S and 25S loci, supporting evidence of post-hybridization chromosomal reorganization.

Table 1
Comparison of rDNA locus numbers in parental species and hybrids (based on present data and literature)

Genotype	5S rDNA (mean)	25S rDNA (mean)
Galant (*B. napus*)	8 ± 1.0	4.3 ± 1.2
Kris (*B. napus*)	9.4 ± 1.3	5.0 ± 1.1
Zolotistaya (*B. rapa*)	8.4 ± 1.4	4.3 ± 1.1
Yantarnaya (*B. rapa*)	9.4 ± 1.6	5.5 ± 1.3
DHGY	10.4 ± 1.6	5.3 ± 1.1
DHKZ	11.4 ± 1.3	6.3 ± 1.3

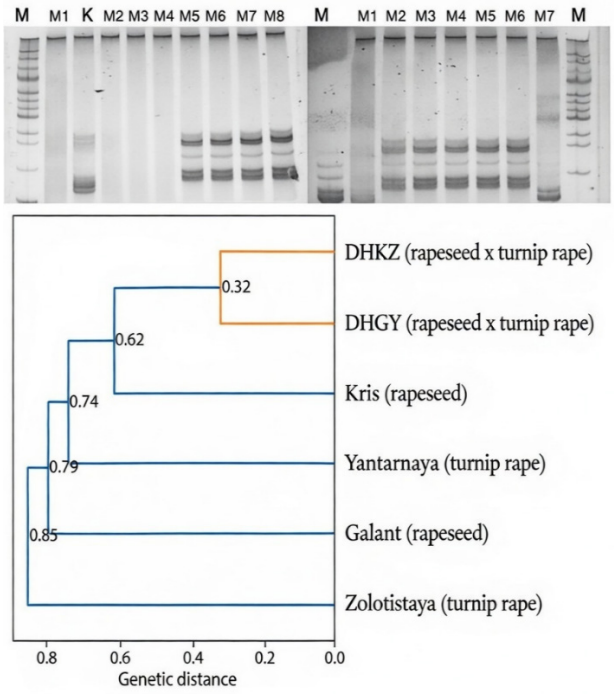
Intergenomic variation was apparent, with stronger green signals (5S) likely originating from the paternal *B. rapa* A genome, and red signals (25S) distributed across both A and C genomes. Some cells showed asymmetric distribution, with extra 5S sites on presumed C-genome chromosomes, hinting at translocation events. Overall, FISH confirmed the presence of rDNA loci from both parents and revealed intraspecific polymorphism, which could influence hybrid fertility and stability.

Molecular marker analysis

A total of 55 SSR markers (primarily from BrGMS, BnGMS, and BnEMS series) were used to assess genetic diversity, polymorphism, and potential functional variation across six *Brassica* genotypes: two rapeseed (*B. napus*) cultivars (Galant and Kris), two turnip rape (*B. rapa*) cultivars (Zolotistaya and Yantarnaya), and two interspecific doubled-haploid hybrid lines (DHGY and DHKZ) derived from rapeseed × turnip rape crosses.

All markers were scored as binary (presence/absence) data due to the dominant-like amplification patterns observed on agarose gels. The marker panel exhibited high discriminatory power, detecting substantial genetic variability among the genotypes. Polymorphism information content (PIC) values ranged from 0.00 to 0.50, with several loci achieving the theoretical maximum of 0.50 for dominant markers (indicating near-equal allele frequencies and optimal informativeness). Only a small proportion of loci remained monomorphic, confirming the overall effectiveness and broad coverage of the selected SSR set.

Figure 5
Molecular analysis of parental cultivars and DH hybrids



A – Representative SSR amplification profiles of rapeseed, turnip rape, and hybrid lines. M – DNA ladder; B – UPGMA dendrogram based on genetic distance coefficients showing relationships among genotypes

A notable fraction of the markers has been previously associated with key agronomic traits in *Brassica* species, particularly those influencing yield and its components. These associations enhance the biological relevance of the detected polymorphisms for breeding applications. The following table summarizes the reported trait associations for the polymorphic loci identified in this study (Table 2):

Table 2
SSR markers and their reported associations with agronomic traits in Brassica

Marker	Associated traits
BrGMS3837	Plant height
BnEMS1119	Yield
BrGMS1490	Heterosis effects; yield-related traits
BrGMS0086	Number of branches; seeds per silique
BoGMS1897	Heterosis for plant height; heterosis for seeds per silique
BrGMS4057	Heterosis for seeds per silique
BnGMS0662	Plant height
BrGMS2252	Heterosis for silique length; heterosis for seeds per silique
BrGMS4252	Heterosis for seeds per silique
BrGMS3688	Heterosis for seeds per silique
BoGMS1740	Thousand seed weight
BrGMS2901	Plant height; heterosis for seeds per silique
BoGMS0454	Plant height; seeds per silique
BnGMS0749	Heterosis for seeds per silique
BnGMS0386	Plant height
BnGMS0509	Thousand seed weight

Polymorphism at these loci (especially those linked to plant height, such as BrGMS3837, BnGMS0662, BnGMS0386, BrGMS2901, BoGMS0454, and BoGMS1897) suggests the presence of allelic variation that may contribute to differences in plant architecture, lodging resistance, and biomass accumulation among rapeseed, turnip rape, and hybrid genotypes. Similarly, markers associated with yield components – including overall yield (BnEMS1119), heterosis for seeds per silique (BrGMS4057, BrGMS4252, BrGMS3688, BnGMS0749, BrGMS2901, BrGMS2252), seeds per silique (BrGMS0086, BoGMS0454), and thousand seed weight (BoGMS1740, BnGMS0509) – indicate functional genomic differentiation with potential economic importance. Numerous studies have shown that SSR loci in *Brassica* frequently co-localize with QTLs for yield-related traits, plant height, and seed quality (Hasan et al., 2008; Raboanatahiry et al., 2022). Thus, the polymorphic markers detected here can serve as indirect indicators of valuable allelic variation for introgressive and marker-assisted breeding programs.

Genetic relationships were analyzed using Jaccard's similarity coefficient converted to genetic distance, followed by cluster analysis with the Neighbor-Joining algorithm. Pairwise genetic distances ranged from 0.32 to 0.85, indicating moderate to high divergence among the accessions.

The dendrogram (Figure 5) revealed the following structure: The two interspecific hybrids, DHKZ and DHGY, showed the smallest genetic distance (0.32), reflecting their close similarity and likely shared breeding background or parental contributions; At a distance of approximately 0.62, the hybrid cluster grouped with the rapeseed cultivar Kris, indicating stronger genomic affinity of the hybrids to *B. napus* than to *B. rapa*. The two turnip rape cultivars (Yantarnaya and Zolotistaya) formed a separate cluster at distances of 0.74–0.79 from the rapeseed/hybrid group. The rapeseed cultivar Galant was the most divergent, joining the overall cluster at the highest distance (≈0.85).

This topology aligns with the expected genomic relationships: allotetraploid *B. napus* (AACC genome) exhibits partial convergence with introgressed *B. rapa* (AA) material in hybrids, but maintains clear species-level separation from diploid turnip rape (Chalhoub et al., 2014; Mason & Snowdon, 2016). The rapeseed-biased intermediate position of the doubled-haploid hybrids is consistent with stabilization of the AACC constitution during DH production and with patterns reported in other SSR- and SNP-based diversity studies of interspecific *Brassica* hybrids (Xu et al., 2018).

To confirm hybrid origin and quantify introgression from *B. rapa* into the *B. napus* background, allele inheritance patterns were examined. The hybrids displayed a near-additive allelic profile, possessing 50-51 alleles across the marker set – markedly more than the rapeseed cultivars (~26 alleles) or turnip rape cultivars (17-18 alleles). This pattern is characteristic of successful interspecific hybridization and retention of parental diversity (Raboanatahiry et al., 2022).

Particularly informative were 12-13 loci where the allele was absent in both rapeseed parental cultivars (scored as 0/0) but present in the hybrids (scored as 1). These markers most likely tag chro-

mosomal segments introgressed from turnip rape. This molecular evidence corroborates cytogenetic results from genomic in situ hybridization (GISH; showing green-labeled alien segments) and fluorescence in situ hybridization (FISH; revealing additive/polymorphic rDNA loci), providing strong support for stable integration of *B. rapa* genomic material into the rapeseed genome. Comparable introgression patterns have been documented in *Brassica* introgression lines and are recognized as promising sources of novel variation for yield, stress tolerance, and other traits (Hasan et al., 2008; Li et al., 2023).

In summary, the SSR marker panel demonstrated high discriminatory capacity, effectively quantified genetic diversity, resolved clear phylogenetic relationships consistent with genomic constitutions, and highlighted functional polymorphisms at loci relevant to key breeding traits. These findings underscore the utility of the marker system for diversity assessment, hybrid verification, and marker-assisted selection in introgressive *Brassica* breeding.

Conclusion

Thus, the analyses presented demonstrated that the doubled haploid interspecific lines exhibit improved yield performance, earlier flowering time, and high seed quality parameters compared with the parental forms. These agronomically valuable traits were consistently expressed across the evaluated generations, indicating good phenotypic stability and adaptability.

Cytogenetic and molecular analyses confirmed the successful integration of the parental genomes. The additive distribution and uniform signal pattern of 25S and 5S rDNA loci in the doubled haploid lines indicate complete homozygosity and chromosomal stability of the hybrids. The consistent rDNA profiles further support that the homozygous hybrids possess fixed genomic configurations without detectable structural irregularities.

Taken together, the combined agronomic, cytogenetic, and molecular data emphasize the high breeding potential of these doubled haploid lines. They represent promising genetic resources for the development of new rapeseed varieties with enhanced productivity, early maturity, and improved seed quality traits.

Funding

This research was funded by the Committee of Science of the Ministry of Science and Higher Education of the Republic of Kazakhstan (grant no. AP26102771).

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Received August 12, 2025
Accepted February 20, 2026