Reviews, challenges

GENE RESOURCES OF PERENNIAL WILD CEREALS INVOLVED IN BREEDING TO IMPROVE WHEAT CROP
(review)

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A b s t r a c t

The reduction of wheat genetic diversity is an urgent problem in modern wheat breeding, which is primarily due to the limited number of varieties had been used in wheat pedigree. As a result of the depletion of the genetic pool of wheat, its resistance to phytopathogens has dropped, that generally reduces the stability of the agrophytocenosis. One of the ways to expand the genetic diversity of wheat is the transfer of genes of economically valuable traits from closely related genera and species, classified into three genetic pools: primary (varieties of hard and bread wheat), secondary (*Triticum* and *Aegilops* species), tertiary (most distant *Triticeae* species). The paper presents a review of success in gene transfer of economically valuable traits into the wheat genome from wheat's wild perennial relatives of the tertiary genetic pool: *Thinopyrum*, *Dasypyrum*, *Pseudoroegneria*, *Elymus*, and *Agropyron*. Representatives of these species have different levels of ploidy (di-, tetra, hexa- and even decaploids) and combine the genomes J (= E), St, W, Y, X, V, H, P, as well as their variants. Various levels of transfer of hereditary material into the wheat genome are considered, i.e. amphidiploids, addition and substitution lines, lines with translocations and small introgressions. Special attention is paid to amphidiploids, namely wheat-wheatgrass hybrids (PPG) combining the wheat genome and a whole or a part of the wheatgrass genome. The wheat-wheatgrass hybrids are considered both as an independent objects of cultivation and as a "breeding bridge", that is, an intermediate step in the transfer of genes from wheatgrass to wheat. The transfer of large chromatin fragments carrying the target gene is often associated with the additional transfer of undesirable genes which reduce the amount and impair the quality of the final wheat products. Therefore, introgressive lines of wheat are considered the most valuable forms, having a small chromatin insertion of an alien genome carrying a useful gene. Since the genomes of the tertiary genetic pool members are the most distant from the wheat genomes, an important problem considered in the review is the production of introgressions by recombination of homeologous chromosomes. The transfer of useful genes in wheat genome from its wild relatives is illustrated by examples, that consider the introgression of genes for resistance to fungal diseases (leaf and stem rust, powdery mildew, Fusarium blight, Septoria blight), viruses (yellow dwarfism streak mosaic), mite colonization, tolerance to drought, salinity and pre-harvest sprouting, storage proteins (glutenins) and perennial lifestyle of the plant. It is noted that wild relatives can serve as donors not only of genes responsible for resistance to stress factors, but also increase yields by increasing fertility, the number of spikelets and other elements of the yield structure, as well as improving the quality of the final product due to new variants of storage proteins. Special attention is paid to the development and use of molecular and molecular cytogenic markers which allow breeders to transfer target genes or regions of chromatin, as well as to monitor their introgression into the wheat genome in segregating populations. At the same time, in practical selection, different types of markers can be successfully used, i.e. those designed for the whole chromosome or its shoulder, linked to the chromatin region carrying the target gene, as well as the marker developed directly to the nucleotide sequence of the gene itself. Whole genome sequencing and genome editing technologies is noted to play in future a significant role in introduction of genetic material of wild relatives into wheat to improve its breeding programs.

Hexaploid wheat as a species arose after the second allopolyploidization nearly 8-10 thousand years ago. Its domestication occurred in the Fertile Crescent area, in the territory of modern south-eastern Turkey. Then, wheat followed the ways of human migration both to the West, Europe, and the East, Asia and finally to America and Australia. As a result, local varieties adapted to local conditions of cultivation appeared [1]. Traditional wheat varieties (landraces) have always been characterized by genetic inhomogeneity and heterogeneity. Due to it, variety populations have higher ecological sustainability and plasticity and are receptive to fluctuations in weather and climatic conditions [2]. Such variety populations of homozygous lines often change the population structure over time but provide resistance to biotic and abiotic stresses [3]. Since the 1970s, i.e., with the beginning of the active stage of the Green Revolution, and to the present time the active substitution of local varieties with commercial genetically homogeneous varieties suitable for high-intensity agricultural technologies has happened, resulting in the loss of biological diversity and a decrease in allelic variation [4]. The term "genetic erosion" [5, 6] was proposed in the early 1970s to describe the effects of these human activities, which reduce the genetic diversity of species until they are lost. Later, this term was adapted in the Russian scientific community both in the literal translation [7-11] and in the formulation "gene pool erosion" [12-15].

A reduction in genetic diversity is a global problem for most plants under cultivation, but in relation to wheat as the world most consumed crop (the area planted as of 2017 is 218 million hectares, the harvest is 772 million tons, 15% of all calories consumed by the world population), these processes are most wide-spread — 65-84% relative to the wild ancestral forms [16, 17]. The depletion of genetic diversity is primarily due to the widespread occurrence of similar varieties with overlapping pedigrees, the selection of which led to yield mainly. The situation is aggravated by the global climate change, urbanization, plowing of new lands, fires, and military actions; these factors lead to the loss of local varieties, as well as the reduction of the natural area of wild relatives of wheat, which could also be used to increase its genetic diversity [18]. As a consequence, more aggressive races of pathogens appear, epiphytoty outbreaks are recorded, the resilience of agroecosystems reduces, the dependence of agriculture on chemicals is growing [19].

In Russia, the analysis of gliadin-coding loci in wheat showed the beginning of genetic erosion in the Krasnodar Territory, Rostov Region and Nonblack Soil Zone and the prevalence of alleles of the Bezostaya 1 and Mironovskaya 808 varieties [20]. The comparison of the genealogical profiles of varieties in spring soft wheat in the Lower Volga Region revealed the degree of similarity higher than among the half-sibs, and in winter wheat in the Central and Volga-Vyatka Regions — at the level of full and half-sibs [21].

It is important to note that in recent years, the positive trend of the increase in the biodiversity of wheat varieties has been observed. Orabi et al. [22] found that the greatest decrease in genetic diversity among European wheat varieties occurred in the 1960s and 1980s; Martynov et al. [21] note that if in the 1970s, the pedigrees of the varieties included one or two landraces, the modern ones include 9-10 of them. However, the character of apparent diversity has changed. Modern breeding has resulted in an unbalanced predominance of wheat germ plasmas from southeastern, southern Europe and the Mediterranean, while genetic resources from East Europe and Asia are least used [1]. Over the past 70 years, the genetic diversity of Russian varieties has increased, however,

due to foreign breeding material. This process is accompanied by the loss of the original Russian material (soft wheat from 35 up to 50%, hard wheat up to 20%) and its substitution with the genetic resources from Europe, the United States and CIMMYT [21].

The main sources of increasing the genetic diversity of wheat are represented by three pools: primary (represented by local and traditional varieties and variety populations − landraces); secondary (other *Triticum* species) and tertiary (other genera — *Secale*, *Aegilops*, *Thinopyrum*, etc.). In the 1970s, a group of varieties with the genetic diversity differing from that of traditional and local varieties appeared, which is associated with the introgressions of foreign genetic material in the genome of wheat from its relatives, primarily rye, with distant hybridization [1]. Nowadays, alleles from 50 species representing 13 genera are known to be transferred to the wheat genome [23]. Among the donors of genes of economically valuable traits in the tertiary genetic pool, a special place is occupied by perennial cereals, in particular, such well-known and well-reputed species as intermediate wheatgrass and pontic wheatgrass [1].

According to modern classification, in perennial wild relatives of wheat, the chromosomal set is formed by a different combination of several genomes in polyploid species. The P genome is represented in di-, tetra-, and hexaploid (including segmental) *Agropyron cristatum* and other wheatgrass forms [24]. An important role is played by the *Pseudoroegneria* species with the St genome, which served, apparently, as the female parent in the polyploid *Thinopyrum* and *Elymus* species [25, 26] and thus represent one of the central genomes in perennial cereal species [27-29]. The members of the *Thinopyrum* genus carry the E gene, also denoted J; the range of ploidy of this genus vary from the diploids *Th. bessarabicum* (J^b) and *Th. elongatum* (J^e) up to the hexaploid forms of *Th. intermedium* ($J^rJ^{vs}St$) and decaploid *Th. ponticum* ($JJJJ^sJ^s$). The matter of the genomic composition of intermediate wheatgrass and pontic wheatgrass is still open and is studied by many researchers with the use of molecular cytogenetic approaches [29-31]. The listed *Thinopyrum* species are widely used in the breeding improvement of soft wheat as donors of economically valuable traits. The gene V is represented in only two species − in annual cereal *Dasypyrum villosum* ($2n = 14$, VV) and perennial cereal *D. breviaristatum*; the latter has both diploid and tetraploid forms. Whether the tetraploid form of *D. breviaristatum* is allo- or autotetraploid VVV^bV^b remains a subject to discuss [32, 33].

As a result of crossing wheat and perennial cereals, the following types of breeding material can be obtained: amphiploids, the hereditary material of which includes the complete genome of wheat and full (in the case of a diploid species) or partial (of a polyploid species) genome of a wild cereal; augmented lines (they have the complete genome of wheat combined with a pair of augmented chromosomes of wild cereal); substituted lines (their chromosome set is formed by the complete genome of wheat, with the exception of one pair of chromosomes, substituted on the chromosome of wild cereal); translocated lines (lines of wheat, one or more chromosomes of which carry translocations); introgressive lines (one or a few chromosomes carry introgressions − small inserts of chromatin of wild cereal in the wheat chromosomes).

A big problem in the transfer of useful genes in the genome of wheat is the so-called "genetic garbage": in the chromatin area of a wild relative embedded in the chromosome of wheat, in addition to the target gene, genes that degrade the final product quality may be situated. Unnecessary chromatin fragments are removed by chromosomal engineering with the use of spontaneous translocations, radiation exposure, tissue culture, and stimulated recombination. Spontaneous translocations, as a rule, centric ones (Robertsonian, occurring as a

result of disruption and fusion of chromosomes on the centromere), as well as exposure to radiation, lead to the formation of non-centric translocations. Stimulated translocations result from the removal from the wheat genome of the *Ph* gene on the chromosome 5BL, which prohibits homo- and homeologous conjugation: it is possible to use nullisomics at 5B or mutants *ph1b* of soft and *ph1c* of hard wheat, which have a deletion of the *Ph*-locus and allele Ph^1 *Aegilops speltoides*. The task of the breeder is to select plants with the target gene among the plants in which the dose of the rest of the chromatin was reduced; in the case of *ph*-mutants, it is necessary to restore the *Ph* allele in wheat after reducing the dose of introgression [34]. If the trait is supported by the group of genes located in different loci of the same chromosome or distributed between chromosomes, it is a hard task to pass it to wheat through separate introgressions; in this case, amphidiploids and augmented (or substituted) forms would show more severe manifestation of the symptom compared to the introgressive forms [35].

Work with wild relatives begins with the exact identification of the species belonging of the sample at the molecular-cytogenetic and molecular levels [36, 37]. An important role is played by the study of genes and allelic diversity in the genomes of wild relatives. This makes it possible to find candidate genes for economically valuable traits, assess the genetic diversity of populations, and develop molecular markers of those genes that can be transferred to the genome of soft and hard wheat [38-42]. Identification of molecular and cytogenetic markers specific to individual chromosomes or their sites plays a significant role, as introgressive forms are often selected not for a specific gene, but for a chromatin site associated (linked) with the target gene [43, 44].

Tall wheatgrass *Th. elongatum* (Host) D.R. Dewey is presented by diploid ($E = J^e$, $2n = 2\times = 14$) and tetraploid (E_1E_2, $2n = 4\times = 28$) forms. Augmented and substituted forms of soft wheat at the chromosome 7E and hard wheat at the chromosome 1E, resistant to Fusarium head blight, were created [45-48]. Disomically substituted lines of soft wheat 1E(1A), 1E(1D) and 6E(6D) showed resistance to Septoria blight, the lines 1E(1B), 2E(2B), 2E(2D) and 3E(3B) − to the yellow dwarf virus of cereals [49]. The salinization resistance genes at the chromosome 3E responsible for removing sodium ions from the cell were introgressed to the distal section of the soft wheat chromosome 3A by stimulated homological recombination [50]. The soft wheat line augmented with the chromosome 4E showed the best capacity for regrowth after harvesting in comparison with other augmented lines [51]. Li et al. [52] obtained substituted, augmented, and translocated lines, most of which showed resistance to wheat striped rust, on the basis of partial amphidiploid Trititrigia 8801 ($2n = 6\times = 42$, ABE), created with the participation of a tetraploid form of *Th. elongatum*.

Bessarabian wheatgrass *Th. bessarabicum* (Savul. & Rayss) Á. Löve (J^b, $2n = 2\times = 14$) is used to improve the resistance of soft wheat to adverse environmental factors. Bessarabian wheatgrass is also interesting as a source of the genes of resistance to salinization and eelworm *Meloidogyne chitwoodi* [53]. With the help of stimulated homologous recombination in the absence of the *Ph1* gene, translocated salt-tolerant forms with translocation of T5AS.5JL were obtained [54]. Low-molecular-weight glutenins have a certain value, which can affect the baking quality of soft wheat grains [55, 56]. In addition, a series of translocated forms of soft wheat with *Th. bessarabicum* chromosome segments was obtained [57, 58]. Grewal et al. [59] developed 1150 molecular SNP (single nucleotide polymorphism) markers for all seven chromosomes of Bessarabian wheatgrass, which can be used in marker-assisted selection (MAS) on the basis of series of recombinant wheat lines [59].

Virgate wheatgrass *Th. junceum* (L.) Á. Löve is a hexaploid ($2n = 6\times = 42$)

with the alleged genomic constitution $E^bE^bE^e$ (or JJE). On the basis of the partial octoploid amphidiploid, a series of wheat lines augmented by *Th. junceum* chromosomes was created [24]. The line AJDAj3 with the augmented chromosome of *Th. junceum* of the second homeologous group showed resistance to Fusarium head blight [60]; based on the salt-resistant line AJDAj5, augmented by the first homeologous group of *Th. junceum*, with the *Ph^1* gene from *Aegilops speltoides*, the recombinant lines of wheat that retained resistance to salinization were created [61]. The relative of virgate wheatgrass, wiry wheatgrass *Th. junceiforme* (Á. Löve & D. Löve) Á. Löve is a tetraploid ($2n = 4\times = 28$), combining the genomes J_1J_2 (J_1 is close to *Th. elongatum* or *Th. bessarabicum*) or JE (E^bE^e) [24, 62]. Based on it with the use of *T. turgidum* subsp. *dicoccon* (BA), a complete amphidiploid resistant to abiotic (drought, flooding) and biotic (Fusarium head blight and striped mosaic virus) stress factors was created [62].

Intermediate wheatgrass *Th. intermedium* (Host) Barkworth & D. R. Dewey [syn. *A. intermedium* (Host) Beauvoir, *Elytrigia intermedia* (Host) Nevski] ($2n = 6\times = 42$) is a wild cereal widely used in the breeding of soft wheat (due to the high combining ability with it) as a unique donor of resistance to biotic and abiotic stressors [63]. Various breeding lines of intermediate wheatgrass are tested for baking quality of the grain; its cultivation and selection is carried out [64-66]. Many wheat-wheatgrass hybrids (WWHs) with high protein content, resistant to yellow dwarf virus and wheat streak mosaic, powdery mildew, yellow leaf, and stem rust [67-70] have been created. In addition to wheat chromosomes, each WWH has its own unique set of wheatgrass chromosomes associated with certain economically valuable traits [71, 72]. WWH forms created by Tsitsin and his students have good baking qualities of grain, resistance to leaf rust, drought and salinization, germination at the root, are capable of regrowth and long-term lifestyle, are characterized by great biological diversity [73-77]. Many traits were subsequently successfully transferred to the genome of wheat directly from wheatgrass or by octaploid amphidiploids to disomically augmented, replaced and translocated lines of soft wheat having resistance to diseases and new protein subunits [78-80]. It is important to note that even disomically substituted forms may eventually become commercially successful varieties; an example of this are the varieties Tulaikovskaya and Belyanka and their derivatives in which resistance to brown rust is provided by the replacement of the chromosome 6D with the chromosome of intermediate wheatgrass 6J of different origin [81, 82]. It is shown that genes of economically useful traits are localized at different chromosomes of wheatgrass, which can be successfully introgressed into the genome of soft wheat through the exchange of sites between chromosomes [83]. Gene transfer from intermediate wheatgrass most often occurs in stages. For example, the resistance gene *Wsm3* was identified on the long arm of the wheatgrass chromosome 7SL in the disomically augmented line of soft wheat DtA7S#3 [84], on the basis of which a Robertsonian translocation in the wheat chromosome T7BS.7S#3L was obtained [85]; using *ph1b*-stimulated recombination, the line of T7BS 7BL-7S#3L with a smaller dose of wheatgrass chromatin that retained the gene *Wsm3* has been created [86]. Similarly, a translocation of the *Bdv2* gene was obtained: on the basis of amphidiploid TAF36, the augmented line with the wheatgrass chromosome 7S, resistant to the yellow dwarf virus of barley was created; by means of *ph*-mutation and tissue culture, a series of translocated lines carrying the target gene at a lower dose of the rest wheatgrass chromatin was obtained [87]. On the basis of the octoploid wheat-wheatgrass amphidiploid Zhong 5, the line Z4 with two non-Robertsonian translocations T3DS-3AS.3AL-7J^{s}S and T3AL-

7J^{s}S.7J^{s}L, among which the second carries the gene for resistance to yellow rust, was obtained [88]. By now, the genes of resistance to fungal rust diseases *Lr38*, *Sr44*, *Yr50*, *YrL693* [78, 84, 89], powdery mildew *Pm40* [90], *Pm43* [91], Fusarium wilt [92], viral diseases *Wsm1*, *Wsm3*, *Bdv2*, *Bdv3*, *Bdv4* [86, 93-96], and cornel aphid [97] were transferred from intermediate wheatgrass in different chromosomes in the form of small introgressions. Most often, resistance genes from the intermediate wheatgrass subgenomes J^r and J^{vs} are introgressed in chromosomes of the D-subgenome of wheat, more rarely in the subgenome A and very rarely in the subgenome B, which is probably due to the high degree of homology between the wheatgrass subgenomes J^r and J^{vs}, on the one hand, and the subgenome of wheat B — on the other hand [91].

Pontic wheatgrass *Th. ponticum* (Podp.) Z.-W. Liu & R.-C. Wang (JJJJ^{s}J^s or E^{e}E^{b}E^{x}StSt, $2n = 10\times = 70$) has a set of valuable characteristics, high resistance to fungal and bacterial diseases, high productivity, a powerful fibrous root system, strong development, etc., making this wheatgrass species very promising for crossing with wheat [67]. Pontic wheatgrass relatively easily crosses with soft wheat, which formed the basis for the creation of a series of WWHs, the genome of which combines chromosomes of both intermediate wheatgrass and pontic wheatgrass [71, 74]. WWHs can grow after harvesting and after wintering, are resistant to fungal and viral diseases and can be grown in the future as an independent culture [98, 99]. The genetic material of pontic wheatgrass is often involved in obtaining introgressive lines of wheat through "breeding bridges" in the form of WWHs, augmented and replaced lines. An example of the transfer of the leaf rust resistance gene *Lr19* from the pontic wheatgrass chromosome 7E to the soft wheat chromosome 7D can be called a classic one. The first step was to create the augmented line 7el1(7D) Agrus; then through γ-radiation, the line T4 (Agatha) with translocation of wheatgrass chromatin in the wheat chromosome 7D was obtained. Due to γ-irradiation and *ph1c*-stimulated homologous recombination, a series of lines with different doses of wheatgrass chromatin on the chromosomes 7D and 7B of soft wheat and 7B of hard wheat was created and it was found that this translocation, in addition to *Lr19*, carries the genes of resistance to striped rust *Sr25*, genes of the yellow pigment in the endosperm *Yp* (one of the possible candidates is the gene *Psy1*), as well as *Sd1* and *Sd2*, aggravating fertility and leading to a shift in the decomposition for translocation [100]. In addition to 7el1, a fragment of chromatin 7el2L carrying genes of resistance to fusariosis, which allows staking different resistance genes of pontic wheatgrass, was transferred in wheat [101-103]. During the introgression of the gene *Lr24*, in a similar manner, first a substituted line 3J^s(3D) TAP 67 was obtained, and on its basis — a translocation at the chromosome 3D; then a chromatin fragment, in addition to the gene *Lr24*, also carried *Sr24* [104]. The effective gene *Sr26* (determines resistance including stem rust race Ug99), was transferred under the scheme of partial amphidiploid ($2n = 56$)—the substituted line 6Ag(6A)—translocation 6AgL-6AL; since this translocation reduced the yield by 15%, its dose was reduced from 90% to 30%, which allowed increasing the yield [105]; at the chromosome 6Ag, also a new resistance gene *SrB* was identified [106]. Pontic wheatgrass genes for resistance to leaf and stem rust *Lr19*, *Lr24*, *Lr29, Sr24, Sr25, Sr26, Sr43* [84, 107-110], colonization by the mite *Eriophyes tulipae Cmc2* [84], an unknown dominant gene for short stem [111], the gene of yellow pigment in the endosperm [112] and anthocyanin staining of the aleurone layer [113] were transferred to wheat chromosomes. Similarly to intermediate wheatgrass, in pontic wheatgrass, a large part of the chromatin introgressions with valuable genes occurs to the chromosomes of the subgenome D of soft wheat, which may be due to its proximity to the subgenomes of pontic wheat-

grass [111].

In breeding practice, the genus *Pseudoroegneria* is used as a donor of salt resistance and drought resistance. Hybrids between *P. spicata* (Pursh) Á. Löve (St, $2n = 2\times = 14$) and different types of wild ruttishness and *Secale montanum* were obtained [114]; new subunits of low-molecular-weight glutenins were identified [115]. The development of molecular markers of chromosomes in the species *Pseudoroegneria* is important, as the St-genome is represented in many polyploid species of perennial wild relatives of wheat, including species important in terms of breeding, such as intermediate wheatgrass, pontic wheatgrass, and in wild ruttishness species [24].

Perennial cereal *D. breviaristatum* (Lindb. F.) Frederiksen ($2n = 4\times = 28$, V^bV^b or VV^b) is represented by the diploid (Vb, $2n = 2\times = 14$) and tetraploid (V^bV^b or VV^b, $2n = 2\times = 42$) forms. On the basis of amphiploids obtained by hybridization of wheat and *D. breviaristatum*, the augmented lines carrying genes of resistance to striped, stem rust, powdery mildew were created [116, 117]. With the help of molecular markers, substitution of $2V^b$(2D) was revealed in lines of soft wheat resistant to stripe rust [118], on the basis of which the introgressive stable form with longer spikes was received [119]. The introgressions of the segments of the $1V^b$ chromosome allowed creating forms of wheat with new high molecular glutenins [119, 120].

The closest relative of *D. breviaristatum* [syn. *Haynaldia villosa*] is annual *Dasypyrum villosum* (L.) Borbás (V, $2n = 2\times = 14$), widely used as a donor of resistance to viral diseases in the augmented and substituted translocated lines [121, 122]. A major role in the involvement of genetic material of *Dasypyrum* in the breeding of soft wheat is played by molecular markers of not genes, but chromosomes and their arms, which allows marking and mapping the segments on the chromosome associated with certain symptoms [43, 44]. Due to the transfer of *D. villosum* chromatin in the genome of wheat, it was found that the chromosome 1V carries the genes of resistance to kernel smut and eyespot, as well as genes that improve grain quality [123-125]; at 2V, the genes that increase yield and genes of resistance to powdery mildew *Pm62* and eyespot [125-127] were discovered; at 3V, the genes of resistance to take-all disease (pathogen *Gaeumannomyces graminis*) and eyespot and striped rust [125, 128, 129] were identified; at 4V, the genes of resistance to eyespot *Pch3*, the virus of spindle streak mosaic of wheat *Wss1* [130-132] were localized; at the chromosome 5V, the genes of resistance to powdery mildew *Pm55* [133] were localized; the 6V chromosome carries the genes of resistance to powdery mildew [134], leaf rust *Lr6V#4* [124], striped rust *SrHv6* [135] and bent-grass leaf-gall eelworm *CreV* [136].

The members of the genus *Agropyron* originally grew in the steppes of European Russia and south-east Siberia and may have been cultivated in the Volga Region to the east of Saratov. This genus is represented by 10 to 15 species, among which *A. cristatum* and *A. fragile* are introduced and grown in North America, and five species grow in China. The most characteristic representative of this genus is the tetraploid form of *A. cristatum*, growing in Central Europe and Central Asia, in Central Asia and Siberia, China and Mongolia, along with rarer diploid forms; hexaploids are found in Turkey, Iran, and Kazakhstan [24]. Based on augmented and substituted lines, applying gametocidal chromosomes, radiation exposure, and other methods, breeders transferred into chromosomes of wheat individual segments that carry genes for resistance to powdery mildew and leaf rust (chromosome 2P) [137, 138]; genes that increase productive tillering capacity and the number of grains per spike, and genes of resistance to leaf rust and powdery mildew (chromosome 6P) [139-142]; genes that increase drought hardiness and thousand-kernel weight (chromosome 7P) [143]. Thus, in

addition to stability genes, crested wheatgrass carries genes and QTL (quantitative trait loci), which positively affect the elements of the crop structure.

The *Elymus* genus is represented by more than 200 exclusively polyploid species combining the genomes St, H, Y, P, and W [24, 35]. In the progeny from crosses and backcrosses of allohexaploid apomictic species *E. rectisetus* with soft wheat, the disomically augmented line with the 1Y chromosome, which is characterized by moderate resistance to Helminthosporium and Septoria diseases [144, 145], was obtained, and the complement of the chromosomes of the 2nd and 5th homeologous groups provided good resistance to Fusarium head blight [60, 146]. *E. tsukushiensis*, which became a donor of the *Fhb6* gene (chromosome 1Ets#1S), transferred to the wheat chromosome 1AS [147], and *E. repens*, the chromatin of which was used to obtain different introgressive Fusarium-resistant lines of wheat [148, 149], also serve as sources of resistance to Fusarium. *E. trachycaulis* was the donor of the resistance gene of soft wheat to leaf rust *Lr55* [150]. Wheat − wild ruttishness hybrids based on *E. farctus* have great perspectives [151].

The use of molecular and cytogenetic markers allows introgressing targeted genes in the wheat genome, thereby greatly facilitating the work of breeders [152, 153]. Genome-wide sequencing data, which is currently being actively developed, and genomic editing technologies will undoubtedly improve the efficiency of the use of genetic resources of wild species [154-156].

Therefore, the successful use of the genetic potential of wild perennial wheat relatives makes it possible to expand the genetic diversity of wheat, significantly impoverished as a result of the limited use of the same varieties in pedigrees. The list of species of perennial wild relatives and useful genes transferred to the genome of wheat is certainly not limited to those listed in this review. This analysis showed that the general trend is the transfer and characterization of genes of wild relatives, which not only increase stability but also positively affect the elements of the structure of the crop and the quality of the final product, that is, clearly improve, and not just worsen these characteristics. Molecular and cytogenetic markers, methods of whole-genomic sequencing and genomic editing technologies will become effective tools for breeders. It is necessary to use all available resources to expand the wheat genetic base, involving in the selection both old varieties and populations of the *Triticum* and *Aegilops* species and new species and genera of *Triticeae* perennial cereals.

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