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Cytogenetic features of intergeneric amphydiploids and genome-substituted forms of wheat

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Abstract. Synthetic intergeneric amphydiploids and genome-substituted wheat forms are an important source for transferring agronomically valuable genes from wild species into the common wheat (*Triticum aestivum* L.) genome. They can be used both in academic research and for breeding purposes as an original material for developing wheat-alien addition and substitution lines followed by translocation induction with the aid of irradiation or nonhomologous chromosome pairing. The chromosome sets and genome constitutions of allopolyploids are usually verified in early hybrid generations, whereas the subsequent fate of these hybrids remains unknown in most cases. Here we analyze karyotypes of five hexa- ($2n = 6x = 42$) and octoploid ($2n = 8x = 56$) amphydiploids of wheat with several species of the *Aegilops*, *Haynaldia*, and *Hordeum* genera, and six genome-substituted wheat-*Aegilops* forms, which were developed over 40 years ago and have been maintained in different gene banks. The analyses involve C-banding and fluorescence *in situ* hybridization (FISH) with pAs1 and pSc119.2 probes. We have found that most accessions are cytologically stable except for Avrodes (genome BBAASS, a hexaploid genome-substituted hybrid of wheat and *Aegilops speltoides*), which segregated with respect to chromosome composition after numerous reproductions. Chromosome analysis has not confirmed the presence of the N genome from *Ae. uniaristata* Vis. in the genome-substituted hybrid Avrotata. Instead, Avrotata carries the D genome. Our study shows that octoploid hybrids, namely AD 7, AD 7147 undergo more complex genome reorganizations as compared to hexaploids: the chromosome number of two presumably octoploid wheat-*Aegilops* hybrids were reduced to the hexaploid level. Genomes of both forms lost seven chromosome pairs, which represented seven homoeologous groups and derived from different parental subgenomes. Thus, each of the resulting hexaploids carries a synthetic/hybrid genome consisting of a unique combination of chromosomes belonging to different parental subgenomes.

Key words: genome stabilization; wheat; amphydiploid; *Aegilops*; *Dasypyrum*; *Tritordeum*; genome-substituted forms; karyotype; C-banding; fluorescence *in situ* hybridization.

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Цитогенетические особенности межродовых амфидиплоидов и геномно-замещенных форм пшеницы

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Аннотация. Синтетические межродовые гибриды (амфидиплоиды) и геномно-замещенные формы пшеницы – важный источник для переноса хозяйственно ценных генов от диких видов в геном *Triticum aestivum* L. Их используют как для решения теоретических задач, так и в практических целях для получения дополненных или замещенных линий, а также для индукции пшенично-чужеродных транслокаций с помощью облучения или

негомологичной конъюгации хромосом. Хромосомный и геномный состав аллополиплоидных форм обычно верифицируется в ранних гибридных поколениях, часто дальнейшая судьба этих гибридов остается неизученной. В настоящей работе с помощью методов С-дифференциального окрашивания хромосом по Гимза и флуоресцентной гибридизации *in situ* (FISH) с ДНК-зондами рAs1 и рSc119.2 мы провели исследование кариотипов пяти гекса- ($2n = 6x = 42$) и октаплоидных ($2n = 8x = 56$) геномно-дополненных амфидиплоидов пшеницы с отдельными видами из родов *Aegilops*, *Haynaldia* и *Hordeum*, а также шести гексаплоидных пшенично-эгилопсных геномно-замещенных форм, полученных более 40 лет назад и поддерживаемых в коллекциях разных научно-исследовательских учреждений. Показано, что большинство исследованных форм цитогенетически стабильны, однако Авродес (геном ВВААСС) – гексаплоидный геномно-замещенный гибрид пшеницы и *Ae. speltoides*, расщеплялся по хромосомному составу после многих репродукций. Хромосомный анализ не подтвердил ожидаемого геномного состава геномно-замещенной форма Авротата, у которой вместо заявленного N-генома от *Ae. uniariostata* Vis. обнаружен D-геном. В данной работе показано, что октаплоидные формы проходят через более сложные преобразования геномов, чем гексаплоидные: в двух исследованных предположительно октаплоидных амфидиплоидах AD 7, AD 7147 произошла редукция числа хромосом до гексаплоидного уровня. У обеих форм были утрачены семь пар хромосом из разных родительских субгеномов, представляющих все семь гомеологических групп. В результате у них сформировался смешанный (гибридный) геном, состоящий из уникальной комбинации хромосом нескольких родительских субгеномов.

Ключевые слова: становление геномов; пшеница; амфидиплоиды; *Aegilops*; *Dasypyrum*; *Tritordeum*; геномно-дополненные формы; геномно-замещенные формы; кариотип; С-бэндинг; флуоресцентная *in situ* гибридизация.

Introduction

Common wheat *Triticum aestivum* L. is one of the most important crops. It ranks third to rice and maize in grain global production (Biodiversity, 2024). It is thought that common wheat arose about 8–10 MY BP in northwestern Iran, near Caspian Sea, as a result of hybridization between a tetraploid wheat and wild goat grass *Aegilops tauschii* Coss. followed by spontaneous chromosome duplication (Kihara, 1975; Dvořák et al., 1998; Feldman, 2001; Feldman, Levy, 2023). Such crosses might have occurred repeatedly and involve different parental wheat and *Aegilops* forms growing in the same region (Hirosawa et al., 2004; Luo et al., 2007). In turn, the resulting hexaploid wheats might cross to each other and to other species, thereby extending and enriching the gene pool of the novel crop (Feldman, 2001; Wang et al., 2013).

Common wheat is more flexible than cultivated tetraploid species (Dubcovsky, Dvořák, 2007); therefore, it is better suited to new environment when spreading to new areas. It is also characterized by better adaptability, higher yield, larger grains, and easier threshing as compared to hulled tetraploid wheat (Tadesse et al., 2016). The addition of the D genome from *Ae. tauschii* conferred grain qualities appropriate for the production of bread, one of the staples in human nutrition. Owing to these advantages, common wheat rapidly penetrated from its center of origin to the neighboring areas; then, to Europe Asia and Africa; and, finally, to North and South America and Australia. It gradually replaced hulled tetra- and hexaploid wheat species. Having been cultivated for over eight millennia, it occupied vast regions with diverse soil and climate conditions.

Meanwhile, intense breeding for high yield, which involved a limited number of founder varieties, narrowed considerably the gene pool of common wheat (Martynov et al., 2006; Girma, 2017; Feldman, Levy, 2023) in the past century. The task of gene pool expansion and search for new donors of commercially valuable traits is increasingly

important (Bespalova, 2015). Wild Crop Relatives (WCR) are considered to be among the most promising donors of new genes for wheat improvement (Prohens et al., 2017; Sharma M.P. et al., 2020; Sharma S. et al., 2021). Species of the *Aegilops* L. genus, wheat relatives, possess many agronomically valuable traits that can be used in wheat breeding: pest resistance, drought tolerance, high micronutrient content, and others (Gill et al., 1986; Monneveux et al., 2000; Schneider et al., 2008; Molnár-Láng et al., 2015; Olivera et al., 2018; Kishii, 2019; Kumar et al., 2019). The close phylogenetic relationship between the *Triticum* L. and *Aegilops* genera facilitates successful transfer of genetic material between them, as plasmon and two of the three common wheat nuclear sub-genomes, B and D, have been inherited from *Aegilops* species (Kihara, 1975; Tsunewaki, 1996).

Nevertheless, the direct gene transfer from *Aegilops* to wheat is a difficult task. Several approaches have been suggested to improve the efficiency of alien genetic material transfer. One of them involves crosses between wheat and a target species, chromosome doubling in the F_1 , and developing wheat-alien addition and substitution lines. These lines are then used for inducing wheat-alien translocations (Peng et al., 2011; Zhang P. et al., 2015; Kishii, 2019; Kroupin et al., 2019). For instance, this approach was used to obtain wheat addition and substitution lines with rye (Gill, Kimber, 1974), barley (Islam, Shepherd, 1990; Cabrera et al., 1995; Molnár-Láng et al., 2000; Trubacheeva et al., 2009), *Aegilops* (Friebe et al., 1992, 2000; Logojan, Molnár-Láng, 2000; Molnár-Láng et al., 2014), *Haynaldia villosa* (L.) Schur (syn. *Dasypyrum villosum* (L.) P. Candargy) (Minelli et al., 2005), *Thinopyrum* Á. Löve (syn. *Elytrigia* Desv.) (Schulz-Schaeffer, Friebe, 1992; Linc et al., 2012; Kroupin et al., 2019), and other cereals. A number of allopolyploid hybrids between various tetraploid wheat species and *Ae. tauschii* have been obtained at CIMMYT, Mexico (Kishii, 2019; Aberkane et al., 2020). Pedigree analyses indicate that the

genetic material of *Aegilops*, mainly *Ae. tauschii*, as well as *Ae. umbellulata* Zhuk. and *Ae. ventricosa* Tausch is present in over 1,350 varieties and 9,000 elite lines of common wheat (Martynov et al., 2015), and their ratio is still increasing.

In addition to commercial breeding, synthetic allopolyploids are extensively used in studies of processes accompanying hybrid genome formation (Özkan et al., 2001; Kashkush et al., 2002; Levy, Feldman, 2004). Addition and substitution lines obtained from such allopolyploids were successfully used for the establishing of genetic relationships (homoeology) of chromosomes of different cereal species (Dhaliwal et al., 1990; Cabrera et al., 1995; Friebe et al., 1995a, b, 2000; Badaeva et al., 2018). However, these studies were primarily focused on processes occurring at early stages of allopolyploid formation, whereas their fate remained unknown in most cases.

Another approach was proposed by Dr. E.G. Zhirov. It is based on the development of genome-substituted common wheat forms, in which their D genome is substituted by the genome of a diploid *Aegilops* or of other cereal species (Zhirov, Ternovskaya, 1984; Davoyan R.O. et al., 2012). The first step of the production of these forms involved the extraction of the tetraploid BBAA component from common wheat cv. Avrora. The resulting tetra-component, tetraAvrora, was crossed to a diploid *Aegilops* species, whose genome was expected to replace common wheat D genome. The hybrids were treated with colchicine to double the chromosome number and obtain fertile amphydiploids. In spite of the fact that some genome-substituted forms obtained by E.G. Zhirov were cytologically characterized and are still used as donors of resistance genes in the breeding of common wheat and triticale (*×Triticosecale* Wittm.) (Davoyan R.O., Zhirov, 1995; Davoyan E.R. et al., 2012, 2023;

Davoyan R.O. et al., 2019), most of these hybrids have not been analyzed by C-banding.

This article is aimed in cytogenetic verification of intergeneric synthetic amphydiploids and genome-substituted accessions of common wheat obtained over 30 years ago and maintained in gene banks of different institutions using C-banding and (for some hybrids) fluorescence *in situ* hybridization (FISH).

Materials and methods

Experiments were conducted with the following artificial genome-substituted hybrids and intergeneric amphydiploids shown in the Table.

Six genome-substituted forms were raised by Dr. E.G. Zhirov at the Lukyanenko Research Institute of Agriculture, Krasnodar, more than 40 years ago. Their detailed description is provided in Zhirov's Dr. Sci. thesis "Wheat genomes: study and reconstruction" (Kyiv, Institute of Plant Physiology and Genetics, National Academy of Sciences, Ukraine, 1989). Two wheat-*Aegilops* amphydiploids were obtained by G.B. Piralov (1976) at the Institute of Genetics and Breeding, Academy of Sciences of the Azerbaijan SSR, Baku. One was accidentally found in the collection of the Institute of Cultivated Plants, IPK, Gatersleben, Germany. Its origin is unknown. The hybrid between emmer and *Haynaldia villosa* was synthesized by P.M. Zhukovsky (1944). The amphydiploid of durum wheat and wild barley *Hordeum chilense* Roem. & Schult. was developed in Spain in the early 1980s (Martin, Sanchez-Mongelaguna, 1982; Fernández, Jouve, 1984).

Karyotypes were analyzed by the conventional Giemsa C-banding protocol (Badaeva et al., 1994). *Tritordeum* was additionally analyzed by FISH (Badaeva et al., 2017) with

Material examined

Name	Cross	2n	Expected genome constitution	Gene bank
Avrodes	<i>T. aestivum</i> × <i>Ae. speltoides</i>	42	BBAASS	NCG
Avrosis	<i>T. aestivum</i> × <i>Ae. sharonensis</i>	42	BBAAS ^{sh} S ^{sh}	
Avrolata	<i>T. aestivum</i> × <i>Ae. umbellulata</i>	42	BBAUUU	
Avrotica	<i>T. aestivum</i> × <i>Ae. mutica</i>	42	BBAATT	ICG
Avrodata*	<i>T. aestivum</i> × <i>Ae. caudata</i>	42	BBAACC	
Avrotata*	<i>T. aestivum</i> × <i>Ae. uniaristata</i>	42	BBAANN	NCG
AD 7*	<i>T. ispathanicum</i> × <i>Ae. cylindrica</i>	56	BBAAD ^c D ^c C ^c C ^c	ICG
AD 7147*	Amphydiploid 4x wheat and <i>Ae. ventricosa</i>	56	BBAAD ^D D ^N N ^N	
AE 1491*	Not known	?	?	IPK
<i>Haynatricum</i> , K-38259	<i>Haynaldia villosa</i> × <i>T. dicoccum</i>	42	BBAAVV	ICG
<i>Tritordeum martinii</i> , K-7997	<i>T. durum</i> × <i>Hordeum chilense</i>	42	BBAAH ^H C ^c	VIR

Note. * Amphydiploids and genome-substituted accessions with unproved chromosome numbers, genome constitutions, or chromosome sets. NCG – National Center of Grain named after P.P. Lukyanenko, Krasnodar, Russia; ICG – Institute of Cytology and Genetics of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia; IPK – Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany; VIR – N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR), St. Petersburg, Russia.

DNA probes pAs1 (Rayburn, Gill, 1986) and pSc119.2 (Bedbrook et al., 1980). Wheat chromosomes were identified according to B.S. Gill et al. (1991), and chromosomes of other species, according to the nomenclatures proposed in (Dhaliwal et al., 1990; Cabrera et al., 1995; Friebe et al., 1995a, 2000; Linc et al., 1999; Badaeva et al., 2008, 2011, 2015a; Liu et al., 2010; Adonina et al., 2015; Molnár et al., 2016; Danilova et al., 2017; Said et al., 2021).

Results and discussion

Genome-substituted forms

Avrodes

Avrodes was cytogenetically proven to be hexaploid form in which the D genome is replaced by genome S from *Ae. speltooides* Tausch (Figs. 1, 2). Avrodes is cytologically unstable, and its chromosome numbers and combinations of the A, B, and S genome chromosomes vary among individual plants.

The plants examined had seven or eight A genome chromosome pairs. All plants had 1A, 2A, 4A, 5A, 6A, and 7A. Chromosome 2A of Avrodes differed from 2A of Avrora in having clear telomeric and terminal C bands. Unlike other chromosomes of the A genome, 6A was present as tetrasome, one pair substituting 6S. Most Avrodes plants had only one 7A pair, but two had an additional copy, substituting 7B (monosomic 7A/7B substitution; Fig. 2c). The karyotype of one plant lacked chromosome 3A, which had been replaced by an additional 3S pair.

Only three of seven chromosomes of the B genome, namely, 2B, 3B and 6B were present in all Avrodes plants examined. The 1BL:1RS wheat-rye translocation inherited from Avrora was seen in all plants, but the translocated chromosome was present in one or two copies (monosomic 1BL:1RS/1S substitution), or it was modified by a translocation of an unidentified fragment onto the distal portion of the long 1B arm (Fig. 2a, red arrow).

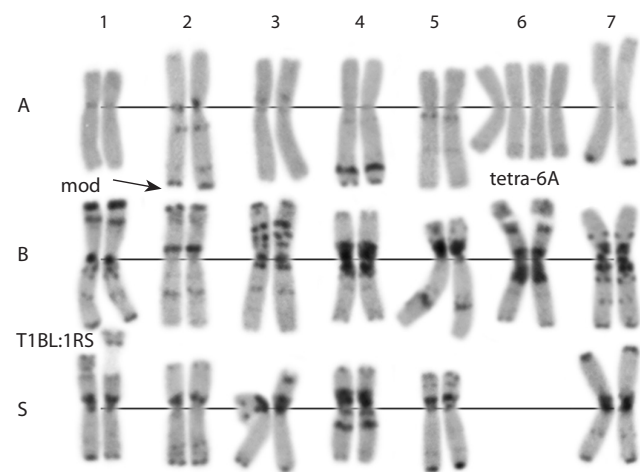


Fig. 1. C-banding karyotype of the Avrodes genome-substituted form. A, B, S – genomes; 1–7 – homoeologous groups.

Some plants were nulli4B-tetra4S (Figs. 2a, b) and others, nulli5B-tetra4S (Figs. 2a, b), where the two 5S chromosome pairs showed different C-banding patterns (Fig. 2c, green arrows). One pair matched exactly chromosome 5S of *Ae. speltooides*, and the other, designated as 5S*, was shorter, and it lacked the large telomeric band in the long arm (Fig. 3). Note that just this modified chromosome pair passed to Avrodes-derived elite accessions resistant to stripe or yellow rust (*Puccinia striiformis* Westend. f. sp. *tritici* Eriks.) (Davoyan E.R. et al., 2023).

The S genomes of different Avrodes plants was represented by 12 to 16 chromosomes, but chromosome 6S was always missing (Fig. 2). Only 2S and 7S were present only in the disomic state. Chromosomes 3S, 4S, and 5S were present as di- or tetrasomics, where 3S replaced homoeologs of the A genome, and 4S and 5S, of the B genome. Most plants had

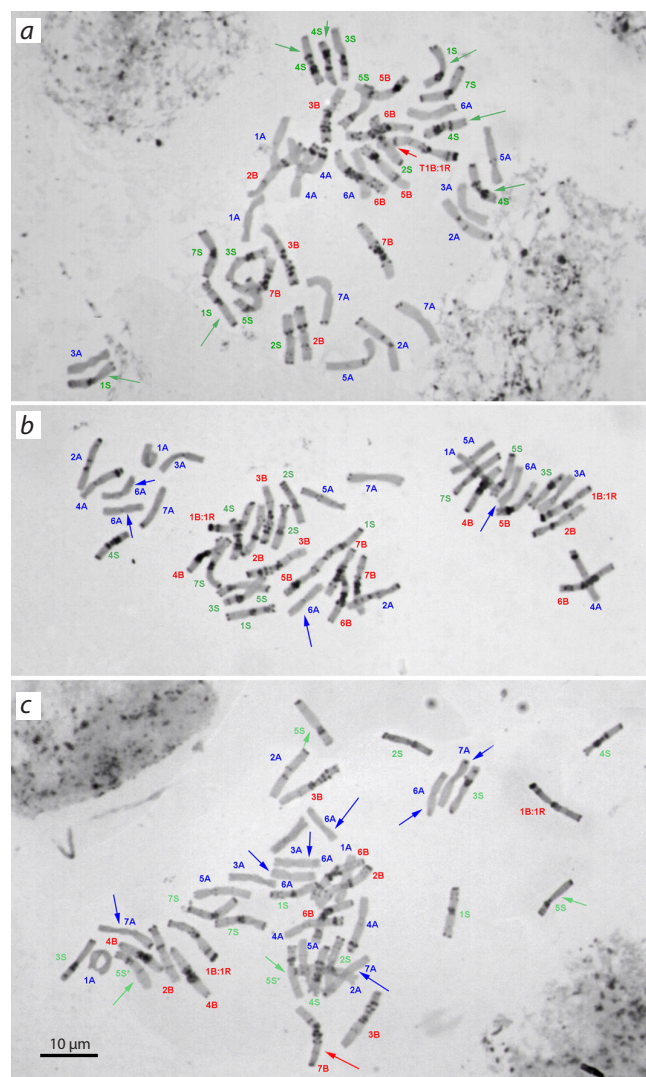


Fig. 2. C-banded metaphase plates in plants of the Avrodes genome-substituted form with different chromosome combinations.

Arrows indicate mono-, tri-, and tetrasomic chromosomes belonging to different genomes: red arrows – B genome; blue – A; and green – S.

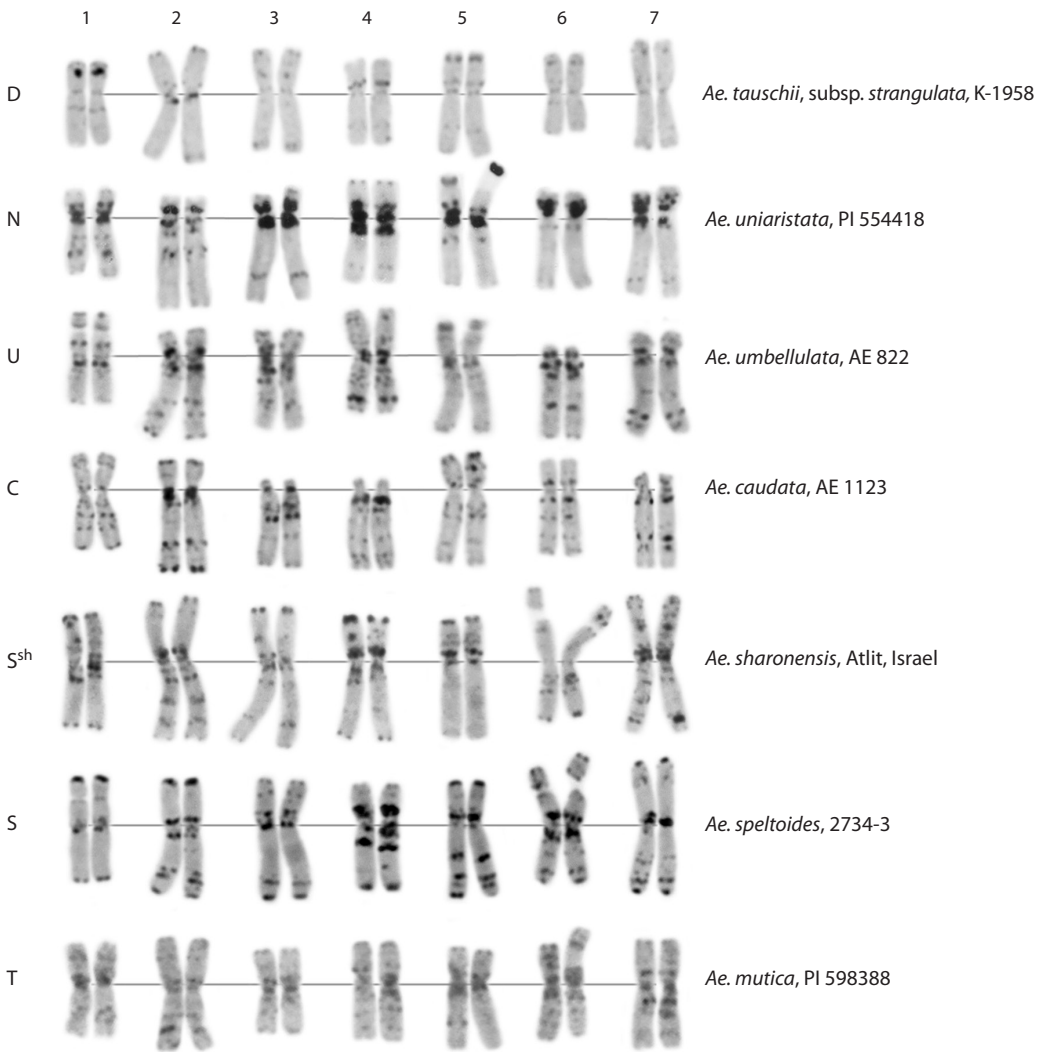


Fig. 3. C-banded karyotypes of diploid *Aegilops* species supposedly or actually involved in the development of genome-substituted wheat forms.

“Type specimens” of species not involved in the development of forms examined are shown for reference. The D–T genome symbols are indicated on the left; species names and origin/accession vouchers, on the right.

one 1S pair, and only two had an additional chromosome 1S, which replaced 1BL:1RS (monosomic 1S/1BL:1RS substitution, Fig. 2a).

The significant cytological instability of Avrodes also manifested itself in an abnormal meiotic chromosome pairing, in particular, high frequency of multivalents, formerly reported by R.O. Davoyan et al. (2012, 2019). This high frequency may be due to both the presence of genes suppressing *Ph1* (the gene regulating homoeologous chromosome pairing) in the S genome (Dvořák et al., 2006), and occurrence of intergenomic B/S or A/S substitutions in most plants, which have three or four copies of some *Ae. speltoides* chromosomes. The genomic instability of Avrodes may also be contributed by gametocidal genes, located on chromosomes 2S and 6S in *Ae. speltoides* (Tsujimoto, Tsunewaki, 1988; King J. et al., 2018; Said et al., 2024). It is worth noting that we found only one of the gametocidal chromosomes, 2S, whereas 6S had been lost.

Avrosis

Avrosis is a hexaploid in which the D genome is replaced by the S^{sh} genome from *Ae. sharonensis*. Eig. The presence of the A, B, and S^{sh} genomes was proven by cytogenetic analysis, including C-banding (Fig. 4). Like Avrodes, Avrosis bears the 1BL:1RS wheat–rye translocation. However, the C-banding patterns of 2A, 2B, 3B, and 5B chromosomes of these forms differed from each other. Unlike Avrodes, Avrosis is cytologically stable: all plants examined had identical chromosome composition and C-banding patterns.

Chromosome T1B:1R was the only exception. In some plants, the distal portion of the short arm was deleted. The chromosomes of the S^{sh} genome showed the morphology and heterochromatin distribution typical of *Ae. sharonensis* (Fig. 4). However, the direct parental accessions of Avrosis had not been indicated by originator, and we could not reveal chromosome changes associated with polyploidization.

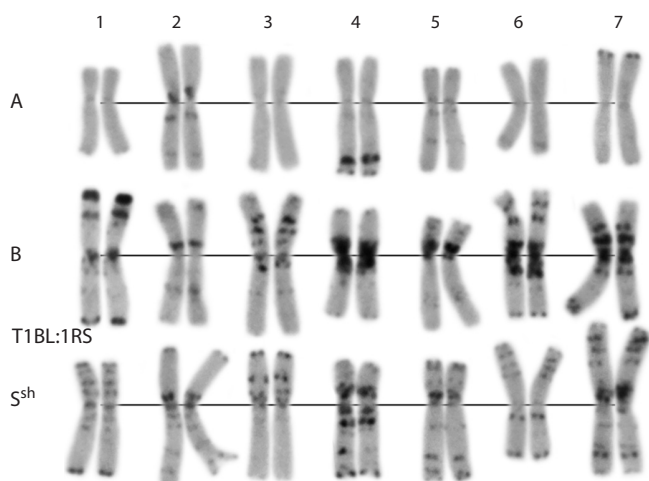


Fig. 4. Karyotype of the genome-substituted form Avrosis.

A, B, S^{sh} – genomes; 1–7 – homologous groups.

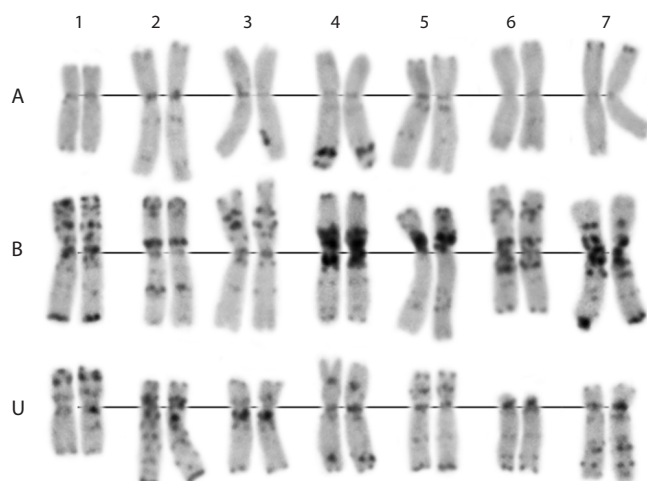


Fig. 5. Karyotype of the genome-substituted form Avrolata.

A, B, U – genomes; 1–7 – homologous groups.

In contrast to Avrodes, Avrosis was used in breeding programs solely as a donor of powdery mildew (*Blumeria graminis* (DC.) Speer f. sp. *tritici* Marshal) resistance (Zhirov, Ternovskaya, 1993), although *Ae. sharonensis* possesses many agronomically valuable traits (Olivera, Steffenson, 2009; Millet et al., 2014). The main difficulty in Avrosis use is that the S^{sh} genome hosts highly efficient gametocidal genes *Gc* (Tsumimoto, Tsunewaki, 1984, 1988; Said et al., 2024). They induce the lethality of gametes that have lost the 4S^{sh} chromosome, bearing this gene. As a result, the 4S^{sh} chromosome is preferentially transmitted to gametes (Miller et al., 1982; King I. et al., 1991).

Nevertheless, some scientists succeeded in obtaining wheat × *Ae. sharonensis* introgression lines for chromosomes of other homoeologous groups, in particular, 1S^{sh} and 5S^{sh} (Millet et al., 2014). Considering these results, we can hope that other S^{sh} chromosomes can be transmitted to the progeny and the genetic potential of Avrodes in common wheat breeding is far from being exhausted.

Avrolata

Avrolata is a hexaploid wheat in which the D genome is replaced by the U genome of *Ae. umbellulata*. It is cytologically stable, like Avrosis. All its plants had identical genome constitutions and banding patterns. We found no chromosome rearrangements in the accession studied. C-banding analysis confirmed the presence of the A, B, and U genomes in its karyotype (Fig. 5). In contrast to Avrodes and Avrosis, Avrolata did not bear the 1BL:1RS wheat–rye translocation; rather, it had the normal 1B chromosome.

The C-banding patterns of chromosomes belonging to the A and B genomes were generally similar to those of Avrosis, and the U chromosomes showed morphologies and banding patterns typical of *Ae. umbellulata* (Figs. 3, 5). As the parental *Ae. umbellulata* form was unknown, we could not assess putative changes of the U genome chromosomes of this hybrid.

The lack of 1BL:1RS in the karyotype of Avrolata may be due to the fact that cv. *Avrora* was *ab initio* heterogeneous for the presence of this translocation, and the direct parent of Avrolata belonged to the biotype lacking it. It is conceivable that durum wheat chromosome 1B survived recurrent crosses in the extraction of the *Avrora* tetra-component.

As reported in (Davoyan E.R. et al., 2012; Davoyan R.O. et al., 2012), Avrolata, along with Avrodes, is a source of novel genes for leaf rust (*Puccinia triticina* Rob. ex Desm. f. sp. *tritici* Eriks.) resistance. It is known that *Ae. umbellulata*, which was the source of the U genome in Avrolata, is extensively used in common wheat breeding, especially in the United States, as donor of the *Lr9* leaf rust resistance gene (Friebe et al., 1996b; McIntosh et al., 2013). Pedigree analysis shows that the ratio of varieties obtained with the use of *Ae. umbellulata* constantly increases and constitutes 25–29% in 2000s (Martynov et al., 2015). Although *Lr9* had been detected in Avrolata, it was not found in its progeny (Davoyan E.R. et al., 2012). Apparently, the resistance in the derived accessions was determined by a novel *Lr* gene or a couple of unidentified genes. Avrolata was also employed in the breeding of other crops. A molecular study demonstrated the transmission of chromosomes 1U and 2U to the progeny of Avrolata crosses with winter hexaploid triticale (Orlovskaya et al., 2015).

Avrotica

Avrotica is a genome-substituted form, whose parents were common wheat cv. *Avrora* and *Ae. mutica* Boiss. (syn. *Amblyopyrum muticum* (Boiss.) Eig, T genome). Cytogenetic analysis proved that Avrotica bears chromosomes of wheat A and B genomes and the T genome of *Ae. mutica*. However, in contrast to previously considered genome-substituted forms, Avrotica has a more complex combination of parental chromosomes.

Specifically, its karyotype maintained two chromosomes of the D genome, 1D and 3D, but lacked wheat 1A and

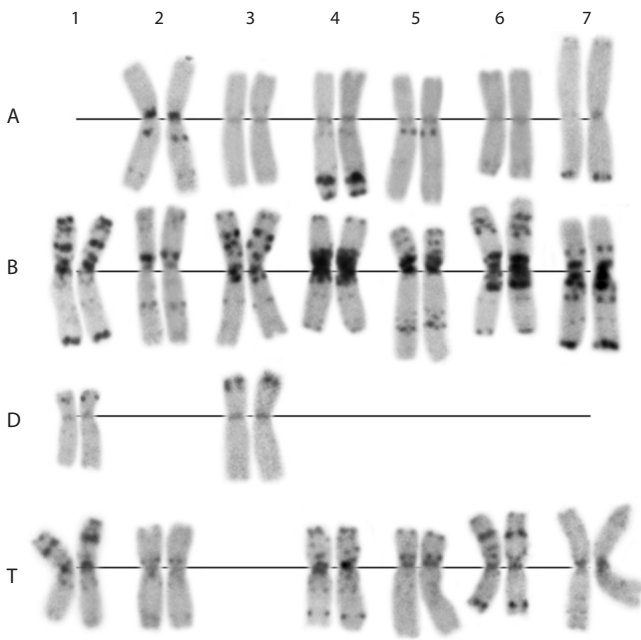


Fig. 6. Karyotype of the genome-substituted form Avrotica.
A, B, D, T – genomes; 1–7 – homoeologous groups.

Ae. mutica 3T (Fig. 6). Thus, the alien genome is represented by only six chromosome pairs. Like Avrolata, Avrotica did not possess the wheat–rye 1BL:1RS translocation, although the C-banding patterns of other chromosomes were similar to those of Avrodes. We could not compare T chromosomes with those of the parental *Ae. mutica* accession, because the originators had not indicated the source of the latter. It should be noted that the homologous T chromosomes of the amphydiploid showed identical banding patterns, whereas the diploid species is highly polymorphic; in particular, is characterized by heteromorphism of homologs (Friebe et al., 1996a).

Although Avrotica is found to be rust resistant (Davoyan R.O. et al., 2012, 2019), this trait has not been transferred to common wheat. A Chinese team (Liu et al., 2015) produced a powdery mildew resistant incomplete amphydiploid of cv. Chinese Spring with *Ae. mutica* and an addition line for chromosome 7T. The allopolyploid had the complete set of the T genome chromosomes but lacked the pair of wheat chromosome 7B.

Another team crossed common wheat cvs. Chinese Spring and Pavon 76 to *Ae. mutica* accession bearing genes – suppressors of the *Ph1* locus (King J. et al., 2017). The F_1 hybrids were twice or thrice backcrossed to the parental cultivar. The plants were scored for alien introgressions by SNP genotyping. Genotypes with single introgressions were used to produce di-haploid plants. This procedure yielded 67 homozygous and stably inheritable introgression lines involving six of the seven *Ae. mutica* chromosomes (King J. et al., 2019). The team failed to obtain introgression lines for chromosome 3T, which was absent from Avrotica as well.

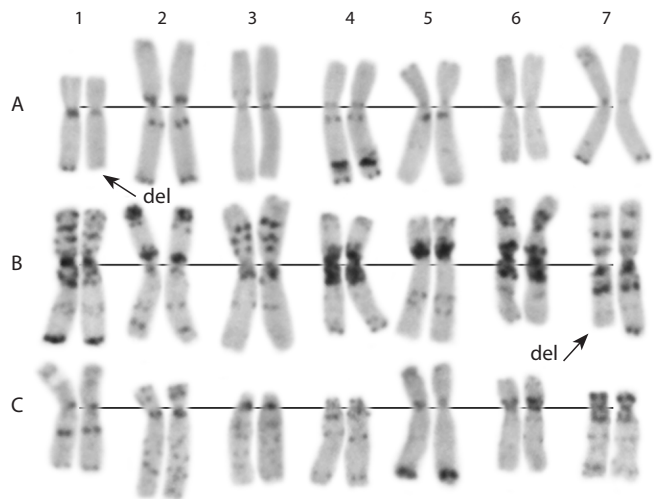


Fig. 7. Karyotype of the genome-substituted form Avrodata.
A, B, C – genomes; 1–7 – homoeologous groups. The arrow indicates a terminal deletion/translocation involving long arms of 1A and 7B chromosomes.

It is reasonable to conjecture that this chromosome bears genes adversely affecting the viability and/or fertility of the *T. aestivum* × *Ae. mutica* allopolyploid; for this reason, plants carrying 3T were abandoned by selection in early hybrid generations.

Avrodata

The pedigree of Avrodata indicates that it was obtained by crossing common wheat Avrora and *Ae. caudata* L. (syn. *Ae. markgrafii* (Greuter) Hammer). Cytological analysis confirmed the presence of the A and B wheat genomes and the C genome of *Ae. caudata* (Figs. 3, 7). All plants examined had identical chromosome sets, but chromosome rearrangements were detected in some of them (Fig. 7). They may have been induced in wheat–*Ae. caudata* crosses by gametocidal genes located on chromosome 3C (Endo, Tsunewaki, 1975).

The Avrodata lacks the 1BL:1RS wheat–rye translocation, and C-banding patterns of most chromosomes of the A and B wheat genomes (e. g., 2A, 4A, 5A, 6A, 1B, 2B, 5B, 6B, 7B) differed from the corresponding chromosomes of other genome-substituted forms obtained with cv. Avrora. In particular, the banding pattern of chromosome 7B was more similar to 7B of durum rather than common wheat. These observations suggest that Avrodata had been obtained from another parental wheat form or that the extraction of the tetra-component from Avrora resulted in the transmission of only part of A and B genome chromosomes of common wheat. The presence of unbalanced chromosome rearrangements in Avrodata plants shows that this genome-substituted form is cytologically unstable. No information on the use of this accession in breeding has been reported.

A genome-substituted amphydiploid of common wheat cv. Alcedo and *Ae. caudata* was synthesized in Germany

(Blüthner et al., 1988). The octoploid amphydiploid and addition lines developed on its basis were analyzed by C-banding, and meiotic chromosome pairing was also studied (Blüthner et al., 1988; Friebe et al., 1992). No deviations in C-banding patterns caused by chromosome rearrangements were detected, although numerous aberrations were noted in meiosis in all studied lines (Friebe et al., 1992). The banding pattern deviations observed in some wheat chromosomes were attributed to putative involvement of other wheat varieties in its origin.

The poor use of Avrotata in breeding may be due to the difficulty of the transmission of C genome material to common wheat associated with (1) a large number of species-specific chromosome rearrangements found in *Ae. caudata* (Danilova et al., 2017; Gong et al., 2017; Grewal et al., 2020) and (2) the presence of gametocidal genes on *Ae. caudata* chromosomes.

Avrotata

We found that Avrotata is a cytologically stable hexaploid form. Its karyotype contains the A and B wheat genomes but no chromosomes corresponding to the N genome of *Ae. uniaristata* Vis have been detected (Figs. 3, 8). The third Avrotata genome showed the greatest similarity to the D genome of diploid *Ae. tauschii* subsp. *strangulata* Eig. (Fig. 3), which differs from the wheat D genome in C-banding patterns of chromosomes 3D and 6D. Presumably, the third Avrotata genome, D^t, is a mix of chromosomes derived from diploid *Ae. tauschii* and the D genome of common wheat, but this assumption cannot be proven by C-banding, because orthologous chromosomes of these genomes are closely similar.

Ae. uniaristata is tolerant to aluminum, and British scientists synthesized a hybrid between Chinese Spring and *Ae. uniaristata* to transmit this trait to the common wheat genome. This hybrid was employed in the development of several addition lines (Miller et al., 1995). The scientists

showed that aluminum tolerance is controlled by chromosome 3N (Iqbal et al., 2000b). Analyses of the lines by *in situ* hybridization (Iqbal et al., 2000a) and later by C-banding (Badaeva et al., 2011) confirmed that they bear *Ae. uniaristata* chromosomes. These data allowed the cytological and genetic classifications of chromosomes of the N genome to be brought into compliance.

The mapping of RFLP markers on *Ae. uniaristata* chromosomes showed that they had been considerably rearranged with regard to homoeologous wheat chromosomes owing to the N genome-specific translocations and inversions (Iqbal et al., 2000b). The deep structural rearrangements of *Ae. uniaristata* chromosomes over the course of speciation were confirmed by the results of chromosome painting with oligo probe cocktail specific to each of the seven homoeologous groups of Triticeae (Li et al., 2020). It is reasonable to assume that the divergence of homoeologous wheat and *Ae. uniaristata* chromosomes impedes the transfer of genetic material between species, including the development of stable viable amphydiploids and genome-substituted forms. Unfortunately, no available data on the cytological verification of the genome constitution of Avrotata during early stages of its development have been reported. For this reason, we cannot decide whether the absence of the N genome from Avrotata was determined by the difficulty in the development of the form itself or the D genome replaced the N over the course of material propagation.

Wheat–*Aegilops* amphydiploids

Amphydiploid AD 7

AD 7 is a spontaneous amphydiploid of tetraploid wheat *T. ispahanicum* Heslot (genome BBAA) and tetraploid *Ae. cylindrica* Host (D^cD^cC^cC^c). The ancestral form of

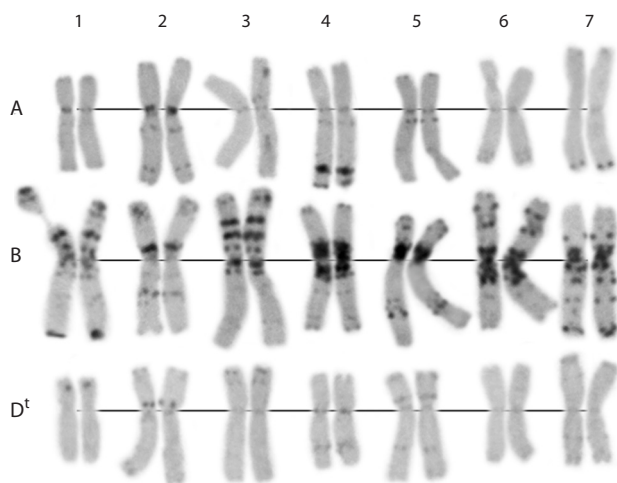


Fig. 8. Karyotype of the genome-substituted form Avrotata. A, B, D^t – genomes; 1–7 – homoeologous groups.

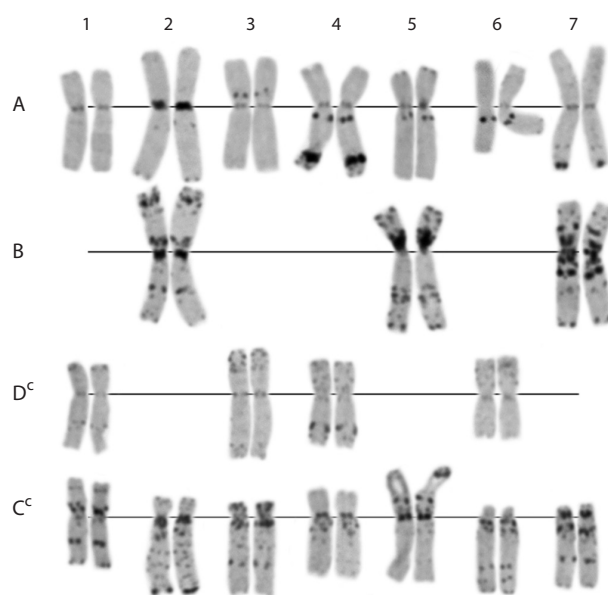


Fig. 9. Karyotype of the AD 7 amphydiploid. A, B, D^c, C^c – genomes; 1–7 – homoeologous groups.

AD 7 was an octoploid $2n = 8x = 56$ with the genome constitution $BBAAD^cD^cC^cC^c$ (Mustafaev, Piralov, 1981). C-banding analysis confirmed the origin of the accession from *Ae. cylindrica* but showed that chromosome number of amphydiploid was reduced to hexaploid level.

Complete set of the wheat A-genome and *Ae. cylindrica* C^c-genome chromosomes were preserved in AD 7. The third genome proved to be mixed. It combined chromosomes of the wheat B genome and *Ae. cylindrica* D^c genome, so that all the seven homologous groups were represented: $1D^c1D^c 2B2B 3D^c3D^c 4D^c4D^c 5B5B 6D^c6D^c 7B7B$ (Fig. 9). The chromosomes of the D^c genome showed banding patterns typical of *Ae. cylindrica* (Linc et al., 1999; Badaeva et al. 2002). Some plants were monosomic for chromosome 6A ($2n = 41$). No chromosome rearrangements were found in the plants studied.

Amphydiploid AD 7147

Amphydiploid AD 7147 was obtained by G.R. Piralov (1976) by crossing tetraploid wheat and *Ae. ventricosa* (Mustafaev, Piralov, 1981). The chromosome number doubled spontaneously; as supposed by G.R. Piralov, owing to the fusion of unreduced gametes. Regular chromosome pairing yielding 28 bivalents was observed in the meiosis of the original 56-chromosome amphydiploid. C-banding analysis of the AD 7147 confirmed that its origin from tetraploid wheat (genome BBAA) and *Ae. ventricosa* (genome D^vD^vN^vN^v) (Fig. 10). However, the C-banding patterns of the A and B genome chromosomes differed from those typical of durum wheat, being closer to *T. carthlicum* Nevski or the European variety of emmer *T. dicoccum* Schrank ex Schübl. (Badaeva et al., 2015b).

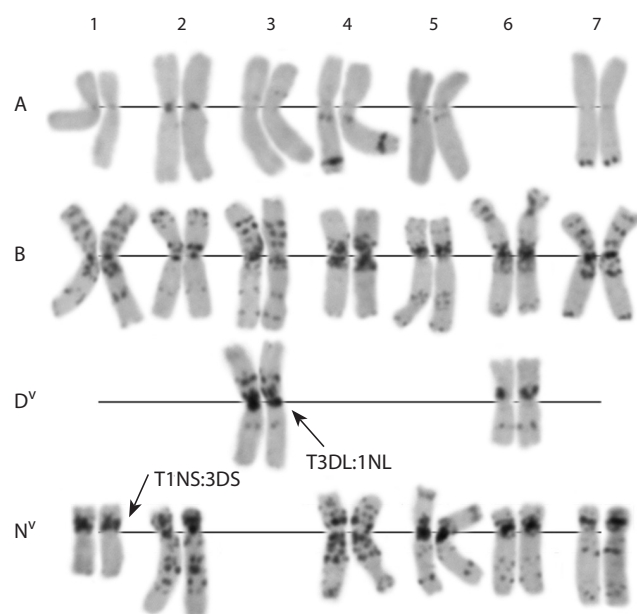


Fig. 10. Karyotype of the AD 7147 amphydiploid. A, B, D^v, N^v – genomes; 1–7 – homologous groups.

We found that AD 7147 bears a $1N^v:3D^v$ translocation, most likely, inherited from the parental *Aegilops* accession. This translocation is common in natural *Ae. ventricosa* populations (Badaeva et al., 2002, 2011). As in the previous amphydiploid, the chromosome number in AD 7147 was reduced to hexaploid level as a result of a loss of one “hybrid” genome. In this case, though, the wheat B genome remained intact, $3N^v$ was lost from the N^v genome, and 6A, from the wheat A genome. Thus, the chromosome number reduction in the hybrid involved mainly the D^v genome of *Ae. ventricosa*, of which only two chromosome pairs were preserved: $3D^v$ (in the form of two translocated chromosomes $T1N^v:3D^v$) and $6D^v$.

Ae. ventricosa is tetraploid species. Presently, it is extensively employed in wheat breeding as donor of pest resistance genes (Dosba, Doussinault, 1978; Garcia-Olmedo et al., 1984; Delibes et al., 1987, 1988). The gene cluster *Sr38/Lr37/Yr17*, inherited from *Ae. ventricosa* (Tanguy et al., 2005), had been mapped on chromosome 2A (Bariana, McIntosh, 1994). Pedigree analysis (Martynov et al. 2015) shows that this introgression is present in more than 34–37% of modern common wheat varieties, mostly of European origin. The introgression originates from the French VPM-1 breeding line, which was produced by Maia in 1967 by crossing common wheat cv. Marne and a synthetic amphydiploid *Ae. ventricosa* × *T. persicum* Vav. (syn. *T. carthlicum* Nevski) (Dosba et al., 1978). Apparently, the genome constitution of this amphydiploid is similar to that of the original AD 7147 accession, but we cannot test the modern constitution of the French hybrid. We have no information on the use of AD 7146 in wheat breeding either, but, by way of analogy with the French *Ae. ventricosa* × *T. persicum*, it could be a promising donor of agronomically important genes.

Amphydiploid AE 1491

Synthetic hexaploid amphydiploid AE 1491 was accidentally identified among *Aegilops* accessions from the gene bank of the Leibniz Institute of Plant Genetics and Crop Plant Research (Germany). Analysis of chromosome morphology and the C-banding patterns (Fig. 11) brought us to suggestion that it is a hybrid of tetraploid *Ae. ventricosa* (genome D^vD^vN^vN^v) and einkorn wheat, presumably, *T. boeoticum* Boiss. (genome A^bA^b) or *T. monococcum* L. (A^mA^m). AE 1491 carried a $1N^v:3D^v$ translocation, and it is conceivable that it was also present in the parental *Ae. ventricosa* accession.

No cases of aneuploidy, significant changes of C-banding patterns in comparison to the parental species (Badaeva et al., 2002, 2015a), or new variants of chromosome structural rearrangements were detected. An amphydiploid *T. aegilopoides* Link (syn. *T. boeoticum*) × *Ae. ventricosa* was produced and studied by (Siddiqui 2009; Siddiqui et al., 2009), but we do not know whether it corresponds to our accession.

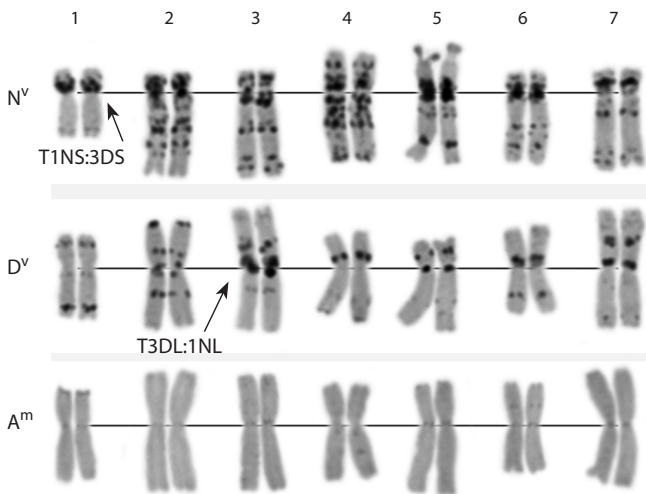


Fig. 11. Karyotype of the AE 1491 amphidyloid.
N^v, D^v, A^m – genomes; 1–7 – homologous groups.

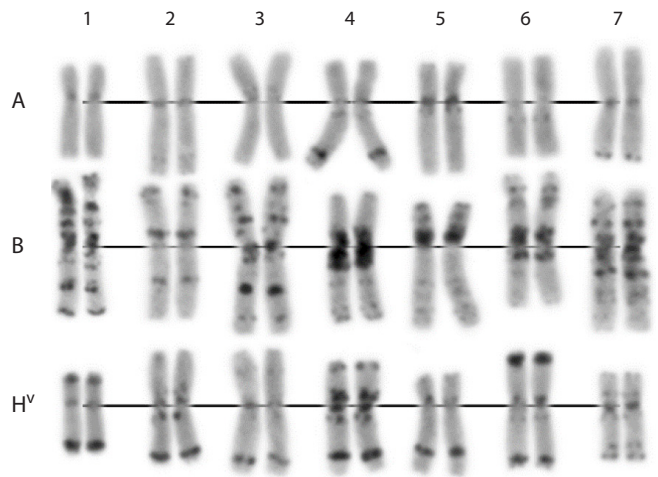


Fig. 12. Karyotype of *Haynaticum*.
A, B, H^v – genomes; 1–7 – homoeologous groups.

Wheat amphidyloids

Haynaticum Zhuk.

Amphidyloids of wheat and *Dasypyrum villosum* (syn. *Haynaldia villosa*) were successfully produced by scientists from different countries starting from the 19th–early 20th century. Crosses to various wheat species, mostly tetraploids (*T. dicoccoides* (Körn. ex Asch. & Graebn.) Schweinf., *T. dicoccum*, *T. turgidum* L., *T. aethiopicum* Jakubz., *T. durum* Desf., *T. araraticum* Jakubz., *T. timopheevii* (Zhuk.) Zhuk.) or, less often, hexaploids (spelt and common wheat) (Pace et al. 2011) were undertaken. Our *T. dicoccum* × *D. villosum* amphidyloid has been developed by P.M. Zhukovsky and named *Haynaticum* Zhuk. (syn. *Triticum* × *turgidovillosum* Tschermak) (Zhukovsky, 1944). It is maintained in the VIR gene bank under accession number K-38259.

The accession was shown to bear the entire sets of wheat A and B genome chromosomes and the H^v genome chromosomes of *D. villosum* (Fig. 12). The C-banding patterns of wheat chromosomes were similar to those of the Transcaucasian group of cultivated emmer (Badaeva et al. 2015). It is likely that the parental form of this allopolyploid was *T. dicoccum* accession from Armenia, Azerbaijan, or neighboring regions of Turkey or Iran. All *Haynaticum* plants examined were euploid ($2n = 6x = 42$). No chromosomal rearrangements were detected. This fact, along with the absence of notable C-banding changes, points to a high cytological stability of the accession, which was obtained nearly 85 years ago.

D. villosum is a good donor of genes for disease resistance. Its amphidyloids and substitution and addition lines derived therefrom are broadly used in wheat breeding in China (Huang et al., 2007; Zhang W. et al., 2013) and other countries. Our accession differs from them in the distribution of heterochromatin blocks on chromosomes of wheat

and *D. villosum* and therefore it is genetically different and may contain a different set of resistance genes.

Tritordeum martinii A. Pujadas

The amphidyloid of durum wheat and wild barley *H. chilense* was synthesized in the early 1980s as a bridge for transferring agronomically useful genes from barley to wheat (Martin, Sanchez-Mongelaguna, 1982). Its karyotype was examined in detail by C-banding (Cabrera et al., 1995) and FISH with various DNA probes (Prieto et al., 2004; Martín, Cabrera 2005).

Analyses of *Tritordeum* chromosomes by C-banding (Fig. 13a) and FISH with pAs1 (green) and pSc119.2 (red) (Fig. 13b) probes confirmed the presence of the A, B, and H^v genomes. Their C-banding and FISH patterns did not differ from those described in the literature. No aneuploidy or chromosome rearrangements were detected, which pointed to a good cytological stability of the accession.

Conclusion

This feature is of great importance for the preservation and propagation of the allopolyploid, which is presently considered to be a new promising man-made crop (De Caro et al. 2024).

The results of the study of genome-substituted and synthetic genome-added amphidyloids of wheat and species of the *Aegilops*, *Dasypyrum*, and *Hordeum* genera bring us to the conclusions that:

- The chromosome sets of allopolyploids having 42 chromosomes are more stable than those of octoploids; however,
- Hexaploid forms containing related genomes (B–S and Avrodes) can remain cytologically unstable over many generations. The cytological instability manifests itself in the heterogeneity of the chromosome sets of plants,

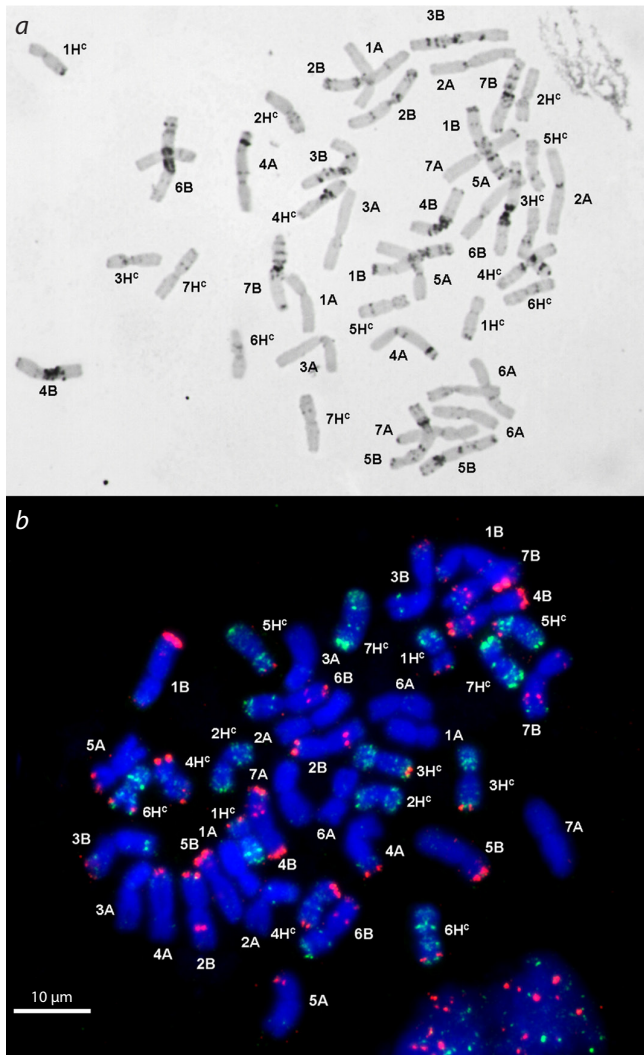


Fig. 13. C-banded metaphase plate (a) and the distribution of probes pAs1 (green) and pSc119.2 (red) on *Tritordeum* chromosomes (b). Chromosome designations: 1A–7A – wheat A genome; 1B–7B – wheat B genome; H^c – *H. chilense* genome.

monosomic or disomic substitutions of chromosomes belonging to related genomes, and more frequent chromosome rearrangements.

- The inconsistency of the chromosome sets in some genome-substituted forms indicates that the use of such materials in breeding and phylogenetic studies should be preceded by their thorough cytological verification.
- The most significant rearrangements of parental genomes were found in octoploids. They included chromosome number reduction to hexaploid level. The elimination involves chromosomes of different genomes (depending on the polyploid origin), covering all seven homoeologous groups.
- Although synthetic amphydiploids lag behind modern wheat cultivars in manifestation, their genes encoding mono- and polygenic characters may be more efficient than common wheat genes. The gene pool of synthetic

wheats may provide new genes for resistance to biotic (Goncharov et al., 2020) and abiotic (Mahmood et al., 2023) stress factors for improving cultivar of common wheat.

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