

Biological and economic characteristics of the allotetraploid with genomic formula DDA^uA^u from the cereal family

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The synthesis of new allopolyploid cereal genotypes is an important task aimed at involving new genetic resources in breeding programs. Diploid species of the genera *Triticum* and *Aegilops* – bread wheat relatives – are an important source of agronomically valuable traits. A tetraploid synthetic with genomic formula DDA^uA^u was obtained by N.A. Navruzbekov through crossing *Aegilops tauschii* Coss. and *Triticum urartu* Thum. ex Gandil. The purpose of this work was to study the chromosomal composition and biological and commercially important traits of the tetraploid. Cytogenetic analysis using fluorescent *in situ* hybridization showed the presence of all chromosomes of the D genome in the chromosomal complement of the synthetic. By means of stepwise vernalization, the winter habit was established for the tetraploid synthetic with the optimum vernalization requirement of 45 days. Under greenhouse conditions, two groups of genotypes were found whose flowering dates differed by 6.5 days, which may indicate an allelism at the *Vrn-3* locus. The coloring of various organs of the tetraploid plant, such as coleoptile, stem, anthers, and glumes of the spike, was revealed. The coloration of the aleurone layer of the grain may indicate that the donor species *T. urartu* is a carrier of the *Ba* gene that controls its blue color. A new morphotype of leaf pubescence was found. In terms of productivity, the tetraploid is comparable to bread wheat. Grains are characterized by a supersoft structure and high wet gluten content, from 39–45 to 65 %, in the field and greenhouse conditions, respectively. Thus, the tetraploid can be used to create new wheat genotypes as a source of untapped genetic diversity, as well as a new genetic model for studying the patterns of evolution of polyploid plants.

Key words: *Triticum urartu*; *Aegilops tauschii*; synthetic allotetraploid; growth habit; flavonoid pigmentation; leaf and spike morphology; yield components; technological properties of grain and flour.

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Биологические и хозяйственные характеристики аллотетраплоида из семейства злаковых с геномной формулой DDA^uA^u

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Синтез аллополиплоидных генотипов злаков – важная задача, нацеленная на вовлечение в селекционные программы новых генетических ресурсов. Диплоидные виды родов *Triticum* и *Aegilops*, сородичей мягкой пшеницы, – существенный источник агрономически ценных признаков. Тетраплоидный синтетик (геномная формула DDA^uA^u) был получен Н.А. Наврузбековым путем скрещивания видов *Aegilops tauschii* Coss. и *Triticum urartu* Thum. ex Gandil. Целью настоящей работы было изучение хромосомного состава, биологических и хозяйственно важных признаков тетраплоида. Цитогенетический анализ с использованием флуоресцентной гибридизации *in situ* показал присутствие всех хромосом генома D в составе генома синтетика. С помощью ступенчатой яровизации установлен озимый образ жизни растений тетраплоидного синтетика с оптимальной потребностью в яровизации в 45 дней. В условиях теплицы обнаружено две группы генотипов с разницей по дате цветения в 6.5 дней, что может указывать на аллелизм по локусу *Vrn-3*. Наличие антоциановой окраски coleoptile, стебля и пыльников предполагает регуляцию этого признака доминантными аллелями локусов *Rc-1*, *Pc-1* и *Pan-1*. Окраска алейронового слоя зерновки может свидетельствовать о том, что донорский вид *T. urartu* является носителем гена *Ba*, контролирующего голубую окраску. Был

также обнаружен новый морфотип опушения листа. По показателям продуктивности тетраплоид сопоставим с мягкой пшеницей. Зерно характеризуется супермягкой структурой, высоким содержанием сырой клейковины – от 39–45 до 65 % – в полевых и тепличных условиях соответственно. Таким образом, тетраплоид может быть использован при создании новых генотипов в селекции пшеницы как источник еще не освоенного генетического разнообразия, а также как новая генетическая модель для исследования закономерностей эволюции полиплоидных растений.

Ключевые слова: *Triticum urartu*; *Aegilops tauschii*; синтетический аллотетраплоид; образ жизни; флавоноидная пигментация; морфологические признаки листа и колоса; структура урожая; технологические свойства зерна и муки.

Introduction

The highland areas of the Caucasus are natural habitats of diploid species of the genera *Triticum* and *Aegilops*, which gave rise to cultural allopolyploid species of wheat. In the second half of the 20th century, many attempts were made to synthesize the new types of allopolyploids in order to engage in breeding and, subsequently, in economic activity, the new genetic resources from diploid species of the above mentioned genera. The tetraploid synthetic with a genomic formula DDA^uA^u was obtained by N.A. Navruzbekov (1982) by crossing *Aegilops tauschii* Coss and *T. urartu* Thum. ex Gandil. The character of meiosis was studied in amphidiploid and the karyotype was shown to do be stabile (Aminov, Navruzbekov, 1985). A similar hybrid with the participation of other initial samples of these species was named *T. erebuni* Gandil. (Gandilyan, 1984). These tetraploids, as well as the tetraploid species *T. palmovae* G. Ivanov (A^bA^bDD) carrying the genome A from the species *T. boeoticum* Boiss., are very limitedly involved in the researches of both applied and fundamental nature. Only the information about the use of two species as donors of fungal disease resistance genes in common wheat is available (Babayants et al., 2012; Davoyan et al., 2018). The biological characteristics of these tetraploid has not yet been conducted in more details. At the Dagestan experimental station of VIR allotetraploid of N.A. Navruzbekov with the genomic formula A^uA^uDD (AT Navruzbekov) is being maintained and successfully propagated. In this work, the chromosomal composition and biological and economically important traits were studied.

Material and methods

The tetraploid was obtained by a direct hybridization of diploid species *Ae. tauschii* and *T. urartu* Thum. ex Gandil. followed by colchicine treatment of the roots of F₁ hybrids (Navruzbekov, 1982).

Tetraploid plants were studied under natural conditions in the city of Derbent (Dagestan) at the experimental station of the VIR branch (St. Petersburg) and under the hydroponic greenhouse conditions of the Institute of Cytology and Genetics of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk). The field study was conducted in a dry subtropical climate of Dagestan, in the southern plane zone. The average annual temperature of the area is +1...–1.4 °C with an annual amount of precipitation of

400–500 mm, 80–90 % of which falls in the autumn-winter period. Summer is hot and dry. Productivity indicators were studied in 2018 on a random sample of 20 plants. Plants were analyzed individually; spike morphology and productivity were assessed on the main spikes. In the hydroponic greenhouse the plants were grown on artificial soil, expanded clay, with daily double top dressing with Knop solution and under 14-hour lighting; day/night temperatures are 18/20 °C before and 20/22 °C after tillering. To determine the growth habit, the plants were grown without vernalization and under 30, 45, and 60 days of vernalizing at +4 °C. The seedlings were sown in bathtubs filled with expanded clay, 7–10 plants in a row with a length of 1 m. The observations were carried out for to the following traits: the day number from seedlings to flowering, the presence of pigmentation and pubescence on the plant organs, spike shape and awnedness, productivity indicators, technological properties of grain and flour.

Fluorescent *in situ* hybridization (FISH) was performed according to a previously published procedure (Salina et al., 2006). For the identification of chromosomes, pSc119.2 and (Bedbrook et al., 1980) and pAs1 (Rayburn, Gill, 1986) probes labeled with the nick-translation reaction were used. The pubescence of the leaf surface was studied in microphotographs of the folds of boot leaves according to the procedure described previously (Genaev et al., 2012). Grain was studied for the nine technological indicators using the methods recommended for variety testing of agricultural crops in Russia (Methods of State Tests of Crops, 1988), with modifications for small portions of grain. Raw gluten content was determined manually from the whole meal using a micro-method based on the state standard of the Russian Federation (State Standard R 54478-2011..., 2012). The diameter of the flour particles (µm) was determined on a PSH-4 device. Physical properties of dough: tenacity (mm), extensibility (mm), the balance of dough and flour strength (u. a.) were determined on a Chopin alveograph with 50-g mixer. Gluten content was determined in grain grown in greenhouse and under field conditions, the other parameters – in grain of field origin grown in Dagestan.

Results

Chromosomal composition. The analysis of the metaphase chromosomes of a tetraploid sample by the FISH method was carried out with the pSc119.2 and pAs1 probes, which

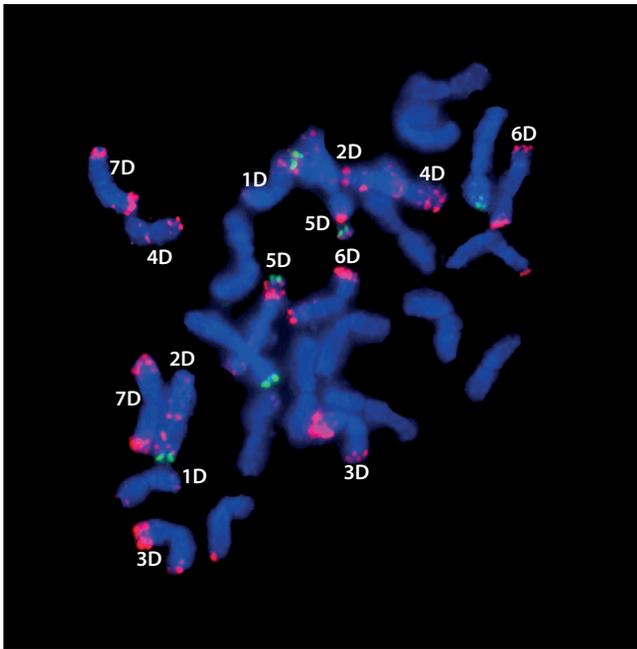


Fig. 1. Identification by fluorescent *in situ* hybridization (FISH) of the D-genome chromosomes of DDA^uA^u tetraploid. Red signal – pAs1 probe, marking D-genome; green – pSc119.2 probe.

are most often used to identify chromosomes in wheat and a number of other cereals including the donors of the B and D genomes of polyploid wheat – *Ae. speltoides* Tausch. and *Ae. tauschii* Coss. (Badaeva et al., 1996; Schneider et al., 2003). The pSc119.2 probe hybridizes mainly with the chromosomes of the B genome of polyploid wheat, and the pAs1 sites are localized mainly on the chromosomes of the D genome. In the result of the study the sample was found to be a tetraploid synthetic wheat ($2n = 28$, DDAA), carrying 14 chromosomes of the D genome in the karyotype (Fig. 1). The sites of hybridization with pAs1 were also found at the ends of the long arms of one of the A-genome chromosome pair, which does not contradict the results of (Badaeva et al., 2015). The presence of the separate pAs1 blocks on different chromosomes of diploid species wheat were showed. The pSc119.2 probe is localized on the short arms of chromosomes 2D and 5D, which corresponds to the previously obtained data for *Ae. tauschii* (Badaeva et al., 1996). The Fig. 1 also contains a pair of submetacentric chromosomes of genome A with pSc119.2 signals in subtelomeric regions of short arms. According to previous studies, pSc119.2 sites on the A chromosomes are few. In tetraploid and hexaploid wheats this tandem repeats can be localized at 5AS and 4AL chromosomes (Schneider et al., 2003; Kubaláková et al., 2005). In diploid wheat, pSc119.2 almost does not occur. However, E.D. Badaeva et al. (2015) reported on the localization of this probe on a long arm, presumably on 2A chromosome, in one of the samples of *T. boeoticum*. Consequently, it is quite possible that the sample of *T. urartu* that participated in the obtaining

of Navruzbekov's AT carries pSc119.2 sites on the short arms of one of the pairs of submetacentric chromosomes, of genome A possibly 5A.

Determination of growth habit. Growth habit and pace of development determine the adaptation of the genotype to environmental conditions through the timely formation of generative organs and successful seed reproduction. Under the conditions of Dagestan, tetraploid was sown in the fall. Due to the mildness of the climate it was not possible to determine the genetic status of vernalization genes. An experiment in the greenhouse showed that without vernalization and with 30-day vernalization, the plants do not pass to the generative phase. The most effective terms of vernalization were 45 and 60 days. This suggests that the sample carries the recessive alleles of the *Vrn-A1* and *Vrn-D1* genes. The winter growth habit was also noted in synthetic allotetraploid *T. palmovae* (DDA^bA^b) (Ivanov, 1984). The vernalized plants studied in the autumn and spring seasons under greenhouse conditions separated into two groups according to the flowering time. In the first group, the number of days was 40.5, while in the second group it was 46.8 days (the differences are significant at $p = 0.0014$). This may indicate that the sample carries different alleles of the *Vrn-3* locus in the chromosomes of the 7th homoeological group responsible for the “fine tuning” of the time of transition to flowering during the growing season, or other minor loci responsible for the timing of flowering *per se*.

Coloration of plant organs. Flavonoid pigments were synthesized at various stages of ontogenesis by various plant organs of the tetraploid synthetic. Their role in life processes is associated with adaptive responses to many abiotic and biotic stresses. The anthocyanin pigmentation was found on the coleoptile, stem and anthers (Fig. 2, a, b). These dominant traits in common wheat are controlled by *Ra*, *Pc-1* and *Pan-1* loci in the chromosomes of the 7th homoeological group (Khlestkina, 2012). Bright and stable color indicates a good expression of these genes in tetraploid. Among these genes, the genes of the 7D chromosome have the highest expression in bread wheat and are probably also determined by the D genome in the tetraploid. The ripened grain had a very rare blue color of the aleurone layer both in the field and in greenhouse conditions (see Fig. 2, c). Previously, the *Ba* gene that determines this trait was localized on chromosome 4A of the species *T. boeoticum* (Singh et al., 2007). No such genes were found in the D genome (Khlestkina, 2012). Thus, it can be assumed that the species *T. urartu*, which donated the genome to the synthetic tetraploid AT Navruzbekov, is the carrier of the dominant allele of this gene.

The tetraploid had colored spike glumes; the trait was well manifested in the field conditions but rather weakly in the greenhouse (see Fig. 2, d). This dominant trait in polyploid wheat is controlled by a series of homoeoallelic genes *Rg-1* in the chromosomes of the 1st homoeological group (Khlestkina et al., 2006). Among the diploid species,



Fig. 2. Flavonoid coloration of different organs in DDA^uA^u tetraploid.

Spike coloration: 1 – in green-house; 2 – the same in field conditions, Derbent; 3 – uncolored spike of hexaploid wheat. S29 – hexaploid cultivar Saratovskaya 29. Explanations in the text.

Average values and variability of yield components of A^uA^uDD tetraploid un field growing on Dagestan experimental station (Derbent town)

Statistical parameter	Plant height, cm	Spike length, cm	Number of spikelets in spike	Spike density	Number of grains in main spike	Grain weight in main spike	1000 grain weight	Grain plumpness, score
(X ± Sx)	128.5 ± 5.62	11.6 ± 0.17	18.5 ± 0.50	19.4 ± 0.50	31.5 ± 1.81	1.2 ± 0.05	38.1	4.1 ± 0.08
Max	139.5	13.5	21.0	22.4	39.0	1.5	42.1	5.0
Min	115.4	8.5	17.0	17.0	19.0	0.8	38.5	3.0

the occurrence of this trait has not been specifically studied. However, it is known that among the varieties of bread wheat the dominant allele is more common in elevated areas and in areas with a cold climate (Yakubtsiner, Savitsky, 1947). The allele of *Rg-D1* gene (chromosome 1D) which determines the gray-smoky (subsp. *cesium*) color of spikelet glumes is characterized of bread wheat. Earlier it was shown that *Ae. tauschii* species carries another than in bread wheat varieties allele of this gene, which gives a dark brown color (Pshenichnikova et al., 2005).

Morphobiological characteristics of the ear. Interestingly, that the studied genotype is close to a bread wheat in terms of the spike shape and density (see Table 1). It is well known that the A genome of the hexaploid precursor of bread wheat *T. spelta* carries the *Q* gene, which determines the speltoid form of the spike (Matsuoka, 2011). It can be assumed that the A^uA^u genome of the tetraploid under study carries an allele of this gene that does not affect the shape of the ear, and its relatively poor threshability is more closely linked to the *Tg* gene in chromosome 2D (McIntosh et al., 2013). The spike of Navruzbekov's AT is

awned which is generally characteristic of wild and poorly cultivated relatives of common wheat.

Leaf blade pubescence and the presence of wax in plants. The presence of pubescence on the leaf blades was a characteristic feature of the AT Navruzbekov. Its morphology differed from the pubescence in bread wheat (Fig. 3). It was long, tough to the touch and rather rare. The adaptive significance of this trait is associated with a protection from damage by leaf-eating insects, as well as with the influence on the energy balance and gas exchange of the leaf by changing the thickness of the air boundary layer adjacent to its surface (Schuepp, 1993). The pubescence protects the photosynthetic apparatus of the leaf from excessive solar radiation and is especially common in plants whose growing areas are steppes, deserts, high mountains and tundra (Johnson, 1975). To date, the genes of bread wheat have been identified in chromosomes 4B and 7B (McIntosh et al., 2013), as well as in chromosome 5A of the diploid and tetraploid species *T. monococcum* and *T. timopheevii* (Jing et al., 2007; Pshenichnikova et al., 2019). Such genes have not yet been found for the D genome. We assume that

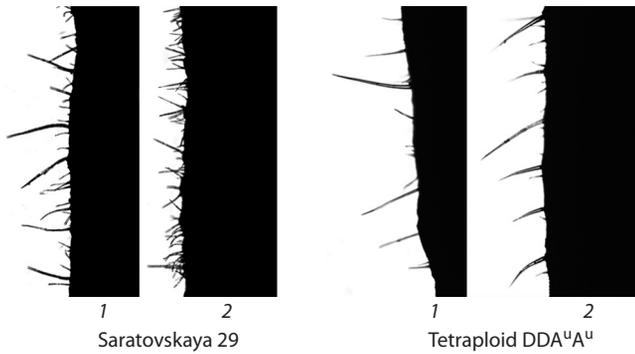


Fig. 3. Microphotograph of booting leaf folds of the hexaploid wheat Saratovskaya 29 (S29) and tetraploid DDA^uA^u .

Leaf surface: 1 – upper; 2 – bottom.

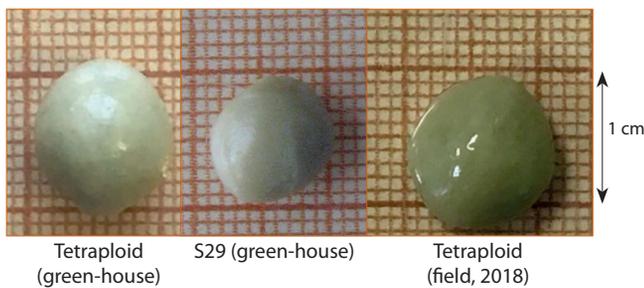


Fig. 4. Hand-washed gluten obtained from the whole meal of grain of DDA^uA^u tetraploid.

S29 – Saratovskaya 29.

the studied genotype is the carrier of a new gene from this genome. Earlier, we showed that among the samples of *Ae. tauschii* some carry the longest leaf pubescence; this expression level of the trait was inherited by the allopolyploid *T. palmovae*, which carries the D and A^b genomes (Pshenichnikova et al., 2017).

The plants of the sample studied were completely waxless. All einkorn wheats are the same (Tsunewaki, Ebona, 1999). No the inhibitor gene has been yet detected responsible for wax formation on einkorn wheat organs, however, the inhibitor gene is known on chromosome 2D (McIntosh et al., 2013).

Economically important traits. For plant height wheat the amphidiploid may be attributed to the intermediate forms, its average straw length is 128.5 cm (see Table). The straw is tough, but lodging resistance is low (3 points of the scale). The length of the ear varies from 8.5 to 13.5 cm. The spike and flower glumes are tough, with poor threshing. Ear density is average. The average weight of grains per spike is 1.2 g, the maximum number of grains per spike is 39. Visual evaluation of grain plumpness was 4,1 points out of 10 possible (see Table). This suggests a lack of uniformity of grain surface (see Fig. 2, c). However, the grain is quite large: thousand-grain weight of the main spike was 38.1 g under field conditions (see Table), and

during the technological analysis of grain yielded in 2017 and 2018 it consisted 33.7 g on average.

Technological properties of dough. Technological properties of grain are the most important breeding characteristics that determine the production purpose of the harvested crop. For the first time in this work, the technological properties of synthetic tetraploid were studied. One of the main technological indicators in the classification of grain according to the production classes in Russia is gluten content in grain. This parameter was studied both in greenhouse and field grain. It turned out to be very high (Fig. 4). In the first case, the content was 65 %. In field conditions this figure was: in 2017 – 39 %, in 2018 – 45 %. Thus, A^uA^uDD tetraploid can be a source of improvement of this trait in breeding. The genotype may be characterized as soft-grained as the diameter of flour particles was 8.7 microns with a total grain vitreousness of 50 %. Such flour can be described as supersoft. Possibly, the tetraploid is the carrier of the dominant alleles of the *Ha* loci in both 5A and 5D chromosomes which synthesize the complete proteins PinA and PinB, providing the soft endosperm structure. This is characteristic of diploid ancestral species of wheat *T. monococcum* and *Ae. tauschii* (Gautier et al., 2000). It should be noted that the tetraploid species with the genomic composition BBAA completely lost the dominant alleles of the genes *Pina-A1* and *Pina-D1* and the DDA^uA^u tetraploid under study is unique in this respect. With its help it is possible to transfer into the bread wheat the dominant allele of *Pina-A1* gene from 5A chromosome, lost in the process of polyploidization. The physical properties of flour (on alveograph) were characterized by relatively high elasticity but low extensibility. The ratio of these rheological parameters was 6.1, which brings the tetraploid closer to durum wheat with the genomic composition of BBAA.

Conclusion

Estimating the breeding value of AT Navruzbekov it can be concluded that due to the noted shortcomings (lodging, poor threshing, low productivity, etc.) its direct use in production is not advisable. At this stage, it is necessary to determine the possible ways of transferring the identified valuable traits to a genotype that is more adapted to industrial cultivation or to obtain a new improved form on the basis of the amphidiploid. At present, there is only one paper concerning crossability of this tetraploid with certain samples of wheat, *Aegilops* and rye (Navruzbekov, 1984). It indicates that the best seed setting and germination is observed under hybridization with a cultivated emmer (over 80 %). With bread wheat this parameters are slightly lower. Seed setting under crossing with rye and various samples of *Aegilops* up to 10 %. These studies indicate the possibility of carrying out the breeding works with this tetraploid. Newly developed allopolyploids are of considerable interest for basic research. They simulate the processes of evolution occurring through polyploidy that is resulted in a simul-

taneous restructuring of the interactions between many genetic networks that existed in separate genomes. These processes largely determine both the adaptive capabilities and the future of the new genotype. The combination of the genomes A and B in cereals was very successful for the formation of a cytogenetically stable tetraploid, which adapted to environmental conditions and later gave rise to a large spectrum of species with the genomic formula BBAA. Later, the addition of the D genome was also evolutionarily favorable and gave the hexaploid *T. aestivum*, which spread widely across the globe.

A comprehensive study of artificial allopolyploids obtained in previous years, including by means of new molecular genetic technologies, will make it possible to master new genetic resources for practical purposes and create new genetic models for studying the patterns of plant evolution through polyploidy. The results obtained in this work indicate the prospects for a deeper genetic and breeding study of the Navruzbekovs' allotetraploid.

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