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ABSTRACT

of the dissertation for the degree of Doctor of Philosophy

MOLECULAR CYTOGENETIC STUDY OF GENETIC VARIATIONS IN WHEAT-*AEGILOPS* HYBRIDS

Speciality: 2409.01 – Genetics

Field of science: Biology

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INTRODUCTION

Relevance and degree of the completion of the topic: Recently, the development of intraspecific hybridization methods in the breeding of common wheat (*Triticum aestivum* L.) has not only significantly increased its yield, but also led to the emergence of the problem of tolerance the crop from diseases and pests, as well as other unfavorable environmental conditions. As the wheat gene pool becomes depleted of benefical genes for traits such as disease and pest resistance, cold and drought, the level of the challenges related to solving the problem also increases. However, this problem can be overcome by using the rich gene pools of wild ancestors and relatives of wheat, and the traditional way to do this is via interspecific and intergeneric, that is, wide hybridization. Distant hybridizations provide the transfer of a number of beneficial traits, including resistance to diseases, pests, cold, drought, and salinity, as well as genes controlling high protein content of grains, from the genera *Aegilops* L. (goatgrass), *Secale* L. (rye), *Hordeum* L. (barley), *Elytrigia* Desv. (einkorn), etc., which are considered to be the wild ancestors and close relatives of wheat, to common wheat.

Cultivated wheat grows together with the *Aegilops* L. genus, *Agropyron* Gaertn., *Secale* L., *Dasypyrum* (Coss.&Durieu) T. Durand (=*Haynaldia* Schur), *Hordeum* L. and *Elymus* L. and is capable of hybridizing with these species.

Aegilops L. is the genus most closely related to wheat. The D genome originated from the diploid species of *Aegilops tauschii* Coss. (= *Ae. squarrosa* L.) and the B genome was derived from a closely related species to *Ae. speltoides* Tausch. In addition, due to the they are wild, the species of this genus are resistant to adverse environmental conditions, biotic and abiotic stresses, and have high content of protein in the grain.

There are several methods for transferring chromosomes carry important genes. *Interspecific hybridization* play an important role in the introgression of agronomically useful genes from wild relatives to cultivated cereal crops. The relatives of wheat have great genetic diversity in most traits. Many desirable traits can be possessed to wheat by crossing it with species belonging to the tribe Triticeae. Homoelogy between wheat and its related species allows alien chromosome segments to compensate for the absend wheat chromosome segments, as well as leading to the introduction of new advantageous genes.

Purpose and Tasks of the Research. The main objective of the was to study the *chromosome* pairing behavior during meiosis that belonging to alien genomes in intergeneric F_1 hybrids obtained from the crossing of wheat with different *Aegilops* species. And for detecting introgressions with alien chromosomes or chromosome segments, hybrids were studied via molecular cytogenetic *techniques*.

To achieve this goal, the following tasks have been set:

- Crossing wheat with different *Aegilops* species, studying their combining ability, and obtaining wheat-*Aegilops* hybrids;
- In order to ensure the fertility of the obtained F_1 hybrids, they backcrossed with wheat again;
- Study of chromosome pairing behavior during meiosis in interspecific F_1 hybrid populations;
- Investigation of the influence of the conjugation between wheat chromosomes and alien chromosomes of *Aegilops* on the fertility of F_1 plants;
- Starting from the second generation, the study of formation in wheat-aegilops hybrid populations, the selection of intermediate forms and the continuation of selection work on them in subsequent generations (F_2-F_7) ;
- The karyotype analysis of agronomically useful hybrid forms with molecular cytogenetic methods (FISH and GISH) in order to identify alien chromosomes or chromosome segments that cause genetic changes;
- Characterization of hybrid forms in which genomic and chromosomal changes have been detected according to economically important traits (yield parameters, high protein content, etc.).

Main points presented to the defense of the dissertation:

- It has been determined that the success of hybridization between common wheat and species of the genus *Aegilops* L. depends on whether the parental forms involved in the cross have a common or identical genome, their ploidy levels and the conjugation between their chromosomes, as well as the direction of hybridization.

- There is a homology between the chromosomes of the common wheat genome and the chromosomes of the U genome of species included in the *Aegilops* section.
- The M genome of *Aegilops* is closer to the N genome, the U genome to the M genome, the S^k genome to the common wheat genome than to the S^v genome, and the *Ae. crassa* (*Vertebrata*) species is closer to the durum wheat genome than to *Ae. neglecta* (*Aegilops*).
- Hybrid populations of *Ae. juvenalis*, a species included in the *Vertebrata* section, and *Ae. neglecta*, a species included in the *Aegilops* section, with common wheats are characterized by a large range of morphogenesis compared to other hybrids.
- Hybrids from the combination of 171ACS × *Ae. umbellulata*, which were studied by molecular cytogenetic methods, had a 1U(1D) substitution, and 7 hybrids had tetrasomic for 5B.
- Hybrid forms 466/1 (171ACS × *Ae. triuncialis*), 450 (*Ae. juvenalis* × 171ACS) and 480 (171ACS × *Ae. neglecta*), as well as lines with 1U(1A) and 5U(5D) substitutions, had statistically significant higher yield than other hybrids.

The scientific novelty of the research. For the first time, hybridization was carried out between bread wheat lines that developed through complex hybridization at the Molecular Cytogenetics Department of the Institute of Genetic Resources and different *Aegilops* species, and their combining ability was studied. For the first time, stable hybrid forms were obtained between these bread wheat lines and *Ae. triuncialis*, *Ae. biuncialis*, *Ae. neglecta*, and *Ae. kotschyi*, and they were analyzed cytogenetically and agronomically. For the first time, F_4 generation hybrid forms, produced by crossing hexaploid common wheat line 171ACS with diploid *Ae. umbellulata* variety, were studied by molecular cytogenetic techniques, and chromosome substitutions and additions in them were identified by GISH and FISH methods.

The scientific and practical significance of the work. The produced and stable hybrid plants can be used as starting material for future wheat breeding programs. Intergeneric hybrids are also very important in terms of enriching biodiversity.

Approbation and application of the work. The main results of the dissertation were presented and discussed at the Russian scientific and practical conference on the topic “Development of N.I. Vavilov's scientific heritage on genetic resources by his successors” dedicated to the 80th anniversary of U.K. Kurkiev (2017), The III International Scientific Conference on “Ecology: Problems of Nature and Society” dedicated to the 110th anniversary of the birth of Hasan Aliyev (2017), the VII Republican Scientific Conference on “Actual Problems of Ecology and Soil Sciences in the 21st Century” dedicated to the 95th anniversary of the birth of Great Leader Heydar Aliyev (2018), the VIII International Scientific Conference of Young Scientists and Researchers on “Innovative Approaches in Modern Biology” dedicated to the 95th anniversary of the birth of Great Leader Heydar Aliyev (2018), the IV International Scientific and Practical Conference held at the Institute of Plant Varieties Expertise on “World Plant Resources: Current Status and Development Prospects” dedicated to the 95th anniversary of variety testing in Ukraine (2018), the Conference of Young Scientists and Students on “Innovations in Biology and Agriculture for Solving Global Challenges” dedicated to the 90th anniversary of Academician Jalal Aliyev (2018), the 1st International scientific and engeenering papers at the Baku Engineering Conference (2018), the VIII International Scientific Conference on "Breeding and Genetics Science and Education" (2019), the conference on "Plant Genetics, Genomics, Bioinformatics and Biotechnology" held in Novosibirsk, Russia (2019), the V International Eurasian Congress of Scientific Research and Recent Trends held at Khazar University (2019), the international scientific conference "Current Problems of Plant Physiology and Genetics" dedicated to the 75th anniversary of the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine (2021), the 6th International Symposium on "Biodiversity in Eurasia" held at the Institute of Dendrology (2023), as well as in the annual reports of the Institute of Genetic Resources of the Ministry of Science and Education (2019, 2020, 2021), as well as at scientific seminars held at the institute.

21 scientific works covering the main provisions of the dissertation have been published, of which 9 are articles (4 were published in periodical scientific publications included in the international summarizing and indexing database).

The organization where the work was carried out. The dissertation work was carried out at the "Molecular cytogenetic" department of the Institute of Genetic Resources of the Ministry of Science and Education of the Republic of Azerbaijan, in 2017-2023.

The total volume of the dissertation in characters with separate volumes of each structural section. The dissertation was written in the Azerbaijani language and consists of 224 pages, introduction, 5 chapters, conclusion, results recommendations, abbreviations and bibliography. In the research, 354 literature data were cited, of which 344 were foreign publications. The total volume of the dissertation is 198.360 characters (chapter I-76.836, chapter II-26.189, chapter III-24.135, chapter IV-21.910, chapter V-25.083 characters). The dissertation is enriched with 12 tables and 86 figures.

MAIN CONTENT OF THE DISSERTATION CHAPTER I. LITERATURE REVIEW

This chapter of the dissertation provides a brief chronological overview of scientific research and literature data related to the use of wild relatives of wheat for the purpose of improving it, the systematics of *Aegilops* and the desirable characteristics of species included in this genus, and the role of molecular cytogenetic methods in chromosome identification.

CHAPTER II. MATERIALS AND METHODS

As research material, F_1-F_7 populations of intergeneric hybrids obtained from crosses of various species, cultivars, lines, and amphidiploids of the genus wheat (*Triticum* L.) with species of the genus *Aegilops* L. belonging to the sections *Sitopsis*, *Cylindropyrum*, *Vertebrata*, *Comopyrum*, and *Aegilops* were used.

During the research, hybridological, electrophoretic, classical and molecular cytogenetic (FISH and GISH), as well as mathematical and statistical methods were used.

Hybridological method. A generally accepted methodology was used to obtain hybrid plants[1,2]. The results were processed using mathematical and statistical methods.

Classical cytogenetic method. Cytogenetic study of hybrids was carried out on the basis of standard methods of meiotic and mitotic chromosomes[3,4] and some of their modifications. After staining both roots and anthers with acetocarmine, temporary slides were prepared from them in a 45% acetic acid solution and examined under Leitz Orthoplan (Germany) and Motic (China) microscopes.

Molecular cytogenetic methods FISH was performed as described by Linc et al[5]. This method was used to analyze the chromosome composition of the obtained intergenic hybrid lines. GISH was performed according to the method of Rider et al[6]. The method was used to analyze the genome composition of the hybrid lines. Chromosomes were examined on a Zeiss Axioskop-2 epifluorescence microscope using filter sets No. 10 for FITC, No. 15 for rhodamine, and No. 01 for DAPI. Images were captured using a Spot CCD camera (Diagnostic Instruments, Sterling Heights, MI, USA) and processed with Image-Pro Plus 4.0 Software (Media Cybernetics, Silver Spring, MA, USA).

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[1] Горин, А.П. Практикум по селекции и семеноводству полевых культур / А.П. Горин, М.С.Дунин, Ю.Б. Коновалов [и др.] // - Москва: Колос, -1968, 439 с.

[2] Тихомирова, М.М. Генетический анализ // Учеб. пособие. Л.: Изд-во ЛГУ, 1990, 280 с.

[3] Паушева, З.П. Практикум по цитологии растений // М.: Агропромиздат, 1988, 271 с.

[4] Пухальский, В.А., Юрцев, В.Н., Соловьев, А.А. // Цитология и цитогенетика. Руководство к лабораторно-практическим занятиям. Учебное пособие, М.: МСХА, 2004, 118 с.

[5] Linc G., Friebe B.R., Kynast R.G., Molnár-Láng M. et al. Molecular cytogenetic analysis of *Aegilops cylindrica* Host. Genome, 1999, v. 42, p. 497–503.

[6] Reader S.M., Abbo S., Purdie K.A., King I.P., Direct labelling of plant chromosomes by rapid *in situ* hybridization. Trends Genetics, 1994, v. 10. p. 265–266.

Electrophoretic method. EF analysis of storage proteins (gliadin) in the grains of hybrid plants was performed on A-PAGE[7].

CHAPTER III. CYTOGENETIC STUDY OF F_1 HYBRIDS BETWEEN WHEAT (*TRITICUM* L.) AND *AEGILOPS* L. AND MORPHOTYPE FORMING IN THEIR LATER GENERATIONS

3.1. Cytogenetic study of intergeneric F_1 hybrids between wheat (*Triticum* L.) and *Aegilops* L.

In the research work, species belonging to the sections *Sitopsis*, *Cylindropyrum* (Jaub. et Spach) Zhuk., *Vertebrata* Zhuk., *Comopyrum* (Jaub. et Spach) Zhuk. and *Aegilops* L. of the genus *Aegilops* L. were hybridized with wheat..

The main purpose of our research was to conduct interspecific hybridizations to transfer useful genes controlling important agronomic traits of the genus *Aegilops* L. to wheat, especially bread wheat lines, and to study the ability of alien chromosomes to conjugate during meiosis in the obtained hybrids.

F_1 plants were uniform in morphology and intermediate in spike shape and plant height. In general, the development of genetic material with different genome allows us to reveal the formation characteristics of cereal genomes and chromosome reconstructions, and is also of great importance in terms of enriching the genetic diversity of agricultural plants, increasing their adaptive potential and sustainability.

As a result of determining the success rate of seed setting in hybrid combinations between bread wheat lines and *Aegilops* L. species and cytogenetic analysis of F_1 hybrids belonging to these combinations, it was determined that even if both parental forms have common subgenomes during interspecific hybridizations, neither the seed setting percentage nor the chromosome conjugation will be high. Additionally, statistically significant correlation was not found between the chromosome pairing and fertility in the

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[7] Попереля, Ф.А., Асыка, Ю.А., Ключко, П.Ф., Определение гибридности семян кукурузы по электрофоретическим спектрам зеина. Доклады ВАСХНИЛ, 1989, № 3, с. 2-4.

studied intergeneric F_1 hybrids.

Since interspecific hybridizations between *Triticum* L. and *Aegilops* L., which is considered the secondary gene pool of wheat, are incongruent crosses, it was expected that the range of conjugation between their chromosomes is low. The differences between the ploidy levels of the parental forms cause the meiotic irregularities, and therefore, the fertilization of unbalanced gametes often results in the weak and sterile, or semi-sterile hybrids.

As presented in Table 1, in hybrid combinations between common wheat lines and *Aegilops* species, seed setting varied between these two upper and lower limits, at best 67.24% (*Ae. vavilovii* (Uzbekistan) k-1389 × 623AO) and at worst 1.25% (171ACS × *Ae. peregrina*). The obtained hybrid seeds were generally small and weak.

In F_1 hybrids of D genome bearing species with common wheats (*T. aestivum*), the pairing between alien chromosomes was slightly higher due to the common D-genome of the parental species in the cross, and the number of bivalents per PMC (pollen mother cells) was on average 5-6, most of which were rod bivalents.

Results of the analysis demonstrated that although the *Ae. kotschyii*, *Ae. columnaris*, *Ae. neglecta* and *Ae. recta* species belonging to the *Aegilops* section do not share a common subgenome with common wheat lines, the F_1 hybrids between them had a slightly higher levels of chiasm frequency, which is an indicator of the conjugation, and amounted to 7 for each PMCs. However, while the F_1 hybrids of the combinations 171ACS × *Ae. kotschyii* and 171ACS × *Ae. neglecta* were semi-fertile, the F_1 hybrids of the combinations 171ACS × *Ae. columnaris* and 171ACS × *Ae. recta* were completely sterile. Again, it is paradoxical that the F_1 hybrids of the last two combinations, despite the fact that the number of chiasmata per PMCs during meiosis was 7, were completely sterile, while the F_1 hybrids of the combinations 171ACS × *Ae. umbellulata*, 171ACS × *Ae. geniculata*, 172ACS × *Ae. triuncialis* and 171ACS × *Ae. biuncialis* were fertile even though the number of chiasmata per PMCs was 4-5. This proves that there is no correlation between the level of conjugation of alien chromosomes and the fertility of F_1

hybrid plants. The high level of conjugation and fertility most likely depend not only on the level of conjugation of alien chromosomes, but also on the nature of the nuclear-cytoplasmic relationship, the ecotype of the samples taken as parental forms, the influence of environmental factors, etc.

It should also be noted that in all the wheat-*Aegilops* hybrids we obtained, meiosis was accompanied by a number of abnormalities typical of incongruent hybrids: rod bivalents and univalents in metaphase I, multivalent associations such as tri- and quadrivalents, fragmentation of univalents into chromatids, lagging chromosome in anaphase I and II, unequal segregation of chromosomes to the poles, chromosome and chromatid bridges, formation of tripolar and multipolar cells, and the formation of micronuclear tetrads and polyadas, as well as numerous micronuclei and fragments, were observed in telophase I and II[8].

The low level of chromosom conjugation than expected in hybrid combinations obtained with the species of the genus *Aegilops* with the D subgenome can also be explained by the effect of the *Ph1* gene, which is located on chromosome 5B of common wheat and has a suppressive effect on the conjugation of homoeologous chromosomes.

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[8] Namazova, L.H. Yumşaq buğda xətləri ilə *Aegilops* L. növləri arasındakı F_1 hibridlərin sitogenetik analizi / L.H. Namazova, A.İ. Şəmşədzadə, A.C. Əliyeva // AMEA Genetik Ehtiyatlar İnstitutunun Elmi Əsərləri, - Bakı : -2017. C.VI, №1, - s. 19-27.

Table 3.1.1.

Meiotic configuration at metaphase I of meiosis in the intergeneric F_1 hybrids between common wheats and species of the genus *Aegilops*

Hybrid combinations	Seed setting, %	PM Cs	Ring bivalenets	Rod bivalents	Univalents	Trivalents	Chiazma frequency	2n
171ACS × *Ae. longissima*	5.71	143	0.41±0.17	3.59±1.66	19.86±0.79	0.04±0.08	4.09±0.44	28
172ACS × *Ae. markgrafii*	25.00	119	0.37±0.12	4.72±0.42	17.55±0.74	0.08±0.12	5.64±0.40	28
cv. Moskovya × *Ae. cylindrica*	32.61	101	2.44±0.11	2.87±2.33	24.22±0.48	0.05±0.10	7.91±0.24	35
Ae. cylindrica (Abs) 172ACS	21.43	139	3.71±0.32	2.65±1.58	22.28±0.62	-	10.07±0.56	35
172ACS × *Ae. ventricosa*	4.35	97	1.75±0.40	2.89±1.78	25.60±0.87	0.04±0.11	6.47±0.91	35
cv. Standart-4 × *Ae. crassa*	3.75	111	-	0.45±2.21	27.55±1.72		0.45±2.21	28
171ACS × *Ae. crassa*	6.90	103	1.43±0.55	4.51±3.63	22.73±1.95	0.13±0.11	7.63±0.77	35
Ae. crassa × 171ACS	50.00	118	0.09±0.12	3.42±1.50	27.18±1.33	0.26±0.19	4.13±0.46	35
cv. Zmitra × *Ae. trivialis*	17.50	108	0.44±0.20	4.73±2.10	31.45±0.66	0.06±0.20	5.75±0.49	42
171ACS × *Ae. trivialis*	6.58	133	1.94±0.41	3.14±2.36	31.50±0.55	0.11±0.08 Quadrival. 0.25± 0.12	6.31±0.42	42
Ae. juvenalis × 171ACS	1.61	125	2.77±0.33	6.85±2.57	22.52±2.13	0.08±0.14	12.55±0.49	42
171ACS × *Ae. umbellulata*	14.52	135	0.31±0.13	2.62±0.31	21.15±0.55	0.33±0.12	3.90±0.30	28
171ACS × *Ae. peregrina*	1.25	135	0.56±0.26	3.36±2.22	26.99±0.94	0.06±0.08	4.61±0.43	35
172ACS × *Ae. kotschyi*	14.63	123	0.36±0.11	5.00±2.15	24.00±0.91	0.10±0.11	4.50±0.47	35

171ACS × *Ae. geniculata*	10.00	119	0.86±0.23	3.43±0.37	25.90±0.82	0.18±0.14	5.52±0.40	35
Ae. geniculata × cv. Asakaze komugi	8.33	101	-	1.55±0.48	31.90±1.38	-	1.55±0.48	35
171ACS × *Ae. triuncialis*	2.70	108	0.18±0.12	1.92±2.82	30.62±0.70	0.06±0.09	2.40±0.46	35
171ACS × *Ae. biuncialis*	5.17	186	0.20±0.09	2.81±0.48	26.97±1.00	0.67±0.29	4.55±0.60	35
171ACS × *Ae. columnaris*	28.26	123	-	3.76±2.22	27.46±0.77	0.01±0.09	3.77±0.38	35
172ACS × Ae. *columnaris*	5.88	117	0.79±0.11	4.04±0.25	21.85±0.33	0.83±0.22	7.27±0.23	35
Ae. neglecta ×172ACS	15.62	95	-	5.99±0.52	22.96±0.83	0.02±0.10	6.03±0.38	35
T. polonicum× *Ae.neglecta*	12.50	110	-	1.73±0.38	24.54±0.42	-	1.73±0.38	28
171ACS × *Ae. neglecta*	1.56	124	0.13±0.12	2.38±2.59	29.69±0.72	0.10±0.12	2.84±0.44	35
171ACS × *Ae. neglecta*	15.79	115	0.22±0.27	6.35±0.39	21.53±0.44	0.11±0.12	7.01±0.48	35
172ACS × *Ae. recta*	14.29	130	1.34±0.19	7.12±0.34	24.66±0.48	0.14±0.11	10.08±0.27	42
T. durum – Ae. tauschi × *Ae. sharonensis*	4,84	112	0,33±0,15	2,81±1,34	21,57±0,55	0,05±0,10	3,62±0,38	28
171ACS × *Ae. sharonensis – Ae. umbellulata*	4,76	79		4,33±0,37	26,30±0,66	0,04±0,11	4,40±0,26	35
Ae. sharonensis – Ae. umbellulata × 172ACS	19,4	88	-	5,29±0,46	24,37±0,86	0,03±0,10	4,25±0,25	35
171ACS × *Ae. ventricosa* TA-1999	142	105	0,53±0,11	4,37±1,46	25,18±0,83	5,44±0,41		35

3.2. Morphotype forming of a F_2-F_7 hybrid populations between common wheat (*T. aestivum* L.) and *Aegilops* L. species

It has been found out that different morphotype forming processes occur in F_2-F_7 hybrid populations between bread wheat and *Aegilops* species, depending on their intensity and range. Fertility in hybrid populations ranged from 0.00-100%, and plant height varieted from 55-160cm. Depending on the genotypes involved in hybridization, partially or completely sterile plants were often found in the segregating progenies.

Almost the majority of the later generation hybrids were of the common wheat type, and at the same time, an increase in fertility was observed towards the later generations.

In general, there is sufficient information in the literature on the very low fertility of not only F_1 but also later generation hybrids between wheat and *Aegilops*. At the same time, *Aegilops* L. × *Triticum* L. hybrids were compared with common wheat and were characterized by better morphological traits.

Starting from the F_2 generation, intensive segregation was observed in hybrid populations obtained with the species of the *Vertebrata* and *Aegilops* sections of the genus *Aegilops* L. with bread wheats. In this regard, *Ae. juvenalis* stands out among the species included in the *Vertebrata* section, and *Ae. neglecta* stands out among the species included in the *Aegilops* section.

Thus, more fractions were recorded in the F_2 (Figure 3.2.1), F_3, F_4 and F_5 populations obtained from the *Ae. juvenalis* × 171ACS combination (20, 13, 44 and 34 fractions, respectively) and in the BC_1F_2 (Figure 3.2.2), BC_1F_3, BC_1F_4 and BC_1F_5 populations belonging to the (171ACS × *Ae. neglecta*) × 172ACS combination (16, 53, 45 and 27 fractions, respectively).

Although fractions with intermediate, spelt, and bread wheat-type spikes predominated in the F_2-F_7 generations of the hybrid populations, those with aegilops, durum, turgidoid, compactoid, persicoid, and vaviloid spikes morphotype were found. This indicates that the process of spike morphotype forming in these populations is intensive and the spectrum of morphotype forming is relatively large.

Figure 3.2.1. Spike morphology of the F_2 hybrid of *Ae. juvenalis* × 171ACS combination

Figure 3.2.2. Intermediate, spelt and common wheat-type spikes of the BC_1F_2 hybrid population of the (171ACS × *Ae. neglecta*) × 172ACS combination

Thus, it was established that in the fourth and fifth generations, wheat hybrids with *Aegilops* species intended towards common wheat morphologically. Most of the hybrid combinations with non-homologous chromosomes were sterile or had low fertility, indicating a low level of chromosomal conjugation between them.

CHAPTER IV. MOLECULAR CYTOGENETIC AND ELECTROPHORETIC STUDY OF WHEAT-AEGILOPS HYBRIDS

4.1. Molecular cytogenetic study of wheat-aegilops hybrids

In the third generation of the hybrid population of the combination 171ACS × *Ae. umbellulata*, fragmentation typical of intergeneric hybrids occurred. And several F_4 hybrid forms were selected, that somatic chromosome numbers ranging from 42-47. In order to identify the introgression of alien chromosomes or chromosome segments of *Ae. umbellulata* into these hybrid plants, they were investigated to molecular cytogenetic studies and the results of their GISH and FISH analyses were comparatively analyzed.

Based on the results of GISH and FISH analysis, three hybrid plants (2n=43) obtained from the combination 171ACS × *Ae. umbellulata*, namely 1, 21 and 22, were determined to be nullisomic for chromosomes 7A and 1D chromosomes, trisomic for 5A, tetrasomic for 5B, and also had 2 U chromosomes. Since one pair of 1U chromosomes replaced by one pair of 1D chromosomes in them, these hybrid samples were considered as 1U(1D) with disomic substitution for 1U (Figure 4.1.1).

FISH and GISH analysis revealed that hybrids, namely 2 and 11 (2n=47) of the 171ACS × *Ae. umbellulata* combination had 4 U chromosomes (one pair of 1U and one pair of 5U), and were nullisomic for 6B and 1D, monosomic for 3D, and tetrasomic for 2B, 3B, and 5B. In both hybrids, it is likely that one pair of 1U chromosomes replaced by one pair of 1D chromosomes, and one pair of 5U chromosomes replaced by one pair of 6B chromosomes. Therefore, this hybrid can be considered disomy substution for 1U and 5U [1U(1D) and 5U(6B), respectively].

Hybrid number 18 (2n=46) was found to have 2 U chromosomes, and was also nullisomic for 1D, monosomic for 3B and 3D, and tetrasomic for 5A, 2B, and 5B. Since one pair of 1U chromosomes replaced by one pair of 1D chromosomes in this hybrid, it was considered as 1U(1D) with disomic for 1U.

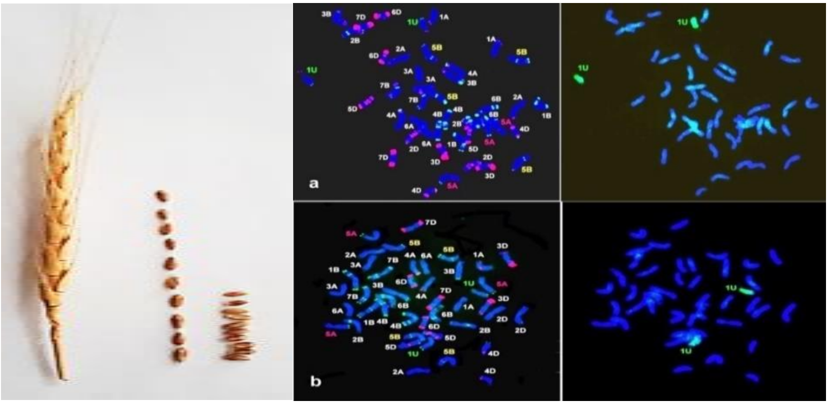


Figure 4.1.1. FISH (left) and GISH (right) on mitotic metaphase chromosomes of hybrid No 1 (a) and 22 (b) (2n=43) selected from the F_4 population of the combination 171ACS × *Ae. umbellulata* (Chromosomes with blue and green colouring represent wheat and *Ae. umbellulata* chromosomes, respectively).

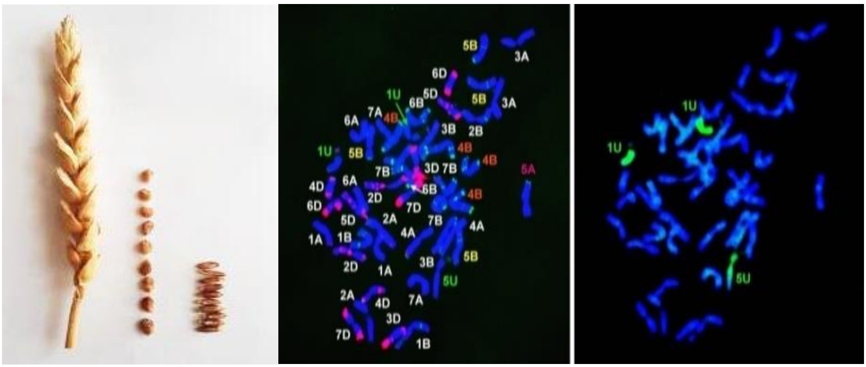


Figure 4.1.2. FISH (left) and GISH (right) on mitotic metaphase chromosomes of hybrid No 17 (2n=46) selected from the F_4 population of the combination 171ACS × *Ae. umbellulata* by FISH (left) and GISH (right) methods (Chromosomes with blue and green colouring represent wheat and *Ae. umbellulata* chromosomes, respectively).

Hybrid number 17 (2n=46), was faund to presence of 3 U chromosomes (two 1U and 1 5U). At the same time, it was found that it was nullisomic for 1D, monosomic for 5A, and tetrasomic for 4B and 5B. Here, since a pair of 1U chromosomes of aegilops replaced by a pair of 1D chromosomes of wheat, it can be considered 1U(1D) with disomy replacement for 1U, 1 chromosome 5A, 1 chromosome 5U, and 1 chromosome 5U, it can be considered 5U(5A) with monosomic replacement for 5U (Figure 4.1.2).

FISH and GISH analysis showed that hybrids 14 and 16 (2n=46) of the combination 171ACS × *Ae. umbellulata* were nullisomic for 2A and 3A and tetrasomic for 5A and 4B. The number of U chromosomes in these hybrids was also 4: one pair of 1U and one pair of 5U. Most likely, in these hybrids, one pair of 1U and 5U chromosomes replaced by one pair of 2A and 3A chromosomes, respectively. In other words, these hybrids can be considered disomic for 1U and 5U, that is, 1U(2A) and 5U(3A).

The investigations about the genom and chromosome composition, chromosome set, monosomic (m) and disomic (d) wheat-aegilops substitutions (S) of the hybrids selected from the F_4 population of the 171ACS × *Ae. umbellulata* combination and whose chromosomes were identified is given in Table 4.1.1.

As can be seen from the table, the number of chromosomes in the hybrids selected from the F_4 population derived from 171ACS × *Ae. umbellulata* combination varied between 42-47, and the number of alien chromosomes of *Ae. umbellulata* varied between 2-5. 1U(1D) disomic substitution was observed in all the studied samples, except for hybrids numer 14 and 16. Only one substitution was recorded in hybrids 1, 18, 21 and 22, two in hybrids 2, 11, 14, 16 and 17, and three in hybrids 8, 9 and 12.

Table 4.1.1.

Genom and chromosome composition of hybrid plants of F4 population of the combination 171ACS × *Ae. umbellulata*

Ge-nom	Chro-mosome	Hybrids					
		1 21 22	18	17	14 16	2 11	8 9 12
A	1	+ +	+ +	+ +	+ +	+ +	+ +
	2	+ +	+ +	+ +	- -	+ +	+ +
	3	+ +	+ +	+ +	- -	+ +	+ +
	4	+ +	+ +	+ +	+ +	+ +	+ +
	5	+ + +	+ + + +	+ -	+ + + +	+ +	+ + + + + + +
	6	+ +	+ +	+ +	+ +	+ +	+ +
	7	- -	+ +	+ +	+ +	+ +	+ +
B	1	+ +	+ +	+ +	+ +	+ +	+ +
	2	+ +	+ + + +	+ +	+ +	+ + + +	+ +
	3	+ +	+ -	+ +	+ +	+ + + +	+ +
	4	+ +	+ +	+ + + +	+ + + +	+ +	+ +
	5	+ + + +	+ + + +	+ + + +	+ +	+ + + +	+ +
	6	+ +	+ +	+ +	+ +	- -	+ +
	7	+ +	+ +	+ +	+ +	+ +	+ +
D	1	- -	- -	- -	+ +	- -	- -
	2	+ +	+ +	+ +	+ +	+ +	+ +
	3	+ +	+ -	+ +	+ +	+ -	+ +
	4	+ +	+ +	+ +	+ +	++	- -
	5	+ +	+ +	+ +	+ +	+ +	- -
	6	+ +	+ +	+ +	+ +	+ +	+ +
	7	+ +	+ +	+ +	+ +	+ +	+ +
U	1	+ +	+ +	+ +	+ +	+ +	+ +
	2	- -	- -	- -	- -	- -	- -
	3	- -	- -	- -	- -	- -	- -
	4	- -	- -	- -	- -	- -	+ -
	5	- -	- -	+ -	+ +	+ +	+ +
	6	- -	- -	- -	- -	- -	- -
	7	- -	- -	- -	- -	- -	- -
S		**1U(1D)d**	**1U(1D)d**	**1U(1D)d U(5A)m**	**1U(2A)d 5U(3A)d**	**U(1D)d U(6B)d**	**1U(1D)d U(4D)m 5U(5D)d**
2n		**43**	**46**	**46**	**46**	**47**	**46**

The chromosome composition of a line from to the F_3BC_1 population of the combination (171ACS × *Ae. neglecta*) × 172ACS was analyzed by the FISH method and it was determined that in this plant, which has a chromosome set of 2n=42, one pair of wheat 1D chromosomes was replaced by one pair of *Ae. neglecta* 1U chromosomes (Figure 4.1.4).

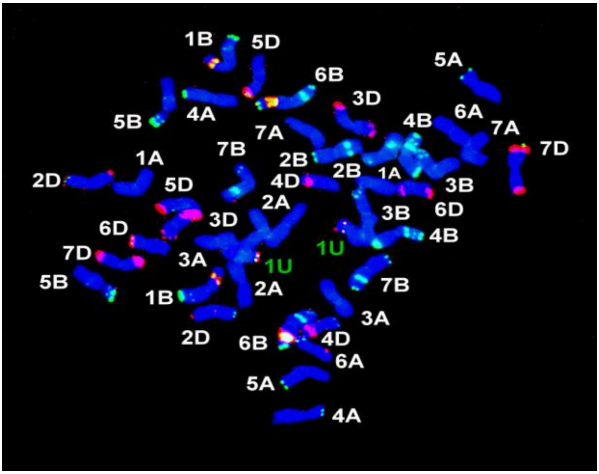


Figure 4.1.3. FISH on mitotic metaphase chromosomes of 1U(1D) substitution line (2n=42) selected from the F_3BC_1 population of the combination (171ACS × *Ae. neglecta*) × 172ACS

The chromosome composition of the hybrid plant obtained from the cross of the bread wheat variety Moskovya with *Ae. cylindrica* was analyzed by FISH and GISH methods. It was determined that the karyotype of this aneuploid plant with a chromosome set of 2n=39 contained 3 chromosomes of *Ae. cylindrica* (1 1C and 2 6C), and that this plant was nullisomic for chromosomes 7A and 2D, and monosomic for chromosomes 3A and 7B.

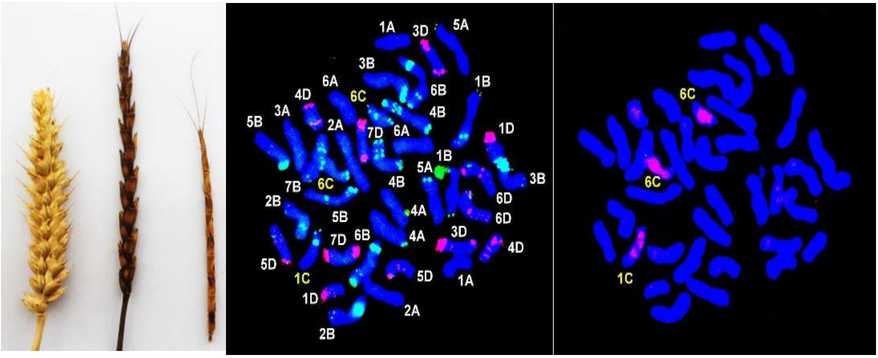


Figure 4.1.4. FISH (left) and GISH (right) on mitotic metaphase chromosomes of Moskovya × *Ae. cylindrica* (Chromosomes with blue and red colouring represent wheat and *Ae. cylindrica* chromosomes, respectively)

Thus, GISH allowed to identify all the chromosomes in the genome. This method allows us to assess the introgression of chromosomes or chromosome segments belonging to the Aeilops genome into wheat. In our experiment, the presence of chromosomes 1C and 6C was determined in the hybrid of the Moskovya × *Ae. cylindrica* combination using the GISH method.

4.2. Electrophoretic study of wheat-aegilops hybrids

In the research work, the hereditary nature of the allelic genes of the gliadin- and glutenin-coding loci, which control the synthesis of electrophoretic components of storage proteins, was studied in the grains of the later generation, stable intergeneric hybrids obtained from the crossing of bread wheat lines with various aegilops species, and the Bezostaya 1 and Anza wheat varieties were used as control samples.

Electrophoregrams of gliadin-coding loci of the grains of the parental forms and hybrids obtained with the modern bread wheat (ABD) lines and *Ae. kotschyi* (SU), *Ae. triuncialis* (CU), *Ae. neglecta* (UM) and *Ae. umbellulata* (U) species are presented in Figure 4.2.1.

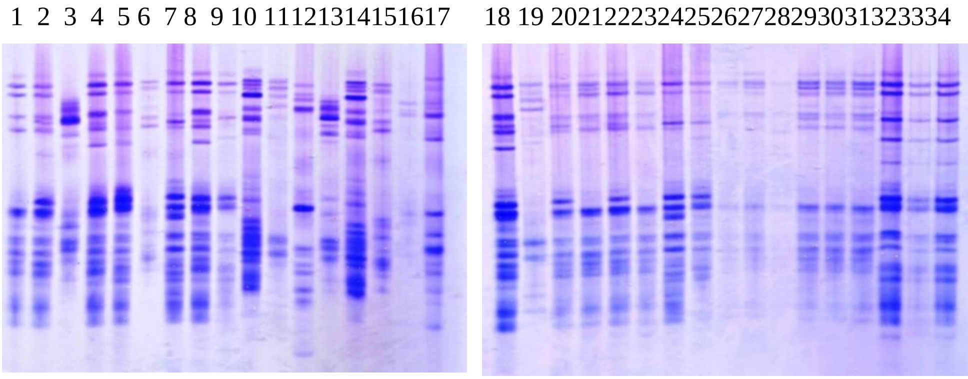


Figure 4.2.1. Electrophoregrams of gliadin storage proteins of bread wheat-*Aegilops* hybrids, bread wheat genotypes, and *Aegilops* L. species: **1**- 172ACS (♀), **2**- hybrid No 443 (172ACS × *Ae. kotschyi*), **3**- *Ae. kotschyi* (♂), **4**-171ACS (♀), **5**- hybrid No (171ACS × *Ae. triuncialis*), **6**- *Ae. triuncialis* (♂), **7**- Bezostaya-1, **8**- 171ACS (♀), **9**- hybrid No 480 (171ACS × *Ae. neglecta*), **10**- *Ae. neglecta* (♂), **11**- *Ae. umbellulata*, **12**- *Ae. tauschii*, **13**- *Ae. kotschyi*, **14**- *Ae. neglecta*, **15**- *Ae. triuncialis*, **16**- *Ae. trivialis*, **17**- *Ae. juvenalis*, **18**- 171 ACS (♀), **19**- *Ae. umbellulata* (♂), **20-23**- hybrid No 485 (171ACS × *Ae. umbellulata*), **24**- Bezostaya-1, **25**- Anza, **26-34**- hybrid No 488, 489 and 491 (171ACS × *Ae. umbellulata*)

The analysis of the obtained results revealed that the electrophoregrams of gliadin-coding loci and the frequency of allelic component blocks forming them in the later generation intergeneric wheat-*Aegilops* hybrids obtained with the participation of common wheats and species of the genus *Aegilops* with different ploidy and genome are different. Thus, the rare allels of the gliadin-coding 2Gli1A2 locus was found only in the hybrid from the combination 172ACS × *Ae. kotschyi*. At the same time, the presence of allelic component blocks of the Gli1A3, Gli1B6 and Gli6D5 loci, which were not found in all the studied hybrids, was recorded in this hybrid. The Gli1A9 and Gli6D6 blocks of the gliadin-coding loci were found only in 171ACS × *Ae. triuncialis*, the Gli1B3 block was found only in 171ACS × *Ae. umbellulata*, the Gli1D1 and Gli6B1 blocks were found only in 172ACS × *Ae. kotschyi* and 171ACS × *Ae. triuncialis*, Gli1B8 block was found in the grains of hybrids from the combinations 171ACS × *Ae. triuncialis*, 171ACS × *Ae. neglecta* and

171ACS × *Ae. umbellulata*, Gli1A5, Gli1D7 and Gli6D7 blocks were found in the combinations 171ACS × *Ae. neglecta* and 171ACS × *Ae. umbellulata*. It was noted that the grains of varieties containing the Gli1A5 block were distinguished by higher quality indicators than those of varieties containing the Gli1A6 block [9]. Gli6B4 is the only block that was found in hybrids of all four combinations (172ACS × *Ae. kotschyi*, 171ACS × *Ae. triuncialis*, 171ACS × *Ae. neglecta* and 171ACS × *Ae. umbellulata*).

CHAPTER V. STUDY OF YIELD PARAMETERS IN INTERGENERİC HYBRIDS BETWEEN WHEAT (*TRITICUM* L.) AND *AEGILOPS* L.

5.1. Characterization and grouping of intergeneric hybrid plants according to yield elements

Increasing genetic diversity in wheat is important for breeding programs and the development of new genotypes. The success of breeding programs depends on the genetic variability of the plant's quantitative traits.

In our practice, genetic and breeding work on intergeneric hybrids obtained from crossing bread wheat lines with *Aegilops* species has been continued each year, and the best populations, resistant to diseases and pests, as well as those with high fertility, have been selected.

In order to reveal the breeding value of 17 intergeneric hybrid plants obtained from distant hybridization in the research study, they were comparatively analyzed according to the main yield elements.

In hybrids, plant height (PH) varied between 89-155, spike length (SL) 8.00-22.50 cm, number of spikelets per spike (NSS) 15.00-28.00, spike density (SD) 1.11-2.37, number of grains per spike (NGS) 12.00-86.00, spike weight (SW) 0.9-5.3, spike width (SW) 0.60-2.00, and kernel weight per spike (KW) 0.40-4.10. According to

[9] Həsənova, Q.M. Yumşaq buğda sortlarının dən keyfiyyətinin formalaşmasının genetik əsasları və onun seleksiyada istifadəsi: biologiya üzrə fəlsəfə doktoru dissertasiyasının avtoreferatı / - Bakı, 2015. – 45 s.

PH, *Ae. juvenalis* × 171ACS, 171ACS × *Ae. umbellulata* (491) and 171ACS × *Ae. neglecta* (18.80, 18.60 and 16.70 cm, respectively), according to NSS *Ae. juvenalis* × 171ACS, 171ACS × *Ae. umbellulata* (491) and 171ACS × *Ae. neglecta* (28.00, 24.20 and 26.20, respectively), according to SD, i.e. the number of spikelets per 10 cm of spike *Ae. juvenalis* × 171ACS (1.91), according to NGS (171ACS × *Ae. neglecta*) × 172ACS and 171ACS × *Ae. neglecta* (85.00 and 86.00, respectively), according to SW 171ACS × *Ae. triuncialis* (4.52 g), according to KW 171ACS × *Ae. triuncialis* (2.92 g) hybrids were higher than other hybrids.

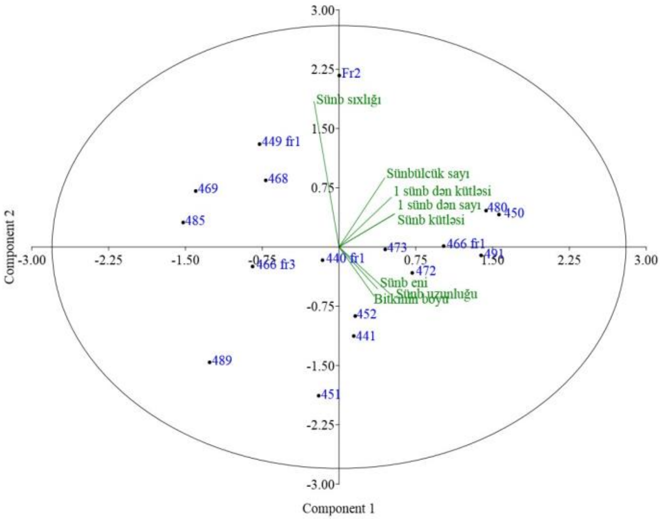
Thus, it was determined that hybrids obtained from combinations of (171ACS × *Ae. neglecta*) × 172ACS, 171ACS × *Ae. umbellulata*, 171ACS × *Ae. neglecta* had higher for almost all of the studied yield elements. At the same time, it was found that the substitutions 1U(1A) and 5U(5D) significantly affect the increase the yield components. The genotypes selected for their high indicators of productivity elements allow them to be used in the future as breeding or starting material. Thus, among the intergeneric hybrid lines, the existence of forms approaching standard wheat varieties in terms of productivity and even surpassing them was revealed. The yield traits of the later generation intergeneric hybrid plants were statistically evaluated. The relationships between the traits were examined by principal component analysis (PCoA). Statistical analyses were performed using R and SPSS 16.0 statistical computer programs and clusters were constructed.

Plant materials with more genetic variation are the more effective for the breeding work based on seed yield[10].

The correlation was established between the yield traits of the later generation wheat-egilops hybrids, and a highly significant (r=0.85) dependence was observed between the number of grains per spike and the kernel weight. Also, a highly significant (r=0.75) dependence was recorded between the length of the spike and the

[10] Moragues, M. Yield formation strategies of durum wheat landraces with distinct pattern of dispersal within the Mediterranean basin: II. Biomass production and allocation // Field crops research, -2006. V.95, №2, -p. 182-193

number of spikelets per spike, as well as between the number of spikelets per spike and the number of grains per spike.



Şəkil 5.1.1. Description of results PCoA analysis

According to the results of the principal component (PCoA) analyzes, some yield components such as NSS, NSG, KW and SW of hybrid plants numbered 466/1 (171 ACS × *Ae. triuncialis*), 450 (*Ae. juvenalis* × 171 ACS) and 480 (171 ACS × *Ae. neglecta*) were higher that other hybrids and shared the same scatter plot.

RESULTS

1. Cytogenetic studies have revealed that in intergeneric F_1 hybrids between wheat and *Aegilops*, the very low conjugation of alien chromosomes during meiosis does not interfere with their fertility, while in F_2 and later generation hybrids, where the level of conjugation is higher, disturbances in the gamete and zygote formation processes usually cause their sterility.
2. Although most F_1 hybrids obtained from a straight combination

between different egilops species and bread wheat are sterile, as a result of the fact that some of the reciproc (inversely) hybrids are fertile, it has been determined that fertility depends not only on the common or identical genome of the parent forms, the degrees of ploidy and the level of conjugation between their chromosomes, but also on the direction of hybridization.

3. As a result of the study of meiosis in F_1 hybrids between species included in the *Vertebrata* and *Aegilops* sections and common wheat, it was found that the M genome is closer to the N genome, the U genome to the M genome, and the S^k genome to the S^v genome than to the common wheat genome.
4. Despite the lack of any homology between the AABB genome of durum wheat and the DDMM genomes of *Ae. crassa* and the UUM^tM^t genomes of *Ae. neglecta*, the fertility of its hybrids with *Ae. crassa* has shown that *Ae. crassa* is genetically closer to durum wheat than to *Ae. neglecta*.
5. During the study of the morphogenesis in intergeneric F_2–F_7 hybrids, a tendency to return to common wheat was observed, and it was determined that the range of morphogenes was wider in hybrid populations of *Ae. juvenalis*, a species included in the *Vertebrata* section, and *Ae. neglecta*, a species included in the *Aegilops* section, with common wheat.
6. As a result of the molecular cytogenetic analyzes, among the hybrids derived from 171ACS × Ae. umbellulata combination, except for hybrids 14 and 16 with a 1U(2A) disosomic substitution, 1U(1D) disosomic substitution was observed in all the remaining hybrids, only one [1U(1D)] was observed in hybrids 1, 18, 21 and 22, two substitutions were observed in hybrids 2, 11 [1U(1D) and 5U(6B)], 14, 16 [1U(2A) and 5U(3A)] and 17 [1U(1D) and 5U(5A)], and three substitutions [1U(1D), 4U(4D) and 5U(5D)] were observed in hybrids 8, 9 and 12. In addition, it was found that hybrids 1, 21, and 22 were tetrasomic for 5B, hybrid 17 for 4B and 5B, hybrids 14 and 16 for 5A and 4B, hybrid 18 for 5A, 2B, and 5B, and hybrids 2 and 11 for 2B, 3B, and 5B, and that tetrasomic occurred most frequently for 5B (in 7 hybrids) and least frequently for 3B (in

2 hybrids).

7. According to the results of the principal component (PCoA) analyzes, some yield components such as NSS, NSG, KW and SW of hybrid plants numbered 466/1 (171 ACS × *Ae. triuncialis*), 450 (*Ae. juvenalis* × 171 ACS) and 480 (171 ACS × *Ae. neglecta*) were higher that other hybrids and shared the same scatter plot. And yield elements of hybrid lines with 1U(1A) and 5U(5D) substitutions were higher than other hybrids.
8. Electrophoregrams of gliadin-coding loci and allelic component blocks of hybrids obtained with bread wheat lines *Ae. kotschyi*, *Ae. triuncialis*, *Ae. neglecta* and *Ae. umbellulata* were identified. Allelic component block Gli6B4 was found in all combinations studied. In lines substituted for 1U, a rare allelic component block of the Gli1B3 locus was found, and in the combination with *Ae. kotschyi*, a rare allelic component block of the 2Gli1A2 locus was found.

RECOMMENDATIONS

1. Addition and substitution lines between *Ae. umbellulata* and bread wheat can be used in breeding programs for genetic improvement of varieties.
2. Wheat-*Aegilops* forms obtained with the of *Ae. neglecta*, *Ae. juvenalis* and *Ae. triuncialis* species can be used to improve the tolerance of wheat to biotic and abiotic stresses.

LIST OF PUBLICATIONS ON THE TOPIC OF THE DISSERTATION WORK

1. Namazova, L.H., Şəmşədzadə, A.İ., Əliyeva, A.C**.** Yumşaq buğda xətləri ilə *Aegilops* L. növləri arasındakı F_1 hibridlərin sitogenetik analizi // - Bakı: Azərbaycan Milli Elmlər Akademiyası Genetik Ehtiyatlar İnstitutunun elmi əsərləri, - 2017. C.VI, №1, - s. 19-27.
2. Namazova, L.H., Əliyeva A.C., Əsgərbəyli O.L. Gəvən (*Astragalus* L.) cinsinin müxtəlif növlərinin sitogenetik tədqiqi // - Bakı: Azərbaycan Milli Elmlər Akademiyası Genetik Ehtiyatlar İnstitutunun elmi əsərləri, - 2019. C.VIII, №1, - s. 16-24.
3. Namazova, L.H. Interspecific hybridization between bread wheat and *Aegilops triuncialis* L. // - Bakı: Research in: Agricultural & Veterinary Sciences, - 2019. C.III, №3, - p. 144-151.
4. Namazova, L.H. İntergeneric hybridization between bread wheat and *Ae. columnaris //* - Bakı: Gənc tədqiqatçı jurnalı, - 2019. C.5, №2, - p. 163-170.
5. Namazova, L.H. İntergeneric hybridization between *T. aestivum* and *Ae. kotschyii* under field conditions // - Bakı: Pedaqoji Universitetin Xəbərləri (Riyaziyyat və təbiət elmləri seriyası), - 2020. C. 68, №1, - s. 168-178.
6. Намазова, Л.Г., Алиева А.Дж. Цитогенетический анализ гибридов F1, полученных от скрещивания линий *Triticum aestivum* L. с видами *Aegilops* L. // Бюллетень науки и практики, - 2023. V. 9, №9, - с. 30-42.
7. Namazova, L.H. Production of hybrids between *T. aestivum* L. and *Ae. ventricosa* Tausch // Journal of Agriculture and Environment, - 2023. V. 37, №9, - p.1-6.
8. Namazova, L.H. Hybridization between diploid Aegilops species and bread wheat // - Baku: Advances in Biology & Earth Sciences, - 2023. V. 8, №3, - p. 313-323.
9. Namazova, L.H. Yumşaq buğda və egilops arasindakı hibrid populyasiyalarda formaəmələgəlmənin tədqiqi // - Gəncə: Azərbaycan Texnologiya Universitetinin Elmi əsərləri, - 2023. V. 44, №3, - s. 35-41.
10. Алиева, А.Дж., **Намазова, Л.Г.** Создание межродовых

гибридов между мягкой пшеницей (*Triticum aestivum* l.) и видами А*egilops* L. // Материалы Всероссийской научно-практической конференции с международным участием посвященная 80-летию Куркиева Уллубия Киштилиевича «Развитие научного наследия Н.И. Вавилова по генетическим ресурсам его последователями», -Дербент: «Дагестанский Государственный Аграрный Университет , -26-29 июня, -2017 , с. 134-138.
11. Namazova, L.H., Əliyeva A.C.Yumşaq buğdalarla (*T. aestivum* L.) *Aegilops* seksiyasına (*Aegilops* L.) mənsub növlər arasındakı F_1 hibridlərin meyotik analizi // Həsən Əliyevin anadan olmasının 110 illiyinə həsr olunmuş "Ekologiya: Təbiət və Cəmiyyət problemləri" mövzusunda III Beynəlxalq elmi konfransın materialları, - Bakı: Bakı Dövlət Universiteti, -26-27 dekabr, -2017, s. 242-244.
12. Namazova, L.H., Aliyeva, A.J. Meiotic analysis of F_1 intergeneric hybrids obtained between a soft wheat line 171 ACS (*Triticum aestivum*) and Vertebrata section species of *Aegilops* L. // Ulu Öndər Heydər Əliyevin anadan olmasının 95 illiyinə həsr olunmuş "XXI əsrdə ekologiya və torpaqşünasliq elmlərinin aktual problemləri" mövzusunda VII Respublika elmi konfransının materialları, - Bakı: Bakı Dövlət Universiteti, -3-4 may, - 2018, s. 197-198.
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