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THE ROLE OF *Aegilops* SPECIES IN THE ORIGIN AND IMPROVEMENT OF COMMON WHEAT

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Abstract

Some *Aegilops s*pecies participated in wheat evolution playing a major role in wheat domestication and therefore the genus *Aegilops* represents a big part of the additional gene pool determining important traits of wheat. Breeders have been using these genes for many years to produce improved cultivars. Wide crosses between its wild relatives are sources of desirable characteristics for genetic improvement of common wheat. *Triticum aestivum* evolution and methods for transfer of alien material into wheat, briefly reviewed in this article, include incorporation of the whole genomes, single chromosomes, small chromosomal segments, single genes and cytoplasm substitution in wheat.

Key words: *Aegilops*, evolution, gene transfer, *Triticum aestivum*, wheat improvement, wide crosses

Aegilops species as a source of valuable traits for common wheat

In the last few decades, the biodiversity of cultivated wheat varieties has become significantly impoverished. It can be increased by introducing economically important genes from wild species, including genes from the genus *Aegilops*, to the wheat genome [1] The *Aegilops* and *Triticum* genera belong to the same family of grasses (Poaceae). *Aegilops* species are annual grasses characterized by strong tillering, found mainly in the Mediterranean Basin, southern Asia, the mountains of the Caucasus and Kashmir, and the Near East. They grow at various altitudes, from 0 to 2,000 m, in dry and degraded environments, at field edges, on roadsides, in grassland, and in or near cultivated fields [2, 3].

Aegilops species are a source of valuable traits for wheat, including long ears [4]; a high content of protein, the amino acid lysine, and the macronutrients iron and zinc in the kernels [5, 6, 7, 8]; resistance to rust [9,10,11,12,13,14,15,16,17,18,19,20,21,22], to powdery mildew (*Blumeria graminis*) [23,24,25], to eyespot (*Pseudocercosporella herpotrichoides*) [26,27], to tan spot (*Pyrenophora tritici-repentis*) [28], to nematodes and insects [29,30,31], and to pre-harvest sprouting [32]; and tolerance for soil salinity, drought [33,34] and soil acidification [35,10].

An example of the transfer of beneficial traits from *Aegilops* species to cultivated wheat is the translocation from *Ae. ventricosa* introduced in France to the winter variety VPM1, conferring resistance – owing to the genes *Pch1* and *Pch2* – to eyespot, caused by *Pseudocercosporella herpotrichoides* [26]. In Great Britain an enzyme marker of the eyespot resistance gene was developed and the Rendezvous variety was produced, which is found in the lineage of many British, French, German and Swiss winter wheats as well as in Australian and North American wheats. In addition to resistance to *Pseudocercosporella herpotrichoides*, a translocation from *Ae. ventricosa* was also found to occur in these varieties, on chromosome 2B, containing a group of three rust resistance genes: *Lr 37*, *Yr 17* and *Sr 38* [36].

The role of *Aegilops* species in the evolution of common wheat

Both selection by man and natural cross-breeding between primitive wheats and wild grasses of the genus *Aegilops* occurring as weeds in wheat crops have played a significant role in the evolution of wheat. Some researchers estimate that hexaploid wheats evolved over 10,000 years [37]. The donor of the A genome for common wheat is probably the diploid wheat *T. urartu* [38]. The origin of the B genome is still a matter of controversy. H u a n g et al. [39] believe it to be similar to the S genome of *Aegilops* species belonging

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to the *Sitopsis* section. The S genome of *Ae. speltoides* is most similar to the B genome of polyploid wheats. This can be seen in the fact that the brittle rachis gene Br_3 has the same position on the short arm of chromosome 3S in *Ae. speltoides* [40] and on the short arm of chromosome 3B in the tetraploid wheat *T. durum* [41,42]. The locus of another brittle rachis gene, Br_2, was localized on the short arm of chromosome 3A in *T. durum* [42]. The B genome, which originated in *Ae. speltoides*, probably underwent a secondary modification in wheat [43]. Tetraploid wheats (AABB) emerged as the result of chance pollination of *Ae. speltoides* with *T. urartu* pollen. Later, the number of chromosomes in the resulting hybrid must have doubled spontaneously. DNA analysis by Haider [44] revealed high similarity of the S genome of *Ae. speltoides* to the B genome of tetraploid and hexaploid wheat. Hexaploid wheats are presumed to have arisen from chance pollination of the tetraploid wheat *T. dicoccoides* with pollen of the diploid goatgrass *Ae. squarrosa* (*Ae. tauschii*) (DD), followed by spontaneous doubling of the number of chromosomes or the pairing of unreduced gametes in the resulting hybrid. Thus, they are natural amphiploids. The similarity between the D genomes of wheat and *Ae. squarrosa* can be seen in the position of the Br_1 brittle rachis gene on the short arm of chromosome 3D of *T. aestivum* and of the gene Br^t on the short arm of chromosome 3D in *Ae. squarrosa* (*Ae. tauschii*) [41,42].

Methods and techniques of gene transfer from *Aegilops* species to common wheat

Some *Aegilops* species occurring as weeds in wheat crops or on unploughed land between fields can spontaneously cross breed with common wheat [45]. The effectiveness of such spontaneous cross-breedings is similar to that of artificial ones. Seed setting in hybrids takes place more often when the maternal form is *Aegilops* and the paternal form is wheat [46,45,3]. Most easily cross-bred with wheat are *Aegilops* species containing the D genome, which has the highest homology to the D genome of wheat [3].

Failures in cross-breeding of wheat with many *Aegilops* species are due to low homology or lack of homology between their genomes and those of wheat, and to an improper number of chromosomes in the endosperm. Underdevelopment of the endosperm leads to the death of the embryos in the early stage of development. Embryos can be isolated and grown on artificial media *in vitro*. Sterility in F_1 hybrids of distant forms is due to disturbances in the meiosis process [47], which results in a lack of functional gametes. Backcrossing with wheat or colchicination is necessary to obtain kernels [48].

Difficulties in obtaining F_1 intergeneric hybrids also result from the genetic barrier posed by the group of *Kr* genes in common wheat. The system controlling the capacity for intergeneric cross-breeding of *T. aestivum* with rye includes four dominant genes, *Kr1*, *Kr2*, *Kr3* and *Kr4*, of which *Kr1* produces the strongest effect and *Kr3* the weakest. In their dominant form, these genes inhibit seed-setting ability in the F_1 generation [49, 50, 51]. There are, however, varieties of wheat, e.g. Chinese Spring with the genotype *kr1 kr1 kr2 kr2*, which are distinguished by adequate ability to cross breed with rye [52].

To overcome barriers to cross-breeding, various methods and techniques are used for transferring genes from *Aegilops* species to wheat. These include the following:

- adding the entire genome of the *Aegilops* species to wheat genomes, i.e. obtaining amphiploids, and from these, via backcrossing with wheat, addition and substitution lines;
- one of the recombination methods, i.e. crossover resulting from homologous or homeologous pairing of chromosomes;
- translocations induced by ionizing radiation, caused by gametocidal chromosomes, or resulting from somaclonal variation;
- obtaining alloplasmic forms of wheat with the cytoplasm of *Aegilops* species;
- transferring single genes to wheat via genetic engineering methods.

Chromosome doubling using colchicin in F_1 hybrids makes it possible to obtain amphiploids [53], and from these, via backcrossing with wheat, addition and substitution lines [54,55]. Amphiploids can also arise spontaneously via pairing of unreduced male and female gametes formed by intergeneric or interspecific F_1 hybrids [56].

By backcrossing amphiploids with wheat and carrying out selection for 43-chromosome plants, addition lines can be produced. One *Aegilops* chromosome is added to the complete set of wheat chromosomes, and following pollination of plants with 43 chromosomes, forms arise that have two *Aegilops* chromosomes. Although addition lines have not found wide application in practice due to disturbances in meiotic divisions leading to the loss of the added chromosome and to low fertility, they are used to identify foreign chromosomes and as initial forms for transferring foreign genetic material to wheat [55,57].

Addition lines are used to obtain substitution lines. These are more stable than addition lines and have more genotypic variation. Substitution lines were obtained in which *Aegilops* chromosomes were substituted in place of wheat chromosomes [6,58,59,60]. Owing

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to the foreign chromosomes, these lines are resistant to fungal pathogens, nematodes, and insects.

The simplest method for transferring foreign genes to wheat is recombination resulting from homologous pairing of chromosomes, usually chromosome D of *Aegilops* and chromosome D of wheat [3]. The species *Ae. squarrosa* (D), *Ae. ventricosa* (UnD), and *Ae. cylindrica* (CD) contain D genomes that are homologous to that of wheat [2]. In this case, gene transfer can take place on the basis of a simple crossing over.

Recombination resulting from homeologous pairing of chromosomes occurs exclusively via inactivation of the *Ph* genes of the homologous pairing system in common wheat. Suppression of homeologous pairing is controlled by the group of dominant *Ph* genes – *Ph1* on chromosome 5 BL and *Ph2* on chromosome 3DS, as well as other unidentified genes on chromosomes 3AS, 4D, 5A, 5B, and 5D. Of these, *Ph1* exhibits the strongest effect [61]. The gene *Ph1* occurs both in common wheat *T. aestivum* and in tetraploid wheat *T. durum*, but is not present in diploid species of wheat or in the *Aegilops* species from which tetraploid wheats with AABB and AAGG genomes were produced. This gene must have appeared at the tetraploid level in the development of hexaploid wheat. The absence of the *Ph1* gene in the goatgrass *Ae. speltoides* indicates that it emerged as the recessive mutation *ph*, enabling pairing of chromosomes of diploid wheat (AA) with chromosomes of *Ae. speltoides* (SS), or as a translocation of a segment of an extra chromosome of the goatgrass *Ae. mutica* with a wheat chromosome [62].

In the absence of dominant *Ph* genes (nullisomy 2n = 40: *ph ph*, monosomy 2n = 41: *Ph ph*) or in the case of a recessive mutation (disomy 2n = 42: *ph ph*), there occurs homeologous pairing of chromosomes of foreign species with wheat chromosomes in F_1 hybrids. The effect of the recessive *ph* allele is manifested only in interspecific and intergeneric hybrids; it does not affect the pairing of chromosomes of the A, B and D genomes in common wheat [63]. During homeologous pairing reciprocal translocations take place, which constitute the main mechanism by which a chromosome fragment from a foreign species is incorporated in the wheat genome, and the transfer of foreign genes sought in *T. aestivum* breeding occurs. Thus, the system of recessive *ph* genes enabling homeologous pairing is exploited in the introgression of foreign genes into common wheat. For this reason work has been undertaken to obtain recessive *ph ph* genotypes in *T. aestivum* wheat [52]. S e a r s [64] obtained the world's first complete sets of 21 monosomic lines (2n = 41) and 21 nullisomic lines (2n = 40) in the Chinese Spring variety. This allowed the heterozygous genotypes *Ph1ph1* (mono-5B) and *Ph2ph2* (mono-3D) and the homozygous genotypes *ph1ph1* (nulli-5B) and *ph2 ph2* (nulli-3D) to be used in breeding. Subsequent monosomic series of wheat were obtained in the cultivars 'Drabant', 'Jara', 'Favorit' and others [52].

Using induced homeologous pairing and crossing over, a number of wheat varieties with *Aegilops* genes have been obtained. One of the first was Compair [65], with resistance to yellow rust transferred from *Ae. comosa*. Resistance to rust was determined by the dominant gene transferred to chromosome 2D of wheat together with a fragment of chromosome 2M of *Ae. comosa*.

On chromosome 5S of the goatgrass *Ae. Speltoides*, Dvorak et al. [61] identified dominant Ph^I suppressor genes which cause inactivation of the gene *Ph1* on chromosome 5BL of common wheat. In the presence of these genes, and despite the presence of the *Ph1* gene, synapsis takes place between homeologous chromosomes of foreign species and of *T. aestivum*. Similar genes were located in *Ae. peregrina* and *Ae. kotschyi* [66]. Suppressor genes were successfully used to transfer genes of resistance to brown and yellow rust from *Ae. umbellulata* [14] and from *Ae. triuncialis* and *Ae. geniculata* [67] to common wheat.

S e a r s [68] distinguished goatgrass species whose S genomes were highly homeologous to wheat B genomes: *Ae. searsii* (S^S), *Ae. longissima* (S^1), *Ae. sharonensis* (S^1), *Ae. bicornis* (S^b), *Ae. speltoides* (S), *Ae. variabilis* (US) and *Ae. kotschyi* (US). The author states that a low degree of homeology to wheat genomes is exhibited by the genomes of such species as *Ae. umbellulata* (U), *Ae. mutica* (Mu), *Ae. caudata* (C), *Ae. comosa* (M) and *Ae. uniaristata* (Un).

If a foreign chromosome is not homeologous to wheat chromosomes and cannot pair with them in F_1 hybrids, genetic material from *Aegilops* can be introduced into wheat by means of translocations. It is then necessary to apply radiation methods in order to physically activate the chromosome [69]. These methods involve irradiation of the anthers or kernels of F_1 hybrids and self-pollination. In both cases, in the F_2 generation translocations with a foreign chromosome must be identified [70, 52]. S e a r s [71] was the first to use ionizing radiation to induce chromosomal aberrations and to transfer the gene for resistance to brown rust (*Puccinia recondita*) from *Ae. umbellulata* to the Chinese Spring variety of wheat.

Gametocidal chromosomes can contribute to the transfer of foreign genes to wheat. It has been observed that certain foreign chromosomes added to wheat are not eliminated from its genome despite successive backcrossings. Gametes with such chromosomes were found to be fertile, while other gametes were incapable of fertilization. The presence of a gene or genes conferring the 'gametocidal' trait was observed on chromosome 3C of *Ae. markgrafii* and *Ae. triuncialis* [72], on chromosome 2C of *Ae. cylindrica* [73], on chromosome 4M of

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Ae. geniculata [74], on chromosomes $2S^{l}$ and $4S^{l}$ of *Ae. longissima,* on $2S^{sh}$ and $4S^{sh}$ of *Ae. sharonensis* [75], and on chromosomes 2S and 6S of *Ae. speltoides* [76]. Gametocidal chromosomes introduced into wheat induced mutations involving structural changes in chromosomes such as deletions and translocations [77].

In vitro breeding conditions can also contribute to translocations between *Aegilops* and *Triticum* chromosomes. Feldman [78] observed the presence of multivalents in meiosis, probably caused by translocations in hybrids of *T. aestivum* with the amphiploid *T. turgidum-Ae. squarrosa*, regenerated from callus obtained from an *in vitro* microspore culture.

Aegilops species can be used as donors of cytoplasmic genes. As a result of the transfer of the common wheat nucleus to the cytoplasm of *Ae. caudata* and *Ae. ovata*, in later generations of backcrossing hybrids there appeared male-sterile forms of wheat that could constitute starting material in heterosis breeding [79]. Cytoplasm substitution can cause changes in grain yield, protein content and resistance to various biological and ecological stresses, due to diverse interactions between the nucleus and the cytoplasm [80]. By cross-breeding the species *Ae. caudata*, *Ae. columnaris*, *Ae. kotschyi*, *Ae. markgrafii*, *Ae. peregrina*, *Ae. umbellulata* and *Ae. triuncialis* with alloplasmic wheat with a translocated 1BL/1RS chromosome, wheat haploids can be induced as the result of parthenogenesis [81]. From these haploids it is possible to obtain double haploids, by colchicination or the use of other mutagens that double genetic material, thus substantially shortening the process of producing new varieties.

Recent years have seen the rapid development of genetic engineering techniques. Transgenic varieties of wheat have been obtained which are resistant to the herbicide glyphosate [82]. One subject of current research is the risk of transfer of such transgenes from wheat to *Aegilops* species, which are often present as weeds in wheat crops [45]. Genetic markers can be used to evaluate the scale of this phenomenon. Areas in which DNA markers have found wide application include evaluation of genetic similarity or distance, selection and identification of desired forms, confirmation of the effectiveness of cross-breeding, and identification of *Aegilops* genes determining important performance features [36, 83, 84, 57, 85, 86, 87, 17, 88]. Using molecular techniques, *Aegilops* genes can be isolated and stored in artificial bacterial chromosomes and then transferred to wheat [89, 90].

CONCLUSION

Transfer of *Aegilops* genes makes it possible to enrich wheat with valuable resistance and quality characteristics and to prevent genetic erosion of the species. The modifications and breeding lines obtained constitute starting material for new varieties which are more fertile, more resistant, and better suited to changing climate and soil conditions.

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Udział gatunków *Aegilops* w powstaniu i doskonaleniu pszenicy zwyczajnej

S t r e s z c z e n i e

Niektóre gatunki *Aegilops* brały udział w ewolucji pszenicy zwyczajnej, odgrywając ważną rolę w jej udomowieniu, dlatego rodzaj *Aegilops* stanowi dużą część dodatkowej puli genów warunkujących ważne cechy użytkowe dla pszenicy. Hodowcy od lat wykorzystują te geny do tworzenia nowych doskonalszych odmian pszenicy. Krzyżowania oddalone napotykają na szereg barier niekrzyżowalności, które należy pokonać, aby uzyskać mieszańce, a następnie wyselekcjonować z nich linie charakteryzujące się pożądanymi cechami dzikich krewniaków pszenicy. W artykule przedstawiono doniesienia na temat ewolucji pszenicy zwyczajnej oraz główne metody i techniki umożliwiające transfer materiału genetycznego gatunków *Aegilops* do pszenicy, w tym dodawanie całych genomów, pojedynczych chromosomów, fragmentów chromosomów, pojedynczych genów oraz substytucję cytoplazmy w pszenicy.

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