Russian Journal of Genetics, Vol. 37, No. 5, 2001, pp. 467–475. Translated from Genetika, Vol. 37, No. 5, 2001, pp. 581–590.

THEORETICAL PAPERS AND REVIEWS

Interspecific Crosses in the Genus *Avena* L.

I. G. Loskutov

Vavilov All-Russia Institute for Plant Production, St. Petersburg, 190000 Russia;
fax: (812) 311-87-68; e-mail: i.loskutov@vir.rw.ru

Received July 14, 2000; in final form, September 19, 2000

Abstract—Problems of crosses between various oat species are considered with regard to establishing their taxonomic positions and genomic compositions of individual species. The evolution of the genus and approaches to the search for the diploid and tetraploid ancestor of the hexaploid species are considered. Use of wild oat species in breeding is demonstrated. The results of studies of the gene pool of wild oat species are presented. These studies were performed at the Vavilov All-Russian Plant Breeding Institute with the purpose of solving problems of phylogeny and practical breeding.

At present the origin of many plant genera and species can be to some extent understood by the use of interspecific hybridization. Data on interspecific hybrids obtained by modern cytogenetic methods are of considerable evolutionary interest. The practical significance of remote hybridization is based on combination of characteristics of evolutionarily distant species, although cultivated crops lost many traits possessed by their wild ancestors. Numerous examination of plant resources revealed valuable properties of individual species whose application for breeding seems very promising.

Crosses between species of equal or different ploidy levels have long attracted the attention of researchers. The genus *Avena* L., which includes many species, has three ploidy levels and is represented by di-, tetra-, and hexaploids (see table). Most of these species are wild. Cultivated crops are present in each ploidy group: *A. strigosa* Schreb. (2*n* = 14), *A. abyssinica* Hochst. (2*n* = 28), *A. byzantina* C.K. (2n = 42), and *A. sativa* L. (2*n* = 42) [1].

Many wild *Avena* species have commercially important traits. The diploid species *A. pilosa* M.B., *A. ventricosa* Bal., *A. hirtula* Lag., and *A. prostrata* Ladiz. are resistant to powdery mildew; *A. wiestii* Steud is highly resistant to septoria leaf rust (*Septoria avenae* Frank.); *A. longiglumis* Dur. is a genetic intermediate in crossing otherwise uncrossable tetraploids with cultivated oat [2]. Tetraploid species, for example, *A. magna* Mur. et Terr. and *A. murphyi* Ladiz., possess high contents of protein (to 30%), lysine, and oil in grains; are resistant to powdery mildew and crown rust; have large grains (the weight of 1000 grains reaches 35 g); and demonstrate great productive tillering. The species *A. barbata* Pott is resistant to powdery mildew, stem and crown rusts, and sensitive to barley yellow dwarf virus (BYDV) [3]. The perennial cross-pollinating species *A. macrostachya* Bal. is characterized by complete resistance to stem and crown rusts, BYDV, aphid injury and is winter hardiness [4].

The wild hexaploid oat species play an important role in breeding. Virtually all commercially important traits are present in *A. sterilis* L.: large grains, high protein content (to 25%) and its balanced amino acid composition, and high contents of oil (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 [6]. The plants are resistant to cold, stem and crown rusts, mildew, smuts, root rots, and nematode injury [6]. Another hexaploid species, *A. fatua* L., is also widely used in oat-breeding programs owing to its early ripeness, short culm, cold resistance, high contents of protein and oil in grain, little grain shedding, resistance to stem and crown rusts, smuts, and tolerance to BYDV [5].

Taxonomic studies of the genus *Avena* L. in Russia were first performed in 1909 by A.I. Mal'tsev [7], who collected, investigated, and systematized wild and cultivated oat species [8]. Specimens were collected in many regions of Russia, Central Asia, and Transcaucasia and received from foreign collections and botanical gardens. Later, the collection was augmented by addition of specimens gathered by field teams of the All-Union Plant Breeding Institute headed by N.I. Vavilov, P.M. Zhukovskii, and other scientists [9, 10].

In 1912, Mal'tsev donated his representative collection of oat species to S.I. Zhegalov, Peter Agricultural Academy, for investigation of the genetics of various morphological and commercial traits, immunity, and species compatibility [11, 12]. The studies involved crosses of the cultivated species *A. sativa* L. with *A. fatua*, *A. sterilis*, *A. ludoviciana* Dur., and *A. strigosa*; later, with *A. barbata* and other wild tetraploid species [13–17].

By analyzing a great body of information on the morphology, ecology, and interspecific crosses of oat species, A.I. Mal'tsev [7, 18] developed the best classification of the genus *Avena* L. type section (*Euavena* Griseb.). This classification was then confirmed by karyological and other studies [19]. In experiments on

1022-7954/01/3705-0467$25.00 © 2001 MAIK "Nauka / Interperiodica"

Crossability of species of the genus *Avena* L.

No.	Species	Ploidy level	Genome	Diploid												Tetraploid								Hexaploid					
				1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	*A. clauda*	7	Cp	–	F	C				0			0		0	0				0									
2	*A. pilosa*	7	Cp		–	C			0	0			0		0	0			0	P			S					P	
3	*A. ventricosa*	7	Cv			–	F			0			0		0	0			0	0			S					P	
4	*A. bruhnsiana*	7	Cv				–						0		0				0	0								P	
5	*A. prostrata*	7	Ap					–	0	P	0		S	C	C	C				C	C		C					C	
6	*A. damascena*	7	Ad						–	0	C		0	C	0	0				0			C						
7	*A. longiglumis*	7	Al							–	0	C	C		C	S			C	P	C		0					P	P
8	*A. canariensis*	7	Ac								–				S			P					C					P	
9	*A. wiestii*	7	As									–	F	F	F	C	C			P									
10	*A. hirtula*	7	As										–	F	F	P	C		C	P			0	C	C	C	C	P	C
11	*A. atlantica*	7	As											–	F			P		P			C					S	
12	*A. strigosa*	7	As												–	P	C		S	P	C	P	0	C	C	C	C	C	C
13	*A. barbata*	14	AB													–	F	P	F	P	0	P	S	S	S	S	S	S	S
14	*A. vaviloviana*	14	AB														–		F	C								C	C
15	*A. agadiriana*	14	AB															–		P	P							P	
16	*A. abyssinica*	14	AB																–	C				C	C	C	C	P	P
17	*A. magna*	14	AC																	–	C	S	S			P	P	P	P
18	*A. murphyi*	14	AC																			S	S			S		P	
19	*A. insularis*	14	CD?																							P		P	
20	*A. macrostachya*	14	AA																				–					S	
21	*A. fatua*	21	ACD																					–	F	F	F	F	F
22	*A. occidentalis*	21	ACD																						–	F	F	F	F
23	*A. sterilis*	21	ACD																							–	F	F	F
24	*A. ludoviciana*	21	ACD																								–	F	F
25	*A. sativa*	21	ACD																									–	F
26	*A. byzantina*	21	ACD																										–

Note: F, fertile progeny; P, partial sterility; S, strong sterility; C, complete sterility; 0, noncrossing.

crossing of diploid and tetraploid species with hexaploid ones, the parents were incompatible or F_1 plants were sterile. Species with the same ploidy levels were intercrossed successfully [7].

Fertile interspecific oat hybrids were obtained in Japan with the use of the tetraploid species *A. barbata* and, later, with the use of cultivated and sand oats [20]. In 1930, an attempt was made to transfer powdery mildew resistance from the wild diploid species *A. hirtula* collected in Spain to cultivated species [21]. Most attempts to cross species of different ploidy levels made at that time were not successful.

Combined field studies performed in the late 1950s and early 1960s in the regions of the origin and maximum diversity of oat species *Avena* L. [22–24] drew the attention of researchers to the karyology and cytogenetics of cultivated oat species and their wild relatives. This added to understanding the mechanisms responsible for reproductive isolation of the species.

Since the 1950s, the investigation of wild and cultivated oat species has involved interspecific crosses conducted for various purposes [25]. On the one hand, the theoretical objective of these studies was to establish the diploid ancestor of cultivated hexaploid oat, which, in turn, would add to understanding the cytogenetics of this species and clarify its genomic formula. On the other hand, the practical task of the studies involved search for commercially important traits in wild species and their introduction into cultivated species to extend their genetic potential.

One of the first studies concerning the genomic formula of cultivated oat was performed by Nishiyama,

who crossed *A. sativa* and *A. strigosa* [20]. The pattern of chromosome conjugation in meiosis demonstrated that the diploid species *A. strigosa* is closely related to cultivated oat. The genomic formula of *A. strigosa* was designated as A. This conclusion was confirmed by karyological studies [26].

In later experiments, crosses of *A. strigosa* with the diploid species *A. hirtula* and *A. wiestii* produced fertile offspring, and their chromosomes were fully homeologous. This suggested that these species belong to one group having the same genome, thereby confirming Mal'tsev [7] suggestion on close relatedness of these forms, which he assigned to one species *A. strigosa*. It was found that these species are identical in chromosome structure because their hybrids regularly formed seven bivalents [27]. Later, this genome was designated as As.

The diploid species *A. atlantica* Baum, discovered in Morocco [28], was crossed with *A. strigosa* and other species of this group and yielded fertile offspring. On this ground, it was classified with the group of species having the As genome. Later, this was confirmed by karyological studies [29]. Some authors regarded *A. atlantica* as a wild analog of *A. strigosa* instead of *A. hirtula* [30].

Other diploid species having chromosome variants of the A genome (*A. canariensis* Baum (Ac), *A. damascena* Rajh. et Baum (Ad), *A. prostrata* (Ap), and *A. longiglumis* (Al)) differ in the results of crosses: *A. prostrata* is quite compatible with all listed species, and *A. longiglumis* is readily crossable with *A. strigosa*, whereas hybrids between *A. canariensis* and *A. damascena* are sterile [29, 30–35].

Crosses of the diploid species *A. pilosa* with cultivated oat revealed partial chromosome homeology of one of the genomes of these species. A high or complete homeology was revealed in crosses between diploid species bearing the A genome and hexaploid species. However, these species do not cross with *A. pilosa*. It was thus concluded that *A. pilosa* has a variant of the C genome [27].

Species with the C genome readily cross with each other and form seven bivalents. At the same time, no interspecific hybrids were obtained between species with the genomic formulae A and C. The species *A. ventricosa* Bal. was generally used in such studies as the donor of the C genome [36]. The range of this species (Algeria and Cyprus) is completely isolated from those of species with the A genome, which confirms their incompatibility. The scarcity of bivalents in the hybrids *A. strigosa* × *A. pilosa*, bearing the A and C genomes, confirmed the significant difference between these genomes [37].

The results of cytogenetic studies of species with the C genome are consistent with the suggestion by Mal'tsev, who pointed to a significant difference in the ecology and morphology of these taxa and recognized two series of diploid species: *Inaequaliglumes* Malz. (*A. pilosa* and *A. clauda* Dur.) and *Stipitatae* Malz. (*A. ventricosa* and *A. bruhnsiana* Grun.) [7]. The species of the former group yielded fertile offspring in crosses with each other [36, 37] and demonstrated reproductive isolation in crosses with the species of the latter group. According to the results of karyological studies, the genome of *A. pilosa* and *A. clauda* was designated as Cp [27, 38] and that of *A. ventricosa* and *A. bruhnsiana*, as Cv [27]. They were considered to be the most primitive species of the section *Euavena* Griseb. [25].

Interspecific crosses between diploid species and species with other ploidy levels demonstrated that the A genome could have been inherited from *A. strigosa* and *A. longiglumis* [39] or *A. canariensis* [31]. Only partial homeology was revealed between the chromosomes of A-genome diploids and those of cultivated oat [25]. The morphological traits of *A. canariensis* suggested that it could have been the ancestor of tetraploid and hexaploid species [31], but cytological studies did not reveal complete homeology between their chromosomes [40].

On the basis of ample factual evidence, it was suggested that *A. ventricosa* could have been the diploid donor of the C genome for tetraploid and hexaploid species [27].

All tetraploid species can be classified into four groups based on their karyotypes, morphology, and the pattern of chromosome conjugation. Group 1 includes *A barbata*, *A. vaviloviana* Mordv., and *A. abyssinica* Hoch. They are genetically uniform and possess the AB genome. According to Mal'tsev, they belong to the series *Eubarbatae* Malz., together with *A. strigosa* and other diploid species bearing the A genome [7]. Their relationships were later confirmed by the fact that the tetraploid species of this group are autotetraploids which originated from the diploid species *A. hirtula* and *A. wiestii* [41–43]. The AB genome was suggested to have resulted from the divergence of the original diploid A genome [25]. In recent studies, it is designated as AA' [44]. These species are readily crossable with all species of the genus *Avena* L., except for diploids with the C genome [45].

Group 2 includes *A. magna* and *A. murphyi*. Crossing of diploid species possessing the As genome with *A. magna* yielded partially sterile hybrids [29]. Cytological examination of the F_1 hybrids *A. barbata* × *A. magna* showed that these species are not related. Crosses *A. sativa* × *A. magna* also yielded sterile F_1 hybrids [2]. The great morphological similarity between *A. magna* and wild hexaploids and the meiotic pattern in pentaploid hybrids obtained with the use of *A. sativa* suggested that *A. magna* could have been involved in the evolution of hexaploid species as an AC tetraploid progenitor [46].

Reciprocal crosses of *A. magna* with cultivated oat and other hexaploid species demonstrated its important role in the evolution of hexaploid species [3]. The

results of interspecific crosses brought some scientists to the conclusion that the tetraploids bearing the AC genome originated from diploid species bearing its components, presumably, *A. canariensis* (A) and *A. ventricosa* (B), which was confirmed by my study [47]. There was an alternative opinion that the A genomes of *A. magna* and *A. strigosa* were identical, and the C genomes of *A. magna* and *A. pilosa* were related. Later, this hypothesis was discarded [45, 48].

Group 3 of tetraploids includes *A. macrostachya* (C), which is a perennial autotetraploid species with the genomic formula AA. According to Mal'tsev's definition for the genus *Avena* [7], the morphological features of this species allow it to be assigned to the most primitive section *Avena*strum Koch. Crosses of this species with diploids bearing various derivatives of the A genome (*A. damascena*, *A. prostrata*, *A. atlantica*, and *A. canariensis*) demonstrate negligible chromosome homeology [4, 49]. According to other studies, the most viable F_1 hybrids were *A. pilosa* × *A. macrostachya*. They often form trivalents in the metaphase. Hybrids with *A. atlantica* formed seven univalents each, and those with *A. prostrata*, seven bivalents each [50]. The mitosis study of crosses *A. barbata* × *A. macrostachya* suggested autotetraploid origin of the latter and the close relatedness of the species, although the hybrids were sterile even after chromosome duplication by colchicine [51].

The apparent differences in the morphology of *A. macrostachya* and a low percentage of chromosome conjugation in the hybrids of *A. macrostachya* with *A. sativa* and *A. murphyi* indicate that *A. macrostachya* was not involved in the evolution of tetraploid or hexaploid species [49]. Further studies demonstrated that the *A. macrostachya* genome is closer to the C (*A. pilosa*) than to the A (*A. strigosa*) genome [52]. This shows that *A. macrostachya* is evolutionarily primitive [53]. In my opinion, the presence of the symmetrical karyotype in this perennial species is not typical of diploid species with the C genome. In this feature, *A. macrostachya* is similar to the oat species having the A genome. In G.A. Levitskii's viewpoint, the presence of perfectly symmetrical karyotype confirms that the species of this group are primitive [54].

Group 4, including the species *A. agadiriana* Baum et Fed. [55], cannot be considered independent since this species is little studied. *A. agadiriana* was discovered by finding tetraploid forms in collections of the diploid species *A. canariensis* rather than discovering it in nature. Later, it was found that these species have different ranges: the diploid *A. canariensis* is endemic to Canary Islands (Spain), and the tetraploid *A. agadiriana* occurs only in Morocco. Nevertheless, it is believed that the latter is more closely related to *A. barbata* than any other tetraploid species and has the AB genome [56]. Moreover, *A. agadiriana* is similar to *A. magna*, *A. murphyi*, and other hexaploids in the structure of lodicules, upper part of the lemma, etc. The participation of *A. agadiriana* in the evolution of hexaploids is indicated by the above evidence and by the good crossability between hexaploids and this species [2, 57].

Interspecific crosses were also used for determining the genomic constitution of the most important group of hexaploids. Crosses of diploid species having the As genome (*A. strigosa* group) and tetraploid species having the AB genome with *A. sativa* demonstrated that the hexaploid species has the A genome but lacks the B genome. Cultivated oat was shown by analysis of chromosome morphology in the hybrids to have the genomic formula ACD [30]. In later studies, the A and C genomes were found to be similar to the corresponding genomes of diploids and tetraploids, whereas the origin of the D genome is still unknown [25]. The following evolutionary pathway was proposed: *A. canariensis* > *A. magna* > *A. sterilis* [31]. Later, the A genomes of *A. magna* and *A. sterilis* proved to be closer to each other than the A genomes of *A. abyssinica* and *A. sativa*. It was suggested that *A. magna* was the donor of two genomes (AC) of the hexaploid *Avena* L. species [2]. According to Leggett [45], the genomes A and D are similar to each other but different from C. The A genome of the diploid progenitor appears to have been the precursor of the A and D genomes of hexaploid species [58]. Recent studies have demonstrated that the D genome is likely to be a variant of the A" genome, like the B genome, but differs from the latter [59].

A new tetraploid species, *A. insularis* Badiz., has been recently reported in 1998. It is suggested to be one of the ancestors of the hexaploid species and is tentatively assumed to have the CD or CA" genome. This species yields fertile hybrids with *A. strigosa* with closely related *A. magna* and *A. murphyi*; hybrids were sterile. Partially fertile hybrids are obtained with hexaploid species [60].

The species *A. sterilis* is a more likely hexaploid ancestor of cultivated oat than *A. fatua* [61, 62].

The ample evidence on interspecific crosses suggests that the evolution of the genus *Avena* L. involved two strikingly different genomes: A and C. Other genomes were their more or less distant derivatives. According to the generally adopted assumption that the diploid species *A. canariensis* and *A. ventricosa* are the progenitors of the A and C genomes, respectively, the evolution of the resulting allopolyploids should have involved structural chromosome rearrangements making them partially homeologous.

Thus, the modern oat species are complex differentiated ecologic systems, whose evolution was affected by certain environmental conditions and selection.

As to the practical significance of interspecific crosses, they allow transfer of agriculturally important traits from wild and weed species to cultivated ones. All *Avena* L. species are subdivided into two groups according to their crossability. Group 1 includes all weed species readily crossable with cultivated oat.

Group 2 includes diploid and tetraploid species either not directly crossable, or yielding sterile hybrids in subsequent generations, or requiring tissue-culture methods for hybridization. The discovery of new species and collection of new specimens have significantly extended the genetic pool for oat selection with the use of wild species.

Crosses of cultivated oat with wild species are subdivided into the following groups: (1) crosses are easily performed, and the progeny is fertile (with all hexaploid species) or partially sterile (with C-genome species, *A. longiglumis*, *A. hirtula*, and *A. magna*); (2) crosses are difficult, and the progeny is substantially (with *A. barbata*) or completely (with *A. prostrata*, *A. vaviloviana*, and *A. murphyi*) sterile.

Successful hybridization of many species in the 1960s confirmed the possibility of transfer of whole chromosomes or their parts from diploid species to the genomes of cultivated hexaploid oat [63, 64]. The gene for crown-rust resistance was transferred from the diploid species *A. strigosa* into a tetraploid line, which was later used for developing multilinear oat varieties [65]. This line also provided the basis for developing the phenoperiod-nonsensitive variety Donald [66]. In 1968, a fertile hexaploid bearing a part of an *A. hirtula* chromosome with an allele of the gene for mildew resistance was obtained in Great Britain [67]. In 1970s, Forsberg transferred the gene *Pc-15* for crown-rust resistance from *A. strigosa* to a hexaploid species [68]. In 1986, a hexaploid line resistant to stem rust was obtained by transferring the *Pg-16* gene from *A. barbata* [69].

Tetraploid species are used in Great Britain for solving the most urgent problem of powdery mildew resistance. This trait was transferred from *A. barbata* to a number of cultivars: Maris Tabard, Maris Oberon, Margam, and Maldwyn [70].

Cross incompatibility presents the greatest difficulty in transferring genes 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 the tetraploid species *A. magna* and *A. murphyi* with cultivated oat, and their fertility can be restored by backcrossing with *A. sativa* pollen. This approach for application of tetraploid species in oat breeding for grain quality and weight was developed in Sweden [71]. Natural backcrossing by sowing pentaploid F_1 hybrids in cultivated-oat plots can be used in crosses involving *A. barbata* and *A. macrostachya*. Cross incompatibility between diploids and cultivated oat is often overcome by colchicine-mediated chromosome duplication. Irradiation with thermal neutrons enabled to transfer genes for crown-rust resistance from *A. abyssinica* to *A. sativa* [72].

The most successful method for overcoming chromosome incompatibility was reported in [73]. It involved the CW-57 specimen of the diploid species *A. longiglumis*, which favored conjugation of homeologous chromosomes during transfer to mildew-resistance genes from the tetraploid *A. barbata* to cultivated oat. A good example of such intermediation is the development of the hexaploid line Amagalon, bearing the allele of the gene *Pc-91* transferred from *A. magna* through *A. longiglumis* [74]. The same approach can be used in other crosses.

At present, interspecific crosses among hexaploid oat species have gained the most widespread acceptance because new alleles can be transferred by routine programs involving cyclic crosses.

Starting from the 1960s, oat selection in the USA was based on wild hexaploid species [5, 75]. Involvement of *A. fatua* and *A. sterilis* in breeding was quite common. It yielded many oat varieties grown in vast areas of the USA, Canada, and Australia: Rapida and Sierra [76, 77]; Mesa [78]; Calif. C.C.II and Montezuma [79, 80]; Marvellous [81]; Dumont, Fidler [82, 83]; Multiline E77, Multiline E76, and Webster [84, 85]; Starter [86]; Panfive, Centennial, and Ozark [87]; etc.

These breeding methods allow many agriculturally important traits to be transferred into cultivated oat for extending its gene pool as well as the gene pool of the entire genus.

In Russia, interspecific crosses and, in particular, use of wild oat species are little used. For this reason, researchers of the Vavilov All-Russia Institute for Plant Production started investigating the gene pool of wild species to extend the genetic potential of cultivated oat species [88, 89].

At present, the Vavilov All-Russia Institute for Plant Production possesses a rich collection of *Avena* L. species. It contains about 10 000 accessions of four cultivated oat species and 2000 accessions of twenty-one wild species. The wild accessions represent numerous morphological variants reflecting their wide geographic distribution in the Mediterranean countries. A representative collection was made in Transcaucasia, where wild oat species are the most diverse in the CIS countries [90, 91].

In addition to taxonomical identification involving morphological traits, the species of the specimens were identified by avenin patterns. This method involves the determination of species-specific storage proteins. In addition, it can be used for establishing phylogenetic relationships between related species and their position in the genus [92].

Former identifications of some specimens were revised by invoking karyological data involving chromosome counts (ploidy analysis) and karyotype description [93].

Most of the collection of wild and weed oat species were investigated in the plots of the Pushkino laboratories of the Vavilov All-Russia Institute for Plant Production to develop approaches to interspecific crosses. The main problem was to recognize early-ripening spring varieties among di- and tetraploid species. This would permit crosses with cultivated oat to be per-

formed under field conditions and high-quality seeds of both hybrids and parental species to be obtained.

The agricultural performance of the species was estimated by several indices: field disease resistance (crown and stem rust, powdery mildew, BYDV, etc.), duration of vegetation (early ripening (74–100 days) forms and those tending to the winter habit), plant height (short-culm forms below 60 cm were found), productivity (weight of 1000 grains exceeding 35 g and a low glumosity), grain yield, and morphological traits closely correlating with agricultural ones [92, 94–100].

Moreover, forms differing in the sensitivity to photoperiod and vernalization were found [101]. Determination of salt tolerance showed that the investigated specimens of wild species outperformed cultivated oat in this index by several times [102].

Protein content, amino acid composition, including lysine, oil content, and fatty acid composition were assayed in a number of oat species. Some specimens contained 28% protein (lysine, 5.7% of the protein) and 10% oil [92, 103, 104, 106].

At the next stage, di- and tetraploid species were introduced into breeding programs. Diploid species were crossed with cultivated oat to investigate their compatibility and the regenerating and callus-forming ability in species of various ploidy levels and their hybrids [105].

The long-term studies involved interspecific crosses conducted for various purposes: increasing oil content in grain and obtaining short-culm hybrids and lines resistant to crown rust.

The comprehensive study of the entire range of species in the genus *Avena* L. allows better understanding of the phylogeny of such a valuable crop as oat. Use of the diverse wild oat species with regard to their morphological traits, geographic occurrence, and ecological preference is the most promising method for preventing the loss of the genetic potential of cultivated varieties. Of great importance is the comprehensive choice and study of the breeding material invoking physiological, phytopathological, biochemical, and molecular-biological evidence.

REFERENCES

1. Rodionova, N.A., Soldatov, V.N., Merezhko, V.E., *et al.*, *Kul'turnaya flora* (Cultivated Flora), vol. 2: *Oves* (Oat), Moscow: Kolos, 1994, ch. 3.
2. Thomas, H., New Species of *Avena*, *Proc. 3rd Int. Oat Conf.*, Lund, Sweden, 1989, pp. 18–23.
3. Ladizinsky, G., Biological Species and Wild Genetic Resources in *Avena*, *Proc. 3rd Int. Oat Conf.*, Lund, Sweden, 1989, pp. 76–86.
4. Leggett, J.M., *A* Further *Avena macrostachya* Hybrid, *Proc. 4th Int. Oat Conf.*, Adelaide, Australia, 1992, vol. 3, pp. 152–153.
5. Frey, K.J., Genetic Resources of Oats, *Use of Plant Introductions in Cultivar Development*, 1991, part 1, no. 17.
6. Pasynkov, V.I., Use of Wild Oat Species in Breeding, *Sel. Khoz. za Rubezhom*, 1971, no. 7, pp. 18–20.
7. Mal'tsev, A.I., Wild and Cultivated Oat Species of Sectio *Euavena* Griseb., *Tr. Prikl. Bot., Genet. Sel.*, L., 1930, suppl. 38.
8. Mal'tsev, A.I., Several Observations on Plant Development in Wild and Undesirable Oat Species, *Tr. Byuro Prikl. Bot.*, 1914, vol. 4, no. 12, p. 788.
9. Loskutov, I.G., Some Historical Aspects of VIR *Avena* World Collection, *Proc. 2nd Int. Crop. Sci. Congr.*, New Delhi, India, 1996, p. 140.
10. Loskutov, I.G., *Vavilov and His Institute: A History of the World Collection of Plant Genetic Resources in Russia*, Rome: IPGRI, 1999.
11. Vavilov, N.I., Materials on Cereal Resistance to Parasitic Fungi, *Tr. Selekts. St. Mosk. S–kh. Inst.*, 1913, no. 1, pp. 16–28, 66–69.
12. Vavilov, N.I., Plant Immunity to Infections, *Ott. Izv. Petrovsk. S–kh. Akad., God 1918*, Moscow, 1919, pp. 25–27, 128–134, 180–184.
13. Zhegalov, S.I., Several Observations on Oat Hybrids, *Trudy III Vserossiiskogo s"ezda po selektsii i genetike* (Proc. III Ros. Meet. on Breeding and Genetics), Saratov, 1920, p. 84.
14. Zhegalov, S.I., Crosses between Chaffy and Naked Oat Species, *Nauchno-Agron. Zh.*, 1924, vol. 1, no. 2, p. 130.
15. Zhegalov, S.I., *Vvedenie v selektsiyu sel'skokhozyaistvennykh rastenii* (Introduction to the Breeding of Cultivated Plants), Moscow, 1927.
16. Mitrofanova, K.S., To the Analysis of Several Interspecific Crosses in Oat, *Nauchno-Agron. Zh.*, 1927, no. 4.
17. Nikolaeva, A.G., Use of the Cytological Method in Studying Certain Genetic Problems, *Trudy III Vserossiiskogo s"ezda po selektsii i genetike* (Proc. III Ros. Meet. on Breeding and Genetics), Saratov, 1920, p. 39.
18. Mal'tsev, A.I., A New System of Sectio *Euavena* Griseb., *Byull. Prikl. Bot., Genet. Sel.*, 1929, vol. 20, pp. 127–149.
19. Emme, E.K., Karyotaxonomic Study of Oat of Sectio *Euavena* Griseb., *Tr. Prikl. Bot., Genet. Selekts., Ser. II*, 1932, no. 1, pp. 147–168.
20. Nishiyama, I., The Genetic and Cytology of Certain Cereals: I. Morphological and Cytological Studies in Triploid, Pentaploid, and Hexaploid *Avena* Hybrids, *Jpn. J. Genet.*, 1929, no. 5, pp. 1–48.
21. Jones, E.T., A Comparison of the Segregation of Wild versus Normal or Cultivated Base in the Grain of Diploid, Tetraploid, and Hexaploid Species of Oats, *Genetica* (The Hague), 1940, no. 22, pp. 419–434.
22. Baum, B.R., Rajhathy, T., Fleischmann, G., *et al.*, *Wild Oat Gene Pool: A Collection Maintained by the Canada Department of Agriculture, publ. 1475*, Can. Dep. Agric., 1972.
23. Rajhathy, T., Zillinsky, F.J., and Hayes, J.D., *Report on Canada–Wales Expedition, 1964*, Can. Dep. Agric., 1964.
24. Rajhathy, T., Zillinsky, F.J., and Hayes, J.D., *A Collection of Wild Oat, Mediterranean Region*, Ottawa: Can Dep. Agric. Res., 1966.

25. Rajhathy, T. and Thomas, H., Cytogenetics of Oats (*Avena* L.), *Misc. Publ. Genet. Soc. Can.*, 1974, no. 2, pp. 5–90.
26. Rajhathy, T., A Standard Karyotype for *Avena sativa*, *Can. J. Genet. Cytol.*, 1963, vol. 5, no. 2, pp. 127–132.
27. Rajhathy, T., Evidence and Hypothesis for the Origin of the C Genome of Hexaploid *Avena*, *Can. J. Genet. Cytol.*, 1966, vol. 8, no. 4, pp. 774–779.
28. Baum, B.R. and Fedak, G., *Avena atlantica*, a New Diploid Species of the Oat Genus from Morocco, *Can. J. Bot.*, 1985, vol. 63, pp. 1057–1060.
29. Leggett, J.M., Interspecific Hybrids Involving the Recently Described Diploid Taxon *Avena atlantica*, *Genome*, 1987, vol. 29, pp. 361–364.
30. Rajhathy, T. and Morrison, J.W., Chromosome Morphology in the Genus *Avena*, *Can. J. Bot.*, 1959, vol. 37, no. 3, pp. 372–377.
31. Baum, B.R., Rajhathy, T., and Sampson, D.R., An Important New Diploid *Avena* Species Discovered on the Canary Islands, *Can. J. Bot.*, 1973, vol. 51, pp. 759–762.
32. Ladizinsky, G., The Cytogenetic Position of *Avena prostrata* among the Diploid Oats, *Can. J. Genet. Cytol.*, 1973, vol. 15, pp. 443–450.
33. Leggett, J.M., Morphology and Metaphase Chromosome Pairing in Three *Avena* Hybrids, *Can. J. Genet. Cytol.*, 1984, vol. 26, pp. 361–364.
34. Rajhathy, T., Chromosomal Differentiation and Speciation in Diploid *Avena*, *Can. J. Genet. Cytol.*, 1961, vol. 3, no. 4, pp. 372–377.
35. Rajhathy, T. and Baum, B.R., *Avena damascena*: A New Diploid Oat Species, *Can. J. Genet. Cytol.*, 1972, vol. 14, pp. 645–654.
36. Rajhathy, T. and Thomas, H., Chromosomal Differentiation and Speciation in Diploid *Avena*: III. Mediterranean Wild Populations, *Can. J. Genet. Cytol.*, 1967, vol. 9, no. 1, pp. 52–68.
37. Nishiyama, I. and Yabuno, T., Meiotic Chromosome Pairing in Two Interspecific Hybrids and a Criticism of the Evolutionary Relationship of Diploid *Avena*, *Jpn. J. Genet.*, 1975, vol. 50, pp. 443–451.
38. Rajhathy, T. and Dyck, P.L., Chromosomal Differentiation and Speciation in Diploid *Avena*: II. The Karyotype of *A. pilosa*, *Can. J. Genet. Cytol.*, 1963, vol. 5, no. 2, pp. 175–179.
39. Rajhathy, T., The Allopolyploid Model in *Avena*, *Proc. 3rd Stadler Symp.*, 1971, pp. 71–87.
40. Leggett, J.M., Chromosome Relationships and Morphological Comparisons between the Diploid Oats *Avena prostrata*, *A. canariensis*, and the Tetraploid *A. maroccana*, *Can. J. Genet. Cytol.*, 1980, vol. 22, pp. 287–294.
41. Holden, J.H.W., Species Relationships in the Avenae, *Chromosoma*, 1966, vol. 20, no. 1, pp. 75–124.
42. Ladizinsky, G. and Zohary, D., Genetic Relationships between Diploids and Tetraploids in Series Eubarbatae of *Avena*, *Can. J. Genet. Cytol.*, 1968, vol. 16, pp. 105–112.
43. Sadasivaiah, R.S. and Rajhathy, T., Genome Relationships in Tetraploid *Avena*, *Can. J. Genet. Cytol.*, 1968, vol. 10, pp. 655–669.
44. Fabijanski, S., Fedak, G., Armstrong, K., and Altosaar, I., A Repeated Sequence Probe for the C Genome in *Avena* (Oats), *Theor. Appl. Genet.*, 1990, vol. 79, pp. 1–7.
45. Leggett, J.M. and Markland, G.S., The Genomic Structure of *Avena* Revealed by GISH, *Proc. Kew Chrom. Conf. IV*, 1995, pp. 133–139.
46. Ladizinsky, G. and Zohary, D., Notes on Species Delimination, Species Relationships, and Polyploidy in *Avena* L., *Euphytica*, 1971, vol. 20, no. 3, pp. 380–395.
47. Loskutov, I.G., On the Taxonomy of Genus *Avena* L., *Proc. XVI Int. Bot. Congr.*, United States, 1999, p. 422.
48. Leggett, J.M., Chromosome and Genomic Relationship between the Diploid Species *Avena strigosa*, *A. eriantha*, and the Tetraploid *A. maroccana*, *Heredity*, 1998, vol. 80, no. 3, pp. 361–367.
49. Leggett, J.M., Interspecific Hybrids Involving the Perennial Oat Species *Avena macrostachya*, *Can. J. Genet. Cytol.*, 1985, vol. 27, pp. 29–32.
50. Pohler, W. and Hoppe, H.D., Homeology between the Chromosomes of *Avena macrostachya* and the *Avena* C Genome, *Plant Breed.*, 1991, vol. 106, no. 3, pp. 250–253.
51. Hoppe, H.D. and Pohler, W., Hybrids between *Avena barbata* and *A. macrostachya*, *Cereal Res. Commun.*, 1989, vol. 17, no. 2, pp. 129–134.
52. Leggett, J.M., A New Triploid Hybrid between *Avena eriantha* and *A. macrostachya*, *Cereal Res. Commun.*, 1990, vol. 18, nos. 1–2, pp. 97–110.
53. Stebbins, G.L., *Chromosomal Evolution in Higher Plants*, London, 1971.
54. Levitskii, G.A., *Tsitologiya rastenii. 1931. Izbrannye trudy* (Plant Cytology, 1931: Selected Works), Moscow: Nauka, 1976.
55. Baum, B.R. and Fedak, G., A New Tetraploid Species of *Avena* Discovered in Morocco, *Can. J. Bot.*, 1985, vol. 63, pp. 1379–1385.
56. Leggett, J.M., Inter- and Intra-Specific Hybrids Involving the Tetraploid Species *Avena agadiriana* Baum et Fedak sp. nov. ($2n = 4x = 28$), *Proc. 3rd Int. Oat Conf.*, Lund, Sweden, 1989, pp. 62–67.
57. Alicchio, R., Aranci, L., and Conte, L., Restriction Fragment Length Polymorphism-Based Phylogenetic Analysis of *Avena* L., *Genome*, 1995, vol. 38, no. 6, pp. 1279–1284.
58. Linares, C., Gonzalez, J., Ferrer, E., and Fominaya, A., The Use of Double Fluorescence *in situ* Hybridization to Physically Map the Positions of 5S rRNA Genes in Relation to the Chromosomal Location of 18S–5.8S–26S rDNA and a C Genome-Specific DNA Sequence in the Genus *Avena*, *Genome*, 1996, vol. 39, no. 3, pp. 535–542.
59. Leggett, J.M., A Revision of Genome Evolution in Hexaploid *Avena*?, *Experimental Biology Online: Aberystwyth cell genetics group meeting*, 1997.
60. Ladizinsky, G., Cytogenetic Relationships between *Avena insularis* ($2n = 28$) and Both *A. strigosa* ($2n = 14$) and *A. murphyi* ($2n = 28$), *Genet. Res. Crop Evol.*, 1999, vol. 46, pp. 501–504.
61. Zhou, X., Jellen, E.N., and Murphy, J.P., Progenitor Germplasm of Domesticated Hexaploid Oat, *Crop Sci.*, 1999, vol. 39, pp. 1208–1214.

62. Jellen, E.N. and Beard, J., Geographical Distribution of a Chromosome 7C and 17 Intergenomic Translocation in Cultivated Oat, *Crop Sci.*, 2000, vol. 40, pp. 256–263.
63. Rajhathy, T. and Sadasivaiah, R.S., The Cytogenetic Status of *Avena magna*, *Can. J. Genet. Cytol.*, 1969, vol. 11, pp. 77–85.
64. Thomas, H. and Thomas, P., Cytology, *Report Welsh Plant Breed. St.*, 1962, pp. 94–96.
65. Zillinsky, F.J. and Derick, R.A., Crown Rust-Resistant Derivatives from Crosses between Autotetraploid *Avena strigosa* and *A. sativa*, *Can. J. Plant. Sci.*, 1960, vol. 40, pp. 366–370.
66. Burows, V.C., Donald Oats, *Can. J. Plant Sci.*, 1984, vol. 64, pp. 411–413.
67. Thomas, H., The Addition of Single Chromosome of *Avena hirtula* to the Cultivated Hexaploid Oat *A. sativa*, *Can. J. Genet. Cytol.*, 1968, vol. 10, pp. 551–563.
68. Thomas, H., Cytogenetics of *Avena*, *Oat Science and Technology*, Marshall, H.G. and Sorrels, M.E., Eds., United States: Agronomy, 1992, no. 33, pp. 473–507.
69. Ohm, H.W. and Shaner, G., Breeding Oat for Resistance to Diseases, *Oat Science and Technology*, Marshall, H.G. and Sorrels, M.E., Eds., United States: Agronomy, 1992, no. 33, pp. 657–698.
70. Jones, I.T., O'Reilly, A.M., and Davies, I.J.E.R., Cereal Breeding: Durable Resistance to Powdery Mildew in Oats, *Annual Report, 1983, Oats*, Welsh Plant Breed. St., 1984, pp. 93–94.
71. Hagberg, P., Interspecific Crosses in Oats (Abstract), *Nordisk-Jordbrugsforskning*, 1983, vol. 65, no. 2.
72. Sharma, D.C. and Forsberg, R.A., Spontaneous and Induced Interspecific Gene Transfer for Crown Rust Resistance in *Avena*, *Crop Sci.*, 1977, vol. 17, pp. 855–860.
73. Thomas, H., Powell, W., and Aung, T., Interfering with Regular Meiotic Behavior in *Avena sativa* as a Method of Incorporating the Gene for Mildew Resistance from *A. barbata*, *Euphytica*, 1980, vol. 29, pp. 635–640.
74. Rothman, P.G., Registration of Four Stem Rust and Crown Rust Resistant Oat Germplasm Lines, *Crop. Sci.*, 1984, vol. 24, pp. 1217–1218.
75. Frey, K.J., Remaking a Crop Gene Pool: The Case History of *Avena*, Toward Enhanced and Sustainable Agricultural Productivity in the 2000's: Breeding Research and Biotechnology, *Proc. SABRAO 7th Int. Congr. and WSAA Symp. Held at Academia Sinica, Nankang, Taipei, Taiwan, November 16–20, 1993*, Special Publication Taichung District Agricultural Improvement Station, 1994, vol. 1, no. 35, pp. 1–14.
76. Suneson, C.A., Registration of Rapida Oats, *Crop Sci.*, 1967, vol. 7, p. 168.
77. Suneson, C.A., Registration of Sierra Oats, *Crop Sci.*, 1967, vol. 7, p. 168.
78. Thompson, R.K., Registration of Mesa Oats, *Crop Sci.*, 1967, vol. 7, p. 167.
79. Suneson, C.A., Registration of Calif. C.C.II Oat Germplasm, *Crop Sci.*, 1969, vol. 9, p. 527.
80. Suneson, C.A., Registration of Montezuma Oats, *Crop Sci.*, 1969, vol. 9, p. 527.
81. Baum, B.R., Pedigrees and Other Basis Data of Cultivars Oats, *World Wide Material That Is Needed for Identification and Registration*, Res. Branch Canada Dep. Agr., 1969.
82. McKenzie, R.I.H., Brown, P.D., Martens, J.W., *et al.*, Registration of Dumont Oats, *Crop Sci.*, 1984, vol. 24, p. 207.
83. McKenzie, R.I.H., Martens, J.W., Brown, P.D., *et al.*, Registration of Fidler Oats, *Crop Sci.*, 1981, vol. 21, p. 623.
84. Frey, K.J., Browning, J.A., and Simons, M.D., Registration of Multiline E76 and Multiline E77 Oats, *Crop Sci.*, 1985, vol. 25, p. 1125.
85. Frey, K.J., Michel, L.J., Murphy, J.P., and Browning, J.A., Registration of Webster Isolines, *Crop Sci.*, 1986, vol. 26, pp. 374–375.
86. Stuthman, D.D., Wilcoxson, R.D., and Rines, H.W., Registration of Starter Oat, *Crop Sci.*, 1990, vol. 30, pp. 1365–1366.
87. McMullen, M.S. and Patterson, F.L., Oat Cultivar Development in the USA and Canada, *Oat Science and Technology*, Marshall, H.G. and Sorrels, M.E., Eds., United States: Agronomy, 1992, no. 33, pp. 573–612.
88. Trofimovskaya, A.Ya., Pasynkov, V.I., Rodionova, N.A., and Soldatov, V.N., Genetic Potential of True Oat Section of the Genus *Avena* and Its Importance for Breeding, *Tr. Prikl. Bot., Genet. Sel.*, L.: VIR, 1976, vol. 58, no. 2, pp. 83–109.
89. Yarosh, N.P., Rodionova, N.A., and Pasynkov, V.A., Biochemical Properties of Several Wild and Cultivated Oat Species, *Byull. Vses. Inst. Rastenievod.*, 1977, no. 73, pp. 14–20.
90. Soldatov, V.N. and Loskutov, I.G., Wild Oat Species from Trans-Caucasia, *Nauchno-Tekhn. Byull. Vses. Inst. Rastenievod.*, 1992, no. 224, pp. 34–37.
91. Loskutov, I.G., Introduction to VIR's Oat Collection: Documentation, Characterization, and Evaluation, *Report of a Working Group on Avena*, Godolo, Hungary: IBPGR, 1993, pp. 30–36.
92. Loskutov, I.G., Chmeleva, Z.V., Gubareva, N.K., *et al.*, *Katalog mirovoi kollektsii VIR, Oves (Kharakteristika zerna obraztsov dikorastushchikh vidov ovsa po soderzhaniyu i aminokislotnomu sostavu belka i po soderzhaniyu i zhirnokislotnomu sostavu masla v usloviyakh Leningradskoi oblasti. Belkovye formuly ovsa po elektroforeticheskim spektram avenina)* (Catalog of the World Collection of the Institute of Plant Breeding: Oat (Characterization of Wild Oat Species by the Content and Amino Acid Composition of Proteins and the Content and Fatty Acid Composition of Oil in Grains Obtained in the Leningrad Oblast; Oat Protein Formulas Inferred from Avenin Electrophoretic Patterns)), St. Petersburg, 1999, no. 704.
93. Abramova, L.I., Karyotypic Characters of Oat (*Avena* L.) Species with Differing Genomes, *Nauchno-Tekhn. Byull. Vses. Inst. Rastenievod.*, 1987, no. 170, pp. 51–55.
94. Loskutov, I.G., Intraspecific Diversity in Oat *Avena barbata* Pott. and *A. sterilis* L., *Nauchno-Tekhn. Byull. Vses. Inst. Rastenievod.*, 1990, no. 201, pp. 53–57.
95. Loskutov, I.G., Wild Oat Species as a Source of Lodging Resistance, *Nauchno-Tekhn. Byull. Vses. Inst. Rastenievod.*, 1992, no. 226, pp. 13–17.
96. Loskutov, I.G., A Collection of Wild Oat Species of the Genus *Avena* L. as a Source of Diversity of Commer-

cially Valuable Traits, *Trudy 1 Vserossiiskoi konferentsii po bot. resursovedeniyu* (Proc. 1st. Rus. Conf. on Plant Resources), St. Petersburg, 1996, pp. 158–159.

97. Loskutov, I.G., A Collection of Wild Oat Species Growing in the Former Soviet Union Is a Source of Diversity of Agronomic Traits, *Tr. Prikl. Bot., Genet. Sel.*, St. Petersburg: VIR, 1997, vol. 151, pp. 81–88.
98. Loskutov, I.G. and Merezhko, V.E., *Katalog mirovoi kollektsii VIR: Oves (Obraztsy s identifitsirovannymi genami, kontroliruyushchimi biologicheskie, morfologicheskie i khozyaistvenno-tsennye priznaki)* (Catalog of the World Collection of the Institute of Plant Breeding: Oat (Samples with Identified Genes for Biological, Morphological, and Commercially Valuable Traits)), St. Petersburg, 1997, no. 687.
99. Loskutov, I.G., The Collection of Wild Species of CIS as a Source of Diversity in Agricultural Traits, *Genet. Res. Crop Evol.*, 1998, vol. 45, no. 4, pp. 191–195.
100. Soldatov, V.N., Merezhko, V.E., and Loskutov, I.G., Evaluation of Cultivated and Wild Oat Species for Tolerant to BYDV, *Oat Newslett.*, 1990, vol. 41, p. 70.
101. Loskutov, I.G., Influence of Vernalization and Photoperiod to the Vegetation Period of Wild Species of Oats (*Avena* spp.), *Euphytica*, 2001, vol. 117, no. 2, pp. 125–131.
102. Kosareva, I.A., Loskutov, I.G., Semenova, E.V., and Davydova, G.V., Study of Aluminum Resistance in Wild Oat Species, *Trudy konferentsii "Aktual'nye problemy selektsii i semenovodstva zernovykh kul'tur Yugo-Vostochnogo regiona RF"* (Proc. Conf. "Urgent Problems in Breeding and Seed Production of Cereals in Southeastern Russia"), Saratov, 1999, pp. 81–82.
103. Loskutov, I.G. and Moskaleva, G.I., Use of the Anatomical Method to Quantify Oil in Oat Grains, *Trudy Mezhdunarodnoi konferentsii po anatomii i morfologii rastenii* (Proc. Int. Conf. on Plant Anatomy and Morphology), St. Petersburg, 1997, pp. 83–84.
104. Loskutov, I.G. and Chmeleva, Z.V., Agronomic Traits and Grain Biochemical Characters in Wild Oat Species, *Tr. Prikl. Bot., Genet. Sel.*, St. Petersburg: VIR, 1997, vol. 151, pp. 98–106.
105. Loskutov, I.G. and Pendinen, G.I., Specific Features of in vitro Regeneration of Wild *Avena* L. Species Differing in Genome Composition, *Tezisy II mezhdunarodnoi konferentsii po biotekhnologii* (Proc. II Int. Conf. on Biotechnology), Moscow, 2000, pp. 137–138.
106. Loskutov, I.G., Some Quality Groat Characters in Oat Wild Species, *Proc. 6th Int. Oat Conf.*, New Zealand, 2000, pp. 248–253.