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RESEARCH ARTICLE

On evolutionary pathways *of Avena* species

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Abstract This article presents literary review and results analysis of evaluation of representative set of oat accessions of all *Avena* L. species. Results of complex study of major morphological characters and utilization of the karyotype structure data confirmed by the results of RAPD and avenin spectrum analysis are presented. Relationships of genomes of different *Avena* species at each ploidy level are discussed. Two genomes form the base of all *Avena* species, namely the A and C genomes. Results of the evaluation of several characteristics of the oat species and their geographical distribution are analysed. Probable evolutionary pathway of *Avena* species are suggested. Most likely the centres of origin of *genus Avena* L. are determined.

Keywords *Avena* species ■ Evolution ■ Centres of origin and diversity ■ Genomes ■ Geographical distribution

Introduction

Evolutionary research is aimed to perceive interactions between species on the basis of morphogeographic data, taking into account the factors of heredity and variability, physiology and biochemistry, cytogenetics and molecular biology. Many researchers have been studying various issues of evolution and geographical distribution of oat species over the continents and localization of the areas of their origin and diversity (Vavilov 1926; Malzev 1930; Baum 1977; Coffman 1977). Domestication of different oat species and some of their forms, as derivatives of wild species, took place simultaneously and independently in some regions (Haussknecht 1899; Thellung 1911; Trabut 1914; Malzev 1930; Mordvinkina 1936). Identifying the foci of morphogenesis both for the cultivated species and their wild progenitors is a subject of contemporary investigations. Very interesting from the evolutionary point of view are cytogenetical and molecular biological analyses of plant forms and interspecific hybrids by modern methods. They have helped to find answers to a number of questions related to the phylogeny of oat species, clarify the degree of relationship between them and identify their genomic composition (Malzev 1930; Loskutov 2001b).

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Literature review

Having analyzed volumes of factual data, it was concluded that the A and C genomes characterizing

diploid species had originated by wide structural divergence from a genome of the progenitor of such species. Minor variants (Cp, Cv and Al, Ad, Ac, As) of each of those genomes were already obtained as a result of insignificant changes in a hypothetic transient form which had preceded the present-day species (Baum et al. 1973; Rajhathy and Thomas 1974; Holden 1979; Thomas 1995). The presence of a strictly symmetrical karyotype confirms to the primitiveness of the species within the group, while an asymmetrical karyotype distinguishes their heterogeneity and evolutional advancement (Levitskii 1931; Stebbins 1971). Thus, on the basis of the karyotype structure in the diploid species some researchers have assumed that the species with the A genome, possessing a symmetrical karyotype, are karyologically more primitive than those with the C genome and an asymmetrical karyotype (Leggett and Thomas 1995). Meanwhile, the species with the C karyotype are morphologically very primitive [according to Maltsev (1930) such species have glumes very unequal, lower glume one-half of upper one, upper glumes with 5-7 veins, callus very long, awl shaped, about 10 mm in length], and therefore they belong to the group of species that underwent the process of evolution slowly. In the opinion of Stebbins (1971), the species which demonstrate high karyotype asymmetry, but according to their morphological traits belong to ancient groups, are very likely archaic and have undergone the bradytelic type of evolution, although they are not really primitive.

According to Maltsev (1930), it is from the primary centre of origin of all diploid oat species the western part of the Mediterranean region (Atlas Mountains/Pyrenees), where the greatest diversity of these forms is concentrated, the axes of modern areas of distribution of all 14-chromosome species radiate to eastwards.

Regarding the evolution of tetraploid oat species, it is possible to trace two main independent branches: the species with the AB genome and those with the AC genome. Genomic structure of the species with the AB genome have most likely originated from the diploids with a variant of the As genome. There are researchers who contend that *Avena barbata* Pott is an autotetraploid of one of the diploid species (Ladizinsky and Johnson 1972). The genome in *A. barbata* could have been engendered by duplication of chromosomes in one of the diploids, because this genome consists of two identical or very similar (AA') genomes (Fabijanski et al. 1990). It is assumed that the weedy species *A. barbata* transferred to Ethiopia together with oat seeds was the source of the cultivated species *A. abyssinica* Hochst. which has been choking up oat fields until the present time (Thomas 1995). On the other hand, species *A. vaviloviana* (Malz.) Mordv. and *A. abyssinica* Hochst. according to a number of morphological characters according to Baum (1971) might be the relics of the ancient African floras.

Another group of species with the AC genome was closely related to the hexaploid species. The origin of *A. magna* Murph. et Fed. is supposed to be hybridogenic, resulting from the contacts on the margins of the areas of distribution of diploid species (probably *A. canariensis* Baum and *A. ventricosa* Balan.), which presumably caused the genesis of this allotetraploid. Some researchers were convinced by the results of interspecific crosses that the tetraploids with the AC genome had originated from the diploid species possessing such genomes: they are supposed to be *A. canariensis* (Ac) and *A. ventricosa* (Cv) (Rajhathy and Thomas 1974).

Rajhathy and Thomas (1974) came to the conclusion that hexaploid forms had been brought to existence in the process of generic evolution by alloploid convergence of the species with the AC genome and an unknown species with the D genome. The evolution of hexaploid species, closely linked with diploid and tetraploid ones, is the most intricate and complicated (Ladizinsky and Johnson 1972; Rines et al. 1988). According to the data of Leggett and Markland (1995a, b), A and D genomes are more similar to each other and at the same time they are expressly different from the C genome. The A genome of the diploid progenitor could have obviously been the donor of A and D genomes in hexaploid species (Linares et al. 1996). The latest data witness that the D genome is supposedly an unknown variant of the As-A’’ genome, similarly to the B genome, but differing from the latter (Leggett 1996, 1998).

Taking into account the karyotype structure, cytogenetic features and interspecific hybridization data, it is possible to conclude that the evolution of the genus *Avena* L. obviously involved two different genomes A and C, while all other genomes to a greater or lesser extent were derivatives from these forms. Supposing that according to the conventional scheme the diploid species *A. canariensis* (A genome) and *A. ventricosa* (C genome) were the progenitors of the corresponding genomes, the evolved allopolyploids may have had structural changes in their chromosomes, which could have caused their partial homology (Baum et al. 1973; Rajhathy 1966).

According to the data of Coffman (1977), the progenitor of the diversity of hexaploid forms was *A. sterilis* L. originated in the Asiatic continent. This species most likely brought the cultivated species *A. byzantina* C. Koch into existence, followed by a harmful weedy *A. fatua* L. that inflicts cultivated crops. Deeper insight into the evolutionary issues of hexaploid species has shown that the study of translocations in oat chromosomes and correlations between geographic distribution of various forms using cluster analysis demonstrated high degree of genetic relationship between the accessions of *A. byzantina* and the forms of *A. sterilis* from the northern Mesopotamia, on the one hand, and the accessions of *A. sativa* L. and the forms of *A. sterilis* from the eastern Anatolia, on the other (Zhou et al. 1999). Further examination of all hexaploid species helped to find out that *A. sativa* L. is characterized by the presence of translocations (97%) in contrast to *A. byzantina* (11%). This finding has led to the assumption that two cultivated species *A. sativa* and *A. byzantina* were domesticated independently from each other. The study of *A. fatua* L. and *A. occidentalis* Dur. has confirmed that most of the forms of these species have the same translocations as *A. sativa* and therefore may be regarded as parallel of the oat evolution (Jellen and Beard 2000).

It is the opinion of Maltsev (1930) that all hexaploid species moved from their Asian centre predominantly westwards, and *A. fatua* occupied mainly northern and middle latitudes, while *A. sterilis* inhabited those to the south, thus reaching the westernmost borders of the Mediterranean region. In view of this, it is possible to surmise that *A. sterilis* originated from the same primary Asian centre as *A. fatua,* but moving away westwards became quite different from the latter. This is witnessed by the very gradualism of such differentiation, according to Maltsev taxonomy (1930) beginning from the small-grain *A. sterilis* subsp. *ludovicianaha* Dur. in the east and ending with the large-grain *A. sterilis* subsp. *macrocarpa* Briq. in the west.

According to Thomas (1995), *A. sterilis* in its northward movement generated *fatua-type* mutations that led to the emergence of *A. fatua,* from which weedy forms of the cultivated hexaploid species *A. sativa* have evolved. Also here in South-Western Asia region was the place of origin of hexaploid naked forms which, according to opinion of some researcher, moved toward China (Holden 1979; Thomas 1995).

As noticed by Vavilov (1926), the diversity of distribution areas attest to the fact that polyploids (tetraploids and hexaploids) generally proved to be more enduring than diploids and more adapted to the northern and alpine environments *(A. fatua).*

Discussion of *Avena* evolution in view of recent studies of the VIR *Avena* collection

In the last decades, *Avena* L. Vavilov Institute of Plant Industry (VIR) collection have been replenished by new accessions and newly described species from all regions of the Mediterranean and Black sea regions. The global oat collection is represented by comprehensive specific and intraspecific diversity of both cultivated (10,000 accessions) and wild (2,000 accessions) species of *Avena* L. Full botanic and ecological diversity of cultivated species is incorporated in the old landraces varieties-populations collected in 1910-1920s. A majority of these forms come from the centres of origin and diversity of this crop, providing a universal overview on the total geographic diversity of oat. With this in view, oat species became the subject of complex investigation in order to specify the system of the *Avena* genus, direction of its evolution and

phylogenetic links between the species (Loskutov 2003). At the same time, further search for taxonomy and utilization of new oat breeding sources for breeding purposes is one of theobjectives pursued by VIR in studying its global germplasm collections (Loskutov 1998, 2002; Loskutov et al. 1999).

It is the availability of total botanical and eco-geographic diversity and its complex study that may provide an opportunity to identify centres of origin and variability of this or that genus or species.

Genomes evolution

On bases of complex study using utilization of the karyotype structure data (Loskutov and Abramova 1999; Badaeva et al. 2005) confirmed by the results of RAPD (Loskutov and Perchuk 2000) and avenin spectrum analysis (Loskutov et al. 1999), it was confirmed identification of two basic genomes, which most likely participated in the formation of species in *Avena* L., namely the A and C genomes. As for the B and D genomes, they seem to be derivatives of the A genome. In addition to the data obtained during the study of the species containing these genomes, clear-cut differences have been discovered in the areas of their distribution (Fig. 1).

Numerous researches have proven that the C genome goes through all ploidy levels unchanged, with small variation, thus being considered one of the basic genomes in oat. Our investigations of the karyotype *A. macrostachya* Balan. have shown that this species is an autotetraploid with the AA genome (Loskutov and Abramova 1999). On the other hand, the analysis of chromosome structure indicates that *A. macrostachya* is related to the C-genome species (Rodionov et al. 2005). At the same time, this species is characterized by a symmetrical karyotype and a set of morphological characters attesting to its true primitivity. All this is confirmed by the most primitive perennial type of development and by cross-pollination, which is typical for a group of species of oat-like grasses within the subgenus *Avenastrum* C Koch (Loskutov 2003). Meanwhile, according to Rodionov et al. (2005), the division of the phylogenetic oat lines carrying A and C genomes was accompanied by accumulation of differences in dispersed repetitions and accumulation of transitions and transversions specific for each branch. Later the C-genome line segregated phylogenetic branches of *A. macrostachya* from the progenitor of the other species with the C genome, and after that the progenitors of *A. macrostachya* doubled their chromosome number and generated large blocks of C-heterochromatin which caused an unusual C-banding pattern of chromosomes in C genomes of diploid and polyploid species.

Afterwards the A genome developed independently from the C genome, which brought about lots of A-genome variants (Al, Ap, Ad, Ac, As), and finally produced a cultivated diploid species *(A. strigosa* Schreb.) with the As genome (Fig. 1). RAPD analysis and studying avenine protein markers made it possible to conclude that in spite of all differences between species with the A genome they have indirect evolutionary affinity (Loskutov et al. 1999; Loskutov and Perchuk 2000). Genesis of tetraploid species became possible either after the doubling of the chromosome number in one of the diploid species (AA) or with spontaneous hybridization of two closely related (AB = AA') diploid species. This resulted in raising ploidy to a higher level and bringing into existence a group of tetraploid species with either AB or AA' genomes, which provided an opportunity for the development of a cultivated tetraploid species *(A. abyssinica)* containing the AB genome. Later, diploid species with A and C genomes united into one genotype *(A. canariensis,* Ac and *A. ventricosa,* Cv), where the A genome in one of intermediate forms transformed by structural divergence into a D genome or, as it is now assumed, into an A" genome. The species with A and AB (AA') genomes and a biaristulate lemma tip [sectio *Aristulatae* (Malz.)] in most cases floret disarticulated (Table 1). Some of them have cultivated analogues with the same ploidy level *[A. wiestii* Steud., *A. hirtula* Lagas.—*A. strigosa* Schreb.; *A. vaviloviana* (Malz.) Mordv.- *A. abyssinica* Hochst.] and wider areas of distribution *(A. wiestii, A. hirtula* and *A. barbata),* being rather active weeds *(A. clauda* Dur., *A. pilosa* M.B., *A. damascene* Rajh. et Baum, *A. longiglumis* Dur. and *A. barbata).*

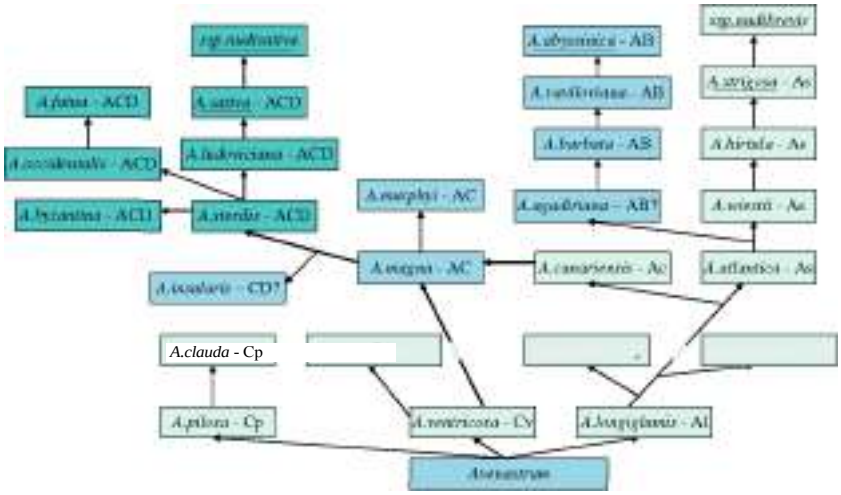

Fig. 1 Phylogenetic relationships of *Avena* species

evolution pathways of the species and forms
probable evolution pathway of hexaploid cultivated species

Table 1 Speciation in the subgenus *Avena* L.

Section	Species			2n	Genome
	Wild		Cultivated		
	Floret disarticulation	Spikelet disarticulation			
Aristulatae (Malz.)	*A. clauda* Dur.	*A. pilosa* M.B.		14	Cp
	A. prostrata Ladiz.				Ap
	A. damascena Raj.et Baum				Ad
	A. longiglumis Dur.				Al
	A. wiestii Steud.	*A. atlantica* Baum	*A. strigosa* Schreb.		As
	A. hirtula Lagas.				
	A. barbata Pott		*A. abyssinica* Hoch.	28	AB
	A. vaviloviana (Malz.) Mordv.				
Avenae (L.)		*A. ventricosa* Balan.		14	Cv
		A. bruhnsiana Grun.			
		A. canariensis Baum			Ac
		A. agadiriana Baum et Fed.		28	AB?
		A. magna Mur.et Terr.			AC
		A. murphyi Ladiz.			
		A. insularis Ladiz.			CD?
	A. fatua L.	*A. sterilis* L.	*A. byzantina* Koch	42	ACD
	A. occidentalis Dur.	*A. ludoviciana* Dur.	*A. sativa* L.		

Obviously, this group seems apparently had no part in the development of hexaploid oats (Loskutov 2003).

In our opinion, the species with the C and AC genomes, whose characteristic feature, i.e. the presence bidentate lemma tip (section *Avenae),* is typical for hexaploid species, are transitional ancestral forms (looks like *A. ventricosa, A. canariensis* or *A. magna)in* the evolution of hexaploid oats (Table 1). This group includes diploid species *A. ventricosa* Balan., *A. bruhnsiana* Grun., *A. canariensis* Baum and *A. agadiriana* Baum et Fed. as well as tetraploid species *A. magna* Murph. et Terr., *A. murphyi* Ladiz. and *A. insularis* Ladiz., that spikelet disarticulated only and do not have direct cultivated analogues.

Significant differences between tetraploid species with AB and AC genomes have been confirmed by the data of RAPD analysis and avenine protein markers (Loskutov et al. 1999;

Loskutov and Perchuk 2000). Further on, the species with three genomes A, C and D underwent hybridization and produced an allohexaploid species, the progenitor of *A. sterilis,* which generated a large group of species, including hexaploid *A. byzantina* and *A. sativa* with the ACD (ACA') genome. Divergence of A and C, two major genomes of the genus *Avena* L., may be traced by the karyotype structure, avenine protein marker spectra and RAPD data (Loskutov and Abramova 1999; Loskutov et al. 1999; Loskutov and Perchuk 2000). Besides, distinctive differences were found in the areas of distribution of the species containing these genomes (Loskutov 2003).

Acting as such transitional progenitors for cultivated hexaploid species of *Avena* L., in our opinion, may be wild diploid and tetraploid forms possessing a characteristic feature typical for hexaploids, that is presence of two denticles on the tip of the lemma (section *Avenae* Losk.) (Table 1).

Presumably in the western part of the Mediterranean region, where the richest specific diversity of *Avena* L. is concentrated, spontaneous hybridization of tetraploid species from the group of transitional forms with genomes A, C and D initiated development of all allohexaploid species (Fig. 1). Occurrence of the largest diversity of polyploids in the eastern part of Anterior Asia, where soil and climate conditions are harder than in the western Mediterranean areas, was confirmed by Vavilov's (1926) statement about greater hardiness of this group of species, as compared with diploid ones, because allopolyploid species promote development of extremely differentiated ecotypes, which played an important role in the evolution. Proceeding from the centre of origin toward the South-Western Asiatic centre, smaller-seeded and more adaptive hexaploid forms of wild species began to occur.

Evolution of cultivated species

The whole diversity of cultivated oats was proven by Vavilov (1926) to have a weedy field origin. As its species moved northwards, oat replaced basic crops by weeding them and became an independent crop for itself. This process may be clearly traced in Spain on the cultivated diploid species *A. strigosa* Schreb., in Ethiopia on *A. abyssinica* Hochst., in Turkey and Iran on *A. byzantina* C. Koch and weedy forms of *A. sativa* subsp. *sativa* convar. *asiatica* Vav. and *A. sativa* subsp. *sativa* convar. *volgensis* Vav. (Fig. 2). At present, all these cultivated forms (non-shattering by themselves) became weeds (Loskutov 2004).

Analyzing the global diversity of local varieties available in the VIR oat collection, much of which was collected by N.I. Vavilov himself during his Mediterranean exploration (1926-1927) (Loskutov 1999), has shown that the greatest intraspecific variability of diploid cultivated species *A. strigosa* Schreb. concentrates in Great Britain, Germany, Spain and especially Portugal. This species, according to the classification of Rodionova et al. (1994), is divided into three subspecies: *A. strigosa* subsp. *strigosa* Thell., *A. strigosa* subsp. *brevis* Husn. and *A. strigosa* subsp. *nudibrevis* (Vav.) Kobyl. et Rod., with distinct geographic differentiation. A majority of diverse forms representing *A. strigosa* subsp. *strigosa* Thell were widespread in Spain, Portugal, Germany and Great Britain; besides, some of the forms had their origin in several other European countries. Local forms of *A. strigosa* subsp. *brevis* Husn. most typically originated from Portugal, Great Britain and, to a lesser extent, Spain. As for the naked forms of *A. strigosa* subsp. *Nudibrevis* (Vav.) Kobyl. et Rod., the only possible centre of their origin is Great Britain; elsewhere these plants could only be exogenous (Fig. 2).

Naked forms have most likely originated as a result of further metamorphosis of the caryopses disarticulation mechanism. If we get a closer view on the cycles of wild, cultivated and naked oat plant forms, the nature of disarticulation of the florets (caryopsis) would vary from complete disarticulation of the caryopsis at maturity (florets or spikelets) with a distinctly expressed callus (wild type) through solid attachment (cultivated covered type) up to unhindered detachment of the caryopsis from the lemma (cultivated naked type).

Distribution of *A. strigosa* Schreb. northwards into Great Britain was accompanied by changes in the environments, thus expanding the habitats

1. Mediterranean centre - Morocco, Algeria, Spain
2. Spain and Portugal - centre of diversity of A. *strigosa*
3. Great Britain - centre of diversity of A. *strigosa* subsp. *nudibrevis*
4. Abyssinian centre - Ethiopia, centre of diversity of A. *abyssinica*
5. South-West Asian centre - Turkey, Iran, Iraq, Syria
6. Tatarstan, Bashkortostan - diversity of A. *sativa* convar. *volgensis*
7. China, Mongolia - centre of diversity of *A. sativa* subsp. *nudisativa*
8. - pathways of distribution of cultivated species and forms.

Fig. 2 Evolution pathways of cultivated *Avena* species

of the forms of *A. strigosa* subsp. *brevis* Husn., and later producing recessive mutations of the type characteristic of naked forms of *A. strigosa* subsp. *nudibrevis* (Vav.) Kobyl. et Rod., which had been described by Linneus as *A. nuda* L.

Avena abyssinica Hochst. has a lot in common with *A. vaviloviana* (Malz.) Mordv. and is considered its cultivated analogue (Fig. 2). Scanty intraspecific diversity of *A. abyssinica* Hochst., represented by six plant forms in the rank of botanical varieties, as described in *Cultivated Flora* (Rodionova et al. 1994), is limited to the territory of contemporary Ethiopia. As regards a majority of its morphological characters, this species is very uniform. Its wild relative *A. vaviloviana* (Malz.) Mordv., widespread only within the same territory, is not rich in morphological forms as well, as witnessed by our investigations and confirmed by avenine protein marker studies (Loskutov 2003). It should that both *A. vaviloviana* (Malz.) Mordv. and *A. abyssinica* Hochst., having found in Ethiopia the most favorable climate and soil conditions for distribution into the south of the Mediterranean centre, were unable to move further on because of more severe arid climate in the countries adjacent to Ethiopia. It should be mentioned that diploid and hexaploid cultivated species incorporate naked forms, while tetraploids do not contain them. The most probable reason, in our opinion, is that the species of this group were unable to disperse far from their centre of origin, had no recessive mutations and consequently produced no naked forms.

The progenitor of the whole group of hexaploid species was the large-seeded *A. sterilis* L., disarticulated by separate spikelets. This species underwent mutations in the manner of caryopses dispersal, which led to the development, on the one hand, of the cultivated species *A. byzantina* C. Koch, and on the other, of the wild species *A. occidentalis* Dur. shattering by separate caryopses and occurring presently only on the Canary Isles (Spain) (Fig. 2). It is highly probable that, owing to the changes in the disarticulation type, *A. occidentalis* Dur. had previously occupied vast areas; besides, its dominating type of development is winter or semi-winter, and we consider it primary, compared to the spring type. In the process of eastward distribution *A. sterilis* L. became differentiated into more adaptive

small-seed forms of *A. ludoviciana* Dur., which underwent mutations in the Anterior Asiatic centre that changed their caryopses disarticulation type. It led, in its turn, to the appearance of weedy field forms of *A. sativa* L. As for *A. occidentalis* Dur., moving eastwards it acquired earlier-ripening, typically spring forms which combined into a separate species, *A. fatua* L. This species, disarticulating by single florets, became a harmful weed and infested vast areas in the north and east of Europe and Asia. Weak sensitivity to vernalization and strong reaction to the length of day was reported to indicate true spring nature of *A. fatua* L., which enabled it to occupy by weeding the most extensive agricultural territories on Earth. True spring nature of this species proves that it was secondary in origin as compared with *A. sterilis* L. and *A. ludoviciana* Dur. (Loskutov 2001a).

Analysis of numerous local plant forms collected by N.I. Vavilov (1926-1927), P.M. Zhukovsky (1925-1927) and V.V. Markovich (1926-1928) during their explorations and collecting missions (Loskutov 1999) has shown that the greatest intraspecific diversity of *A. byzantina* C. Koch may be found in Mediterranean region. The primary centre of morphogenesis for *A. byzantina* C Koch is within the territories of Algeria and Morocco, where its richest endemic botanical diversity is available. The presence of multiple intermediate plant forms in Turkey suggests that this region has been a secondary centre of diversity for this species. Another direction of distribution for hexaploid forms was the northward course. New climate conditions provoked mutations of a *sativa* type, which, as it was initially with *A. byzantina* C. Koch, contaminated wheat and barley fields. RAPD analysis (Loskutov and Perchuk 2000) helped to ascertain that plants representing cultivated species *A. sativa* L. and *A. byzantina* C. Koch formed comparatively small groups, remote from each other, which may serve as a proof of their geographic isolation during domestication: *A. byzantina* C Koch entering cultivation from the western part of the Mediterranean and *A. sativa* L. from the South-Western Asiatic centres of origin of cultivated plants (Fig. 2).

Studying intraspecific diversity of covered accessions of *A. sativa* subsp. *sativa* L. (Rodionova et al. 1994) has shown that weedy field forms of this subspecies *(A. sativa* subsp. *sativa* convar. *asiatica* Vav. and *A. sativa* subsp. *sativa* convar. *volgensis* Vav.) are localized in the territories of Iran, Georgia and Russia (Daghestan, Tatarstan, Bashkortostan and Chuvashia). The groups of intraspecific variability of *A. sativa* subsp. *sativa* convar. *asiatica* Vav. and *A. sativa* subsp. *sativa* convar. *volgensis* Vav., characterized by primitive or transitional traits and weeding crop fields, demonstrated distinct attachment to certain areas (Fig. 2). Analysis of the VIR collection data on attribution of local accessions collected in 1920-1930s to different species has shown that forms of *A. sativa* subsp. *sativa* convar. *asiatica* Vav. have their richest diversity only in Iran and Georgia, where all three botanical varieties of this group were identified, while in Daghestan only one of these varieties was found. Another group, *A. sativa* subsp. *sativa* convar. *volgensis* Vav., has four botanical varieties, and Tatarstan harbors the greatest diversity of them (all four botanical varieties). Three varieties were identified in Bashkortostan, Chuvashia and Ulyanovsk Province, two were found in Udmurtia, and only one of them in Kirov Province, Saratov Province and Mordovia. In other regions of covered oat distribution these forms are absent. It is very likely that covered forms of *A. sativa* subsp. *sativa* L., weedy from the beginning, started to be introduced into cultivation and spread in all directions from the South-Western Asiatic centre across Iran farther into Georgia, Daghestan and Middle Volga Region (Saratov and Ulyanovsk Provinces, Tatarstan, Chuvashia and Bashkortostan).

One more subspecies, *A. sativa* subsp. *nudisativa* (Husnot.) Rod. et Sold., or naked hexaploid oat, according to Vavilov (1926), originated from specific mountain region of north-west part of China. It is reported in publications that hull-less oat was known in China as early as in the 5th century A. D. (Zhukovsky 1964). Getting farther eastwards from its main centre of diversity (South-Western Asiatic centre of crop origin), with a change of growing conditions, *A. sativa* L. produced naked-seeded mutations, which finally settled in new habitats.

While analyzing data on intraspecific diversity of naked landraces of *A. sativa* L., it came out that

among the Mongolian germplasm samples collected by V.E. Pisarev's mission (1922-1923) (Loskutov 1999), where all four botanical varieties of the subspecies were identified. Three botanical varieties had their origin in China, four in Mongolia (two of them are strictly endemic for these regions), two in one of the adjacent Russian provinces, and another two in the other. The remaining forms of naked oat, representing two most widespread variants, originated from the European part of Russia or other European countries. It leads to the conclusion that the centre of diversity for hull-less hexaploid oat forms lies in Mongolia and North-Western China (Fig. 2).

Conclusions

Complex study of specific diversity and analysis of geographic distribution of the habitats of oat forms and species confirmed that most important in the formation of species in *Avena* L. were two basic genomes, namely the A and C genomes. It is suggested that the probable evolutionary pathway of species of section *Aristulatae* (Malz.) apparently reached their evolutionary climax, but diploids and tetraploids species of section *Avenae* Losk. were involved in the evolution of hexaploid wild and cultivated oats.

Most likely the centre of origin of genus *Avena* L. lies in the western part of the Mediterranean region, where species *A. byzantina* C. Koch originated too, while the secondary centre of formation of *Avena* L. species and origin of cultivated oat *(A. sativa* L.) is situated within the Asia Minor centre of crop origin.

Besides, the analysis of intraspecific diversity of landraces helped to identify centres of morphogenesis for all cultivated oat species. The centre of origin and diversity for the diploid species *A. strigosa* Schreb. is Spain with Portugal, for the naked forms *[A. strigosa* subsp. *nudibrevis* (Vav.) Kobyl. et Rod.] designated by Linnaeus as *A. nuda* L. it is Great Britain, for the tetraploid species *A. abyssinica* Hochst. it is Ethiopia, for the hexaploid species *A. byzantina* C. Koch it is Algeria and Morocco, for the hulled forms of *A. sativa* subsp. *sativa* L. it is Iran, Georgia and Russia (Tatarstan), for its hull-less forms *[A. sativa* subsp. *nudisativa* (Husnot.) Rod. et Sold.] it is Mongolia and China.

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