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The oat gene pools – review about the use of wild species in improving cultivated oat

Pule genowe owsa – przegląd informacji na temat wykorzystania dzikich gatunków w ulepszaniu owsa uprawnego

Tomasz OCIEPA

Institute of Plant Genetics, Breeding and Biotechnology, University of Life Sciences in Lublin, Akademicka 15, 20-950 Lublin, Poland, correspondence: tomasz.ociepa@up.lublin.pl

Abstract

The search for agronomic traits and the use of new sources of variability in oat farming is very important in terms of breeding. Wild species of *Avena* are grouped into three gene pools depending on their interfertility with cultivated hexaploid oat. The primary and tertiary gene pools are extensive and diverse, the secondary gene pool is relatively small and poorly represented in *ex situ* gene banks. Appropriate wild species are a valuable source of many appropriate traits such as: high protein, oil, ß-glucan and balanced amino acids composition contents in grain; short culm; cold and drought tolerance. Moreover, they are a source of resistance genes for oat diseases, such as: powdery mildew, crown and stem rust, smuts or barley yellow dwarf virus (BYDV). Note, however transfer of genes from wild to cultivated species is a long and laborious process. These types of methods are used in the species *Avena* with various end effects. The purpose of this article is to collect information on attempts of transferring different genes from wild oat species to cultivated oats.

Keywords: agronomic traits, *Avena* L., disease resistance, ploidy level, wild species

Streszczenie

Poszukiwanie cech agronomicznych i wykorzystanie nowych źródeł zmienności w hodowli owsa jest bardzo ważne z punktu widzenia hodowli. Dzikie gatunki *Avena* są zgrupowane w trzy pule genowe w stosunku od ich płodności z uprawnym owsem heksaploidalnym. Pierwsza oraz trzecia pula genowa są rozległe i zróżnicowane, z kolei rośliny należące do drugiej puli genowej są stosunkowo małe i słabo reprezentowane *ex situ* w bankach genów. Poszczególne dzikie gatunki są cennym źródłem wielu wartościowych cech, takich jak: wysoka zawartość białka, oleju, ß-glukanu i zbilansowana zawartość aminokwasów w ziarnie; krótka łodyga; tolerancja na zimno i suszę. Ponadto są źródłem genów odporności na choroby

owsa, takie jak: mączniak prawdziwy, rdza koronowa i źdźbłowa, głownia lub wirus żółtej karłowatości jęczmienia (BYDV). Należy jednak pamiętać, że przenoszenie genów z gatunków dzikich do uprawnych jest długim i żmudnym procesem. Tego typu metody są stosowane w gatunku *Avena* z różnymi efektami końcowymi. Celem tego artykułu jest zebranie informacji na temat prób przenoszenia różnych genów z dzikich gatunków owsa na formy uprawne.

Słowa kluczowe: *Avena* L., cechy agronomiczne, dzikie gatunki, odporność na choroby, poziom ploidalności

Taxonomy

The genus *Avena* L. belongs to the tribe Aveneae Dumort., family Poaecae Barnh. (United States Department of Agriculture, NRCS, 2018). It is divided into three groups based on polyploidy: diploid (2n = 14), tetraploid (2n = 28) and hexaploid species (2n = 42). Species are classified according to the number and morphology of chromosomes, shape of the panicle, shape of the plant, characteristics of the chaff, and in the case of wild species, spreading (Rajhathy and Thomas, 1974; Baum, 1977). Most species of the genus *Avena* are wild and recognized as weeds. Cultivated crops include *Avena sativa* (about 90% of world crop) and rarely other cultivated species: *Avena strigosa* Schreb. (2n = 14), *Avena abyssinica* Hochst. (2n = 28) and *Avena byzantina* C.K. (2n = 42) (Leggett, 1992a).

The use of modern cytological and molecular methods has allowed to address many issues. However, some problems, such as the distinctness of *Avena* species, their evolution or genetic structure have not been clarified and are still controversial (Paczos-Grzęda, 2003). Several authors have isolated or merged individual species. Zeller (1998) distinguished 31 species of the genus *Avena* genus within 7 sections. Without going into details of systematics, Rajhathy (1991) claimed that 4 hexaploid species could be distinguished (*A. fatua* L., *A.sterilis* L., *A. byzantina* C. Koch, and *A.sativa* L.) based solely on the example of hexaploid species. On the other hand, Leggett (1992a) listed 8 hexaploids with 4 additional species (*A. trichophylla* C.Koch, *A. hybrida* Peterm., *A. occidentalis* Dur., and *A. atherantha* Presl.) by following the numerical taxonomy of Baum (1977). Zeller (1998) distinguished 7 hexaploids, assuming that *A. byzantina* was a subspecies of *A. sativa*, while Loskutov (2007) proved that the genus consisted of 6 hexaploid species (*A. fatua*, *A. sterilis*, *A. byzantina*, *A. sativa*, *A. occidentalis*, and *A. ludoviciana* Dur.).

World distribution and use in practice

Oat is predominantly grown in American and European countries, mainly Russia, Canada and United States of America (Table 1). The most popularly cultivated species is *Avena sativa* L. (White, 1995).

Table 1. Oats area, yield, and production (United States Department of Agriculture, August 2018)

Country/ Region	Area (Million hectares)			Yield (Metric tons per hectare)			Production (Million metric tons)		
	2016/ 2017	Preliminary 2017/18	Projected 2018/ 2019 Jul	2016/ 2017	Preliminary 2017/18	Projected 2018/19 Jul	2016/ 2017	Preliminary 2017/18	Projected 2018/19 Jul
World	9.67	9.54	9.53	2.5	2.46	2.46	24.18	23.51	23.48
Russia	2.75	2.78	2.75	1.73	1.96	1.75	4.75	5.44	4.8
United States	0.4	0.32	0.41	2.37	2.21	2.36	0.94	0.72	0.96
Canada	0.93	1.05	1	3.49	3.52	3.45	3.23	3.7	3.45
Total foreign	9.27	9.22	9.12	2.51	2.47	2.47	23.24	22.79	22.51

At present, oats are widely used primarily for animal feed, however, they are also used in human nutrition, because of their high nutritional value. Oat grains are distinguished from other cereals by a different nutrient composition. First of all, it contains significantly more protein rich in exogenous amino acids (Bartnikowska et al., 2000; Gąsiorowski, 2003). It is used mostly for animal feeding and to some extent as human food (Ahmad et al., 2010). Oat is also applied in the pharmaceutical and cosmetic industry (Budzyński and Szempliński, 2003). Oats have a significantly higher fat content compared to other cereals. This fat is rich in unsaturated acids, characterized by high levels of linoleic, oleic and palmitic acids (Petkov et al., 1999; Gąsiorowski, 2000). In addition, oats are characterized by high levels of micro- and macronutrients, and are also an excellent source of B vitamins (Gąsiorowski, 1992). Many applications of oat also include the possibility of using it for energy purposes (Kwaśniewski, 2010).

How to transfer desirable genes

Data on interspecific hybrids obtained using modern cytogenetic methods have significant evolutionary significance. The practical importance of distant hybridization is based on the combination of the characteristics of evolutionarily distant species, although the crop has lost many attributes possessed by their wild ancestors. Numerous plant resource studies have revealed the valuable characteristics of particular species, which seem to be promising in breeding (Loskutov, 2001).

Oat is a species despite the lack of crossing barriers, it is characterized by a very low efficiency in comparison to other cereals (Thomas, 1992). The crossing of plants involves castration, i.e. removing the immature anthers in the maternal form, and then applying the pollen of the parental forms to the mature markings of the maternal forms few days after castration. Castration is usually performed manually, the alternative is the use of chemical sterilizers (Rodkiewicz et al., 1996).

Avena sativa is distinguished from other cereals by a very narrow gene pool. Many research studies have focused on "cheating" by producing and introducing foreign genetic variation into oats. The most commonly used method of transferring desirable genes is interspecific and intercross crossbreeding. The potential sources of favourable genes are wild species of the genus *Avena.* Altered variability is not always sufficiently available to breeders due to the strong genetic barriers separating wild forms from cultivars. Certain degree of sterility is encountered in triploid hybrids even when chromosomes of diploid and tetraploid species are homologous, because of irregular chromosome segregation during meiosis. Four basic methods have been employed to overcome sterility arising from ploidy differences: directly hybridizing taxa at different ploidy levels; raising the ploidy level of the wild species (or species hybrids) to the same ploidy level as the cultigen before hybridizing with it; doubling the chromosome number of the species at a higher ploidy level (usually the crop species) before hybridizing with the wild species; reducing the ploidy level of the cultigen to that of the wild species, creating a hybrid, and then resynthesizing the chromosome number to equal the cultigen (Stalker, 1980).

The first attempts at intersex crossbreeding in oats did not produce the intended results. In Japan, oat hybrids of different species were obtained using tetraploid *A. barbata* species, followed by the use of cultivated and sand oats (Nishiyama, 1929). In the 1960s, it was possible to transfer whole chromosomes or their parts from diploid species to the genomes of cultivated hexaploid oat (Thomas and Thomas, 1962; Rajhathy and Sadasivaiah, 1969). Cross incompatibility presents the greatest barrier in gene transfer from diploids and tetraploids to hexaploids. This can be overcome by the use of backcrosses, mutants and genetic intermediates. Sterile pentaploid hybrids can be obtained simply by crossing tetraploid *A. magna* and *A. murphyi* species with cultivated oat, and their fertility can be restored by backcrossing with *A. sativa* pollen (Hagberg, 1983).

Gene pool for oat breeding

Wild species of *Avena* are grouped into three gene pools depending on their interfertility with cultivated hexaploid oat. The tertiary gene pool contains all diploid *Avena* spp. as well as the remaining tetraploids (*A. barbata* Pott. ex Link., *A. vaviloviana* Mordv., *A. abysinnica* Hochst., *A. agadiriana* Baum et Fedak, and *A. macrostachya* Bal. ex Coss. et Dur.). Whereas the primary and tertiary gene pools are extensive and diverse, the secondary gene pool is relatively small and poorly represented in *ex situ* gene banks (Harlan and de Wet, 1971; Jellen and Leggett, 2006).

Primary gene pool

The primary gene pool consists of hexaploid taxa where hybrids between wild and cultivated forms are readily produced; they are fertile and have no recombination restrictions.

A. sterilis genotypes are frequently used in the primary gene pool. These genotypes are the source of resistance genes for oat diseases, such as powdery mildew (Lawes and Hayes, 1965; Roderick et al., 2000; Okoń et al., 2016), crown rust (McKenzie et

al., 1981; Thomas, 1992; Chong et al., 2000; Brown et al., 2001; Carson, 2008) and stem rust (McCallum et al., 2002; Fetch and Jin, 2007). Introducing new genes from wild species is intended to improve agronomic traits. Takeda and Frey (1979) investigated the relationships of various traits to protein yield of oats. They used an interspecific oat cross *Avena sativa* x *A. sterilis* for this purpose. In turn, the cultivar "Ozark" (Table 2), with improved winter hardiness, was derived from a cross between the winter-susceptible Florida 501 x *A. sterilis* PI 29625 (Bacon, 1991). *A. sterilis* is a potential donor of desirable traits, such as large grains, high protein content (to 25%) and its balanced amino acid composition as well as high contents of oils (to 10%) and β-glucans (to 6%) in the grain. In hybrids, cytoplasmic genes of this species increase the yield of grain and green mass. The plants are resistant to cold, smuts, root rots and nematode injury (Pasynkov, 1971).

Another hexaploid species, *A. fatua* L., has also been widely used in oat-breeding programmes owing to its short culm, cold resistance, drought tolerance, high contents of protein and oil in grain, little grain shedding, resistance to stem and crown rusts, smuts and tolerance to BYDV (Frey, 1991; Peltonen-Sainio and Mäkelä, 1994; Gallagher et al., 2013). *A. fatua* has been used to develop resistant traits in wheat (Tang et al., 1997).

According to Loskutov (2005), *A. ludoviciana* can be a valuable source of resistance to crown rust (caused by *Puccinia coronata* Cda. f. sp. *avenae* Faser et Led.). Interestingly, some accessions have high groat oil content (7-10%) and high level of unsaturated fatty acids (>46% oleic acid). In the opinion of many researches, *A. sterilis* and *A. ludoviciana* species are the most promising and important both in terms of grain quality and the potential for transferring this trait to cultivated oat.

A. occidentalis exhibit generally better BYDV resistance than *A. fatua*, *A. byzantina* and *A. sativa* (Comeau, 1984). Moreover, it belongs to the group resistant to major obligate fungal diseases – crown and stem rust. Genotypes of this species are also potential sources of high protein content – over 19% (Loskutov, 2005).

Secondary gene pool

A. murphyi, *A. maroccana* and *A. insularis* (*Pachycarpa* section) tetraploids constitute the secondary gene pool. *A. sativa* hybrids with these species are partially female fertile, and this fertility increases with backcrossing (Jellen and Leggett, 2006).

A. murphyi could be a potential source of resistance to powdery mildew (Okoń et al., 2018), crown rust (Tan and Carson, 2013; Sowa et al., 2016), and some accessions also have high protein content and high groat oil content (Loskutov, 2005).

A. maroccana (formally known as *A. magna*) accessions have high contents of protein (to 30%), lysine and oil in grains. In addition, they are also resistant to powdery mildew (Okoń et al., 2018) and crown rust (Sowa et al., 2016), they have large grains (the weight of 1,000 grains reaches 35 g) and demonstrate highly productive tillering. The best-known example of gene introduction from the second gene pool into the cultivated oat variety is the CDC Bell line (Table 2) and a sister line, CDC Baler, forage oats developed at the Crop Development Centre, University of Saskatchewan (Rossnagel, 1999). These lines have been derived from the Av2401/2×SO86044 cross, where the Av2401/2 parent was an *A. sativa* breeding

line derived from a cross between tetraploid species *A. maroccana* and *A. sativa*, with the resulting pentaploid hybrid backcrossed to *A. sativa* (Thomas et al., 1980). *A. insularis* have several desirable traits, such as resistance to major obligate fungal disease like crown and steam rust (Loskutov, 2005).

Table 2. Examples of using wild oat species from each gene pool in the improvement of varieties (Bacon, 1991; Rossnagel, 1999; Loskutov, 2005)

Gene pool	Name of the variety	Important trait	Source of trait
Primary	Starter	High-protein content	*A. sterilis*
	Ozark	Winter hardiness	*A. sterilis*
	Jay	Crown rust resistance	*A. sterilis*
Secondary	Amagalon	Crown rust resistance	*A. maroccana*
	CDC Bell	Annual green feed or oat hay	*A. maroccana*
Tertiary	Hexaploid cultivated oats	Powdery mildew resistance	*A. eriantha*
	Hinoat, Gemini, Foothill	Crown rust resistance	*A. strigosa*

Tertiary gene pool

The tertiary gene pool comprises all diploid oat species and tetraploids *A. barbata*, *A. vaviloviana*, *A. abyssinica*, *A. agadiriana* and *A. macrostachya* (Clifford, 2012).

A. abyssinica accessions carry resistance genes to crown rust (Marshall and Myers, 1961). In turn, *A. agadiriana* exhibit resistance to crown and stem rust (Loskutov, 2005). *A. atlantica* and *A. damascena* have genes responsible for high glucan content (Welch et al., 2000). The species *A. barbata* Pott is resistant to powdery mildew (Thomas, 1992), stem and crown rust (Marshall and Myers, 1961; Carson, 2009, 2010), BYDV (Comeau, 1984), and it additionally have the highest content of oleic acid (Ladizinsky, 1988; Loskutov, 2005). *A. canariensis* carries resistance genes to crown and stem rust (Loskutov, 2005).

A. hirtula has mildew resistance genes (Thomas, 1992). *A. longiglumis* is a genetic intermediate in the crossing of otherwise uncrossable tetraploids with cultivated oat (Thomas, 1989).

The perennial cross-pollinating species *A. macrostachya* Bal. is characterized by complete resistance to stem and crown rust, BYDV (Comeau, 1984), aphid injury and is winter hardening (Baum and Rajhathy, 1976; Leggett, 1992b). *A. prostrata* and *A. pilosa* contain mildew resistance genes (Thomas, 1989, 1992). *A. strigosa* shows resistance to crown rust (Aung et al., 1996; Rines et al., 2018) and BYDV (Comeau, 1984). *A. vaviloviana* has the highest content of oleic acid (Loskutov, 2005). *A. wiestii* exhibits resistance to septoria leaf rust (Thomas, 1989).

Conclusions

Based on the quoted literature there is a large group of wild oat species with useful traits. Changes within the natural environment force the breeders and scientists to seek alternative source of valuable traits. Crossbreeding problems make it difficult to introduce these valuable genes into cultivated oats. Despite this, there are increasingly successful attempts at transferring valuable traits from wild species to cultivated forms.

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