COLLECTIONS OF THE WORLD'S CROP GENETIC RESOURCES FOR THE DEVELOPMENT OF PRIORITY PLANT BREEDING TRENDS

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Assessment of oat varieties with different levels of breeding refinement from the Vavilov Institute's collection applying the method of metabolomic profiling

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Metabolomic profiling data obtained through gas chromatography coupled with mass spectrometry are presented. Thirty oat accessions from the collection of the N.I. Vavilov Institute of Plant Genetic resources (VIR) served as the material for the research. Those accessions of Russian and French origin showed different degrees of breeding refinement: from local landraces (the early 1920s) and primitive cultigens (1920–1930s) to modern improved cultivars. Twenty-seven hulled and three naked oat varieties were selected for the study.

The main objective of the work was to identify differences among common oat varieties with different degrees of breeding refinement at the level of metabolomic profiles. The resulting data reflected the metabolic state of oat genotypes with different ecogeographic backgrounds. They were compared to assess the content of main metabolite groups important for the formation of the crop's stress resistance traits as well as nutritional, medicinal and dietary properties of oat grain products. The most informative indicators were identified (fucosterol, chiro-inositol, xylitol; undecylic, threonic, glutamic, ribonic and phosphoric acids; sorbose, fructose, glucose-3-phosphate, and myo-inositol), which helped to make statistically significant differentiation among oat accessions of different origin with various degrees of breeding refinement. Comparing metabolomic profiles of different oat variety groups (landraces, primitive cultigens, and modern cultivars, developed by Russian and French breeders) mirrored distinctive features of the trends followed by different plant breeding schools.

This study showed that breeding efforts to improve biochemical indicators in oat grain would require the use of the genetic diversity found in landraces and primitive cultigens collected or developed in the 1920–1930s. This diversity is still preserved and maintained in the global germplasm collection at VIR.

Keywords: *Avena sativa* L., landraces, primitive cultigens, improved cultivars

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КОЛЛЕКЦИИ МИРОВЫХ ГЕНЕТИЧЕСКИХ РЕСУРСОВ КУЛЬТУРНЫХ РАСТЕНИЙ ДЛЯ РАЗВИТИЯ ПРИОРИТЕТНЫХ НАПРАВЛЕНИЙ СЕЛЕКЦИИ

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Дифференциация сортов овса из коллекции ВИР по степени селекционной проработки на основе метаболомного профилирования

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Объектом данного исследования были 30 образцов овса из коллекции Всероссийского института генетических ресурсов растений им. Н. И. Вавилова (ВИР) российского и французского происхождения разного уровня селекционной проработки – местные (начало 1920-х годов), примитивные селекционные (1920–1930-х годов) и современные селекционные сорта.

Основная задача работы – выявление различий между сортами овса разной степени селекционной проработки на уровне метаболомных профилей. Полученные результаты отражали метаболическое состояние генотипов различного эколого-географического происхождения. Проведено сравнение по основным группам метаболитов, имеющим важное значение для формирования признаков устойчивости культуры к стрессорам, а также пищевых, лечебных, диетических достоинств зерновой продукции. Выделены наиболее информационно ценные признаки (фукостерол, хиро-инозитол, ксилит, ундециловая, треоновая, глутаминовая, рибоновая, фосфорная кислоты, сорбоза, фруктоза, глюкозо-3-фосфат, мио-инозитол), позволившие достоверно разделить образцы овса различного происхождения и с разной степенью селекционной проработки. Сравнение метаболомных профилей групп сортов овса российской и французской селекции – местных, примитивных, а также современных – отражает особенности направления работ различных селекционных школ.

Наше исследование показало, что при проведении селекционных работ на улучшение биохимических показателей зерновок овса необходимо использовать ресурсы генетического разнообразия российских местных и примитивных селекционных сортов, собранных и созданных в 20–30-е годы XX столетия, которые до настоящего времени сохраняются и поддерживаются в мировой коллекции ВИР.

Ключевые слова: *Avena sativa* L., местные, примитивные и селекционные сорта

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Introduction

Lately, qualitative indicators have been catching up with grain yield in their value for crop production. Traditional trends in cereal crop breeding are higher protein, lysine and starch content in grain, while its dietetic properties are gaining more and more attention among breeders. In addition to protein, cereal grains are rich in other compounds as well, including essential amino acids and antioxidants. Besides, the breeding value of source material is determined by the characteristics underpinning resistance to biotic and abiotic environmental stresses.

The thoughts published almost a hundred years ago by N.N. Ivanov and N.A. Bazilevskaya, Vavilov's associates and VIR's employees, characterized the present-day situation in the best of ways: "At present, a breeder who ignores chemistry while selecting cultivars… cannot work in the manner… that we now require. Such a breeder has already played his role in the history of plant breeding… Now he needs to rely on biochemistry with its entire arsenal of achievements and methods." (Ivanov, 1935, p. 991); "The modern industry is no longer satisfied with our offer of cultivars. One of the ways to solve this problem is the selection of forms found on the border of quantitative variations within a species, containing optimal amounts of the required chemical compound" (Bazilevskaya, 1935, p. 1038).

The most important chemical compounds that determine valuable dietary, medicinal and biological properties of cultivated plants are secondary metabolites and main products of primary metabolisms, such as polysaccharides, proteins and lipids. To measure the content of known bioactive compounds and search for new ones, plant genetic resources need to be screened using the most advanced techniques (Konarev, Horeva, 2000; Konarev et al., 2015; Horeva et al., 2018; Konarev et al., 2019).

The common oat (*Avena sativa* L.) is presently one of the most promising and popular crops in the context of its valuable properties that meet the requirements of 'functional food' producers and favor its use for animal feed or medical and prophylactic purposes (Loskutov, 2007; Leonova et al., 2008; Loskutov, Rines, 2011). Oat grain proteins are better balanced in their amino acid composition than those of other cereals. Oat oil contains unsaturated fatty acids essential for the human organism – linoleic, linolenic and arachidonic acids, aggregately composing the so-called 'vitamin F' (Loskutov, 2007; Leonova et al., 2008). Oat is also a valuable source of β-glucans, pectins, vitamin E, avenanthramides and other phenolic antioxidants, and phytosterols. The presence of these and other health-friendly bioactive compounds makes oat an indispensable ingredient in the human diet (Loskutov, 2007; Konarev et al., 2015; Leonova et al., 2020).

Metabolomic profiling one of the most significant methodological achievements in the past decades, which are (Lokhov, Archakov, 2008; Shulaev et al., 2008) effective in disclosing the 'implementation' mechanisms of such complex characters as resistance to stressors, in studying the dynamics of biochemical composition in ontogenesis, under various agricultural practices and growing conditions, and in the context of different cultivar attribution (specificity) of seeds, etc. (Konarev et al., 2019; Smolikova et al., 2015; Schauer, Fernie, 2006; Langridge, Fleury, 2011; Balmer et al., 2013).

Searching for known and unexplored compounds that directly or indirectly influence the solution of the human nutrition problems requires a detailed and scientifically informed study of plant genetic resources using high-performance biochemical techniques (Loskutov et al., 2017), which means "… to rely on biochemistry with its entire arsenal of achievements and methods." (Ivanov, 1935, p. 1003).

It is well known that crop wild relatives and closely related species are an inexhaustible source of valuable traits for new cultivars. VIR maintains a rich collection of wild oat species, which has been studied for many years, including analyzing biochemical indicators of quality, resistance to biotic and abiotic stressors, etc. (Konarev, Horeva, 2000; Loskutov, 2007; Loskutov et al., 2019; Leonova et al., 2008; Loskutov, Rines, 2011; Loskutov et al., 2017).

Metabolomic profiling of cultivated and wild oat grains showed that the range of variability in the content of the studied groups of compounds was considerably narrower in improved cultivars than in wild oat species. Metabolites were identified, whose content had decreased in the process of domestication, or which distinguished wild oat species from oat cultivars. It may be associated with the formation of environmental adaptability traits, such as resistance to diseases, pests, and abiotic stressors (Žilić et al., 2011; Loskutov et al., 2017). Several properties specific to adaptability could be lost in the breeding process that was aimed at the development of highly specialized lines and intensive-type cultivars, because such process entails a decrease in the genetic polymorphism of improved cultivars, compared with the plant population composition characteristic of wild species and local varieties produced by folk breeding (Shulaev et al., 2008; Perkowski et al., 2012; Gu et al., 2015; Loskutov et al., 2017).

Accumulation of certain metabolites in cells is associated with the integrated drought resistance mechanism in plants (Sánchez-Martín et al., 2015). The presence of other secondary metabolites in many cereal crops is linked with their resistance to diseases and pests (Shelenga et al. 2005, Bolton, 2009, Bushnell et al., 2009, Sitkin et al., 2013, Warth et al., 2015, Kokubo et al., 2017, Loskutov et al., 2019).

Statistical significance of the differences between metabolomic profiles of naked and hulled oats was confirmed mathematically. The revealed significant differences between naked and hulled oat accessions attest to genetic differentiation among common oat subspecies (Loskutov et al., 2020; Loskutov et al., 2017).

Previous findings (Harrigan et al., 2005; Hollywood et al., 2006; Shulaev, 2006; Yandeau-Nelson et al., 2015) verified that the specificity of a metabolomic profile is determined by the interplay between a certain genotype and environmental conditions (Žilić et al., 2011; Björck et al., 2012; Khakimov et al., 2014; Kokubo et al., 2017). It is a promising tool to identify relationships between biochemical indicators and genetic features in cereal crops and to open new opportunities for quality-targeted breeding efforts (Fernie, Schauer, 2009).

Analyzing grains of Polish landraces collected in close geographic proximity showed a distinct similarity in morphological characters and metabolomic profiles, although they differed much when judged by the results of a molecular-genetic analysis with the use of ISSR-markers. All three levels of analysis demonstrated the presence of selection resulting from environmental pressures, specifically the temperature pattern at the sites of origin of those landraces. The same research also showed the importance of coupling genetic polymorphism with metabolomic profiling, which markedly extended the description of the studied landraces (Boczkowska et al., 2017).

Research showed that the metabolomic approach opens new prospects for a complex study of crop genetic resources and their wild relatives – from identifying traits vitally important for breeders to solve fundamental problems of plant breeding, taxonomy, phylogeny, evolution, crops genetic resources identification, etc. (Loskutov et al., 2019).

Metabolomic profiling coupled with other modern 'omics' helps to solve crucial plant breeding problems that remained unsolved earlier, so the efforts of researchers should be targeted at the crops that have already been provided with detailed information on the wide-ranging expression of the studied characters (Langridge, Fleury, 2011; Jonas, de Koning, 2013).

The mQTL (metabolite quantitative trait loci) and mGWAS (metabolome-based GWAS) approaches will make it possible to analyze the nature of quantitative characters useful for plant breeding. Such analysis can produce information not only on the number of metabolites identified in plants but also on their interrelations among themselves and with other characters important for breeding, which may lead to the development of more rational models binding a certain metabolite to such indicators as plant productivity or quality of end products. Even more promising is the possibility to study the interplay among quantitative changes in metabolites and, as a consequence, the variation of the plant's phenotype (Carreno-Quintero et al., 2013). It is noteworthy that the ongoing research on metabolic responses to biotic and abiotic stresses has confirmed the potential efficiency of the breeding practice based on metabolomic profiling in the development of more stress-resistant crop cultivars (Fernie, Schauer, 2009). The role of such an approach in crop productivity and quality breeding is expected to become more and more important in the future (Hong et al., 2016).

Attempts to compare modern oat cultivars with earlier local and primitive varieties have never been ignored by experts: these attempts served to gain a deeper understanding of the oat's population structure and genetic architecture. Besides, a boost of interest has recently been observed towards studying crop landraces and old (forsaken) varieties due to the reduced diversity in the genetic base of contemporary cultivars. When such diversity was analyzed with the use of modern molecular-genetic techniques (SSR, AFLP or DArT), oat landraces and abandoned old varieties demonstrated a notably richer genetic diversity than modern cultivars in a wide range of studied traits. Research showed that landraces exceeded commercial oat cultivars in their genetic diversity, thus confirming the value of local varieties as breeding sources (He, Bjørnstad, 2012; Montilla-Bascón et al., 2013). Other scientists also ascertained that local varieties possessed a wider genetic diversity in the studied characters than modern cultivars preserved in the Polish genebank (Boczkowska et al., 2016). DNA markers were used to disclose differences between oat landraces and commercial cultivars developed through selection from the collection of NSGC (National Small Grains Germplasm Collection of the U.S. Department of Agriculture) (Winkler et al., 2016), while DNA microsatellites helped to find genetic differences between wild relatives, local varieties and contemporary cultivars of oat and barley preserved in the collections of Prague-Ruzyně Gene Bank and Agricultural Research Institute in Kroměřížc (Leišová et al., 2007).

The N.I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR) holds a large collection of the genus *Avena* L. (14,000 accessions), including wild species and a worldwide diversity of cultivated ones, represented by landrace populations, primitive (abandoned) cultigens, modern commercial cultivars, and breeding lines. All this germplasm is geographically diverse, having originated from all the continents. A complex study of this diversity helps to identify source material for breeding and distribute it to leading breeding centers of the Russian Federation where it could be included in their breeding programs (Loskutov, 2007; Loskutov, Rines, 2011).

This research aimed to study Russian and French oat varieties with various levels of breeding refinement using metabolomic profiling to find differences between groups of accessions and identify plant forms with a high content of compounds determining valuable nutritional and functional qualities of food products, which could be used to develop new oat cultivars.

Materials and methods

Thirty oat accessions of Russian and French origin with various breeding levels were selected from the VIR collection for analysis. This material included landraces (the early 1920s), primitive (obsolete) cultivars (primitive cultigens) selected from landraces (1920–1930s) and modern improved cultivars represented by 27 hulled and 3 naked oat varieties. Sowing, observations and harvesting were conducted according to the Guidelines for Studying and Conservation of the Global Barley and Oat Collection (Loskutov et al., 2012) under the conditions of Pushkin and Pavlovsk Laboratories of VIR in 2018 and harvested at the stage of maturity. Cv. 'Privet' (k-14787, Moscow Province), approved for large-scale agricultural production in Leningrad Province, served as the reference; in the sowing pattern it was planted after every 20 plots. Sowing time was optimal for the area of studies. The plot square was 1 m^2. Table 1 presents the accessions of cultivated oats selected for the research.

Table 1. List of oat varieties from the VIR collection used as research material

Таблица 1. Список сортов овса из коллекции ВИР, использованных в качестве материала для исследования

VIR catalogue No.	Origin	Variety name	VIR catalogue No.	Origin	Variety name
k-1461	Russia	Local	k-2108	France	Avoine Janne de Ardennes
k-1512	Russia	Local	k-2122	France	Avoine Nue Grosse**
k-1539	Russia	Local	k-2113	France	Avoine de Hiver
k-1711	Russia	Local	k-7795	France	Avoine Noire Intersable
k-1733	Russia	Local	k-11145	France	Trophee Vilmorin
k-1670	France	Local	k-14787	Russia	Privet

Таблица 1. Окончание

Table 1. The end

VIR catalogue No.	Origin	Variety name	VIR catalogue No.	Origin	Variety name
k-1722	France	Local	k-15276	Russia	Borrav 2
k-5336	France	Local	k-15439	Russia	Gavrosh**
k-5337	France	Local	k-15494	Russia	Medved
k-5338	France	Local	k-15495	Russia	Vsadnik
k-2199	Russia	Smolents	k-14516	France	Negrita
k-2306	Russia	Selektsionny 33	k-14641	France	Criniere
k-2896	Russia	Chervony	k-14712	France	Noire de Michamps
k-2919	Russia	Shatilovskiy	k-15399	France	Avoine Nue Renne**
k-2938	Russia	Zhelanny	k-15401	France	Chantilly

Note: * – 1–10 – landraces; 11–20 – primitive cultigens; 21–30 – modern improved cultivars;
** – naked oat varieties

Примечание: * – 1–10 – местные; 11–20 – примитивные селекционные; 21–30 – современные селекционные сорта;
** – голозерные сорта овса

Sample preparation and metabolomic profile analysis. A metabolomic profile was analyzed using gas chromatography with mass spectrometry according to a protocol (Perchuk et al., 2020). Ten grams from a mix of harvested seeds of each accession was milled in a Lab. mill-I preparation mill (Labor Muszeriparimuv, Hungary), then 0.2 g of powder was homogenized with appropriate amounts of methanol at the ratio of 1:10. The resulting extract was centrifuged at 14,000 rpm for 10 min, and 100 µL was evaporated using a CentriVap Concentrator (Labconco, USA). Then 50 µL of bis(trimethylsilyl) acetamide reagent was added to the solid residue and kept for 40 min under 100°C in a DigiBlock digester (Laboratory Devices, Inc., USA). Tricosane (normal hydrocarbon $C_{23}H_{48}$) was added as an internal standard in the following concentration: 1µg/µL. The analysis was performed on an HP-5MS capillary column (5% phenyl, 95% methylpolysiloxane, 30.0 m, 250.00 µm, 0.25 µm) using an Agilent 6850 gas chromatograph with a quadrupole mass selective detector Agilent 5975B VL MSD (Agilent Technologies, USA). Conditions of the analysis: helium flow – 1.5 mL/min; heating program – from +70°C up to +320°C; heating rate – 4°C/min; detector temperature – +250°C; injector temperature – +300°C; injection volume – 1.2 µL, with splitless flow. The peaks were registered on an Agilent 5975B mass selective detector in the total ion recording mode with a frequency of 1.8 scans per second within the range of 50–850 m/z. The recording of a chromatogram started after 4 min required for solvent removal and went on for 62 min. There were three biological and three analytical replications of the analysis, average data was obtained and used for statistical processing.

Deconvolution and metabolite identification were processed with AMDIS (Automated Mass Spectral Deconvolution and Identification System). Chemical compounds were identified by their mass spectra and retention indices using several databases. In addition to NIST2010 (National Institute of Standards and Technology, USA), the libraries of the Research Park of St. Petersburg University and the Komarov Botanical Institute of the RAS were also applied. These last two databases were developed as the result of previous standard-based chemical determination performed at St. Petersburg University and the Botanical Institute (Shtark et al., 2019, Puzanskiy et al., 2018, Smolikova et al., 2015). The retention indices (RI) were estimated by the calibration of saturated hydrocarbons with the number of carbon atoms ranging from 10 to 40. A semi-quantitative assay of the metabolite profiles was performed by calculation of the total ion peak areas with the internal standard method using UniChrom software (New Analytical Systems, Belarus, www.unichrom.com). The relative content of biochemical components is expressed in ppm DW (µg/g dry weight).

The results of the analysis were processed using STATISTICA 12.0 software for Windows. Statistical processing included calculation of main parameters of variation, analysis of variance, and classical discriminant analysis.

Results

Our research indicated that oat landraces contained higher levels of nucleosides (Table 2), which may be explained by the active metabolism of purine and pyrimidine bases (Deng, Ashihara, 2010), and of acylglycerols, associated with not only lipid metabolism but also stress resistance (Loskutov et al., 2020) as well as phytosterols, free fatty acids and oligosaccharides. On the other hand, this group of accessions demonstrated a lower amount of free amino acids and monosaccharides.

Grains of the primitive cultigens had higher relative contents of organic acids, free amino acids, polyols, monosaccharides and total sugars, and phenolic compounds, but lower levels of free fatty acids, acylglycerols and sugar derivatives (*α*-methyl glucofuranoside, and glucose-3-phosphate; see Table 1).

The grain of modern improved cultivars was observed to have the lowest content of phytosterols, nucleosides and phe-

Table 2. **Main groups of metabolites in the grain of Russian and French oat varieties with different levels of breeding refinement (ppm DW)**

Таблица 2. **Основные группы метаболитов зерен русских и французских сортов с разной степенью селекционной проработки**

Metabolic group	Landraces		Primitive cultigens		Modern improved cultivars	
	I*	II**	I	II	I	II
Total organic acids	694.8*** ± 69.1****		1044.0 ± 168.7		633.6 ± 36.0	
	670.5 ± 86.2	719.2 ± 117.4	1157.7 ± 333.7	930.2 ± 101.2	684.7 ± 29.1	582.5 ± 60.6
Total free amino acids	681.3 ± 113.1		918.7 ± 95.7		726.5 ± 108.7	
	679.7 ± 114.3	682.9 ± 210.9	818.8 ± 98.0	1018.5 ± 163.3	937.0 ± 152.9	515.9 ± 87.5
Total free fatty acids	4250.5 ± 393.5		3552.6 ± 257.5		4078.4 ± 566.9	
	3758.0 ± 468.1	4742.9 ± 597.0	4173.7 ± 306.8	2931.5 ± 105.9	3758.6 ± 679.1	4398.1 ± 966.3
Total acylglycerols	207.7 ± 26.4		181.9 ± 21.5		190.2 ± 23.2	
	194.0 ± 31.0	221.4 ± 45.7	215.2 ± 37.5	148.5 ± 10.5	183.6 ± 32.5	196.8 ± 36.7
Total polyols	2211.5 ± 174.2		3027.3 ± 818.4		2193.6 ± 170.5	
	2172.5 ± 320.1	2250.5 ± 182.4	3895.2 ± 1600.2	2159.4 ± 276.5	2103.5 ± 241.9	2283.7 ± 261.2
Total phytosterols	357.9 ± 31.8		292.5 ± 29.4		277.2 ± 35.0	
	406.2 ± 40.9	309.5 ± 41.4	267.8 ± 21.9	317.3 ± 55.6	274.2 ± 56.6	280.2 ± 48.0
Total mono saccharides	2543.9 ± 509.1		4091.9 ± 1322.5		2571.9 ± 431.3	
	3059.3 ± 966.3	2028.5 ± 315.7	5486.5 ± 2609.2	2697.4 ± 300.2	3129.4 ± 655.3	2014.4 ± 502.4
Total oligo saccharides	31324.1 ± 2212.9		31080.0 ± 1445.7		30495.6 ± 2157.9	
	31162.8 ± 4436.8	31485.4 ± 1529.0	31091.9 ± 1759.7	31068.2 ± 2511.6	34222.6 ± 1913.2	26768.5 ± 3217.0
Total sugar derivates	113.9 ± 21.5		111.9 ± 6.7		129.1 ± 19.8	
	153.2 ± 35.6	74.5 ± 5.4	108.9 ± 9.2	114.9 ± 10.8	108.4 ± 10.3	149.7 ± 38.1
Total sugars	33981.9 ± 1903.9		35283.9 ± 1559.1		33196.6 ± 2322.4	
	34375.3 ± 3806.8	33588.4 ± 1320.0	36687.2 ± 2128.6	33880.5 ± 2328.8	37460.5 ± 1615.2	28932.7 ± 3545.6
Total phenolic compounds	58.9 ± 22.3		74.9 ± 16.4		36.1 ± 4.4	
	72.1 ± 44.5	45.7 ± 13.3	67.7 ± 20.7	82.0 ± 27.4	42.6 ± 4.5	29.5 ± 6.6
Total nucleosides	35.7 ± 19.4		18.9 ± 1.9		14.9 ± 1.6	
	55.6 ± 38.6	15.7 ± 2.3	22.7 ± 2.2	15.2 ± 2.0	16.3 ± 0.9	13.5 ± 3.1

Note: * – Russian varieties; ** – French varieties, *** – arithmetic mean, **** –"±" – standard error of the arithmetic mean, ***** – metabolite content with statistically significant differences

Примечание: * – русские сорта; ** – французские сорта, *** – среднее арифметическое, **** – «±» – стандартная ошибка среднего арифметического, ***** – содержание метаболитов со статистически значимыми различиями

nolics, which may attest to a decrease in the synthesis of the compounds responsible for stress resistance (Loskutov et al., 2019). They also had the lowest relative content of organic acids, polyols, oligosaccharides, total sugars. Lower relative levels of organic acids in the grain of cultivated oats compared with wild species were observed by us earlier (Loskutov et al., 2017). The differences described above between groups of accessions taken in the study may reflect the breeding trend that had been followed in their development.

Russian primitive cultigens and modern improved cultivars showed higher relative values of organic acids; landraces and modern cultivars: phenolics; only landraces: phytosterols and sugar derivatives; primitive cultigens: free fatty acids, acylglycerols and polyols; modern cultivars: free amino acids, versus French varieties. Accessions of French origin contained more free fatty acids, acylglycerols, polyols; landraces and primitive cultigens: free amino acids; primitive cultigens and modern cultivars: phytosterols; primitive cultigens: phenolics; landraces: free organic acids and oligosaccharides; modern cultivars: sugar derivatives, versus the grain of Russian accessions. Compared with French varieties, relative levels of monosaccharides were higher in all accessions of Russian origin, while oligosaccharides were higher in Russian modern improved cultivars. The content of nucleosides was higher in the grain of Russian landraces, primitive cultigens and improved cultivars. The lowest total fatty acid content was observed in French primitive cultigens (see the Table 1).

In the organic acid group, malic, phosphoric and methylated derivative of phosphoric acid dominated in all accessions. The prevailing free amino acid for all accessions was tyrosine. Besides, French landraces and Russian modern improved cultivars had a higher content of α-alanine, while French primitive cultigens prevailed in α-alanine and valine. Main free fatty acids for all studied accessions were palmitic, oleic and linoleic acids. Dominating acylglycerols (monoacylglycerols) were MAG 1-C16:0 and MAG 1-C18:0. As for polyols, glycerol and dulcitol dominated in all oat accessions, while ononitol prevailed in Russian primitive cultigens. Among phytosterols, the most representative in the studied oat grains was sitosterol; besides, high content of fucosterol was recorded for the accessions of Russian landraces and French modern cultivars. Glucose was dominant among monosaccharides and sucrose among oligosaccharides. The highest content of glucose and raffinose was observed in Russian primitive cultigens, and that of sucrose in Russian modern improved cultivars. The prevailing phenolic compound for Russian landraces and French primitive cultigens was α-tocopherol; for Russian primitive cultigens and modern improved cultivars, quinic and 2,3-dihydroxybenzoic acids. All grains of the studied oat accessions contained the nucleoside uridine and adenosine.

The results of the analysis of variance helped to assess the statistical significance of the effect produced by the breeding process and origin on the biochemical composition of oat grains. The first source of variation was the degree of breeding refinement: landraces, cultigens obtained by primitive breeding, and modern improved cultivars; the second one was the differentiation of the accessions by their origin, Russian or French; the third, the combined effect of the first two sources on biochemical indicators of oat grain.

Of the studied 90 characters, statistically significant differences among the accessions with various levels of breeding refinement at $p = 0.05$ were observed in the content of fucosterol, chiro-inositol, xylitol, ethanolamine, GABA; glutamic, maleic, ribonic, phosphoric acids, and a total of organic acids. Differences close to significant ($p \leq 0,1$) were found in the content of threonic, nicotinic, ferulic, gluconic, tridecylic acids, and stigmasterol.

When the accessions of different origin were compared, significant differences were identified in the content of behenic, threonic, methyl malonic, nicotinic and ferulic acids, fructose, sorbose, glucose-3-phosphate and phthalate; differences close to significant in the content of myo-inositol, chiro-inositol, stigmasterol, caffeic, gluconic, lauric, pipecolic and ribonic acids, adenosine, tyrosine, and total sugars *en masse*.

Significant differences between the groups of oat accessions in the interplay Status × Origin, where 'Status' means the degree of breeding refinement and 'Origin' means countries of original cultivation, were registered in the content of fucosterol, chiro-inositol, xylitol, valine, glutamic, threonic, gluconic and ribonic acids, and sorbose. Differences close to significant were observed in the content of fructose, glucose-3-phosphate, and tridecylic, malic and phosphoric acids (Table 3).

Assessing the differentiated impact of the sources of variation (Status × Origin) on biochemical characters revealed their independent effects on the metabolomic profile of oat grains. The group of Russian primitive cultigens significantly differed from other groups in the largest number of indicators (methyl malonic, maleic, malic, threonic, ribonic, gluconic, tridecylic, behenic acids, fructose and sorbose), followed in descending order by Russian landraces and French primitive cultigens (ferulic, nicotinic, behenic acid, chiro-inositol, fucosterol, and phosphoric and glutamic acids, and valine, respectively), Russian and French modern improved cultivars (tridecylic acid and sorbose, and behenic acid and xylitol, respectively) (see the Table 3).

According to the results of the discriminant analysis, the most informative for plotting classificatory functions were such indicators as the levels of 3-hydroxypropionic, behenic and hydroxydecanoic acids, valine, xylitol, fucosterol, sorbose and maltose. The classification functions developed in the course of analysis helped to make a clear differentiation between Russian and French landraces ($\rho = 1$). All accessions of primitive cultigens and modern Russian cultivars also manifested explicit differentiation into groups (100% of correct solutions). It should be noted that one of the French modern cultivars (k-14641, 'Criniere') was close to French landraces in its biochemical composition. The grouping pattern was confirmed for 80% of the accessions representing French modern cultivars.

According to the calculated canonical variables (Table 4), each operational unit (oat grains accession) occupies a definite place on the classification 'tree'. In the first variable (Root 1, 79.4% of variance), the most informative indicators were the content of hydroxydecanoic acid and fucosterol. The first variable differentiates between Russian landraces and all other varieties. As for the second variable (Root 2, 13.2% of variance), the major role in variability is played by the levels of valine, behenic acid and sorbose; it differentiates primitive French cultigens. The third variable (Root 3, 5.3% of variance) includes 3-hydroxypropionic and hydroxydecanoic acids and xylitol; it determines the differences of French modern improved cultivars. The fourth variable (Root 4, 1.4% of variance) and the fifth variable (Root 5, 0.7% of variance) have little value for distinguishing the varieties.

Landraces of Russian and French origin formed separate groups (Figure). Four French modern improved cultivars exactly complied with their group, but the cultivar 'Medved' (k-15494) showed similarity with French landraces ($p = 0.679$). Scattering of the studied accessions under the impact of canonical variables was in line with the results of the discriminant analysis.

Table 3. **Metabolites that demonstrated statistically significant differences among oat accessions of different origin and breeding status (ppm DW)**

Таблица 3. **Метаболиты достоверно различающие образцы овса разного происхождения и разной степени селекционной проработки (ppm сухого веса)**

Character	Landraces		Primitive cultigens		Modern improved cultivars	
	I*	II**	I	II	I	II
Fucosterol	236.6 ± 26.9*****	81.3 ± 14.7	45.3 ± 7.8	75.9 ± 18.2	70.0 ± 18.2	113.7 ± 38.6
Chiro inositol	21.0 ± 6.9*****	8.7 ± 2.0	9.1 ± 0.6	5.2 ± 0.9	3.6 ± 0.5	5.2±1.1
Xylitol	16.7 ± 4.4	9.9 ± 2.7	14.9 ± 1.6	11.7 ± 3.8	17.6 ± 1.3	25.0 ± 2.5*****
Valine	59.2 ± 12.8	49.1 ± 18.5	60.8 ± 13.9	106.7 ± 13.6*****	81.5 ± 18.1	41.3 ± 8.4
Glutamic acid	7.6 ± 4.9	4.6 ± 3.6	27.3 ± 11.8	60.7 ± 22.4*****	29.9 ± 9.0	9.1 ± 6.0
Threonic acid	5.6 ± 1.1	5.6 ± 1.0	15.0 ± 4.6*****	6.3 ± 0.8	8.3 ± 1.6	4.3 ± 0.9
Gluconic acid	0.6 ± 0.6	0.0 ± 0.0*****	9.5 ± 5.5*****	0.9 ± 0.3	0.8 ± 0.4	0.3 ± 0.3
Ribonic acid	4.5 ± 2.5	3.2 ± 1.1*****	43.8 ± 21.5*****	13.1 ± 6.0	11.7 ± 4.1	3.5 ± 2.6
Sorbose	188.0 ± 25.2	161.2 ± 27.2	242.3 ± 38.1*****	214.0 ± 25.2	284.1 ± 47.2*****	144.8 ± 34.5
Fructose	702.7 ± 161.8	435.2 ± 91.2	899.1 ± 168.0*****	499.6 ± 66.2	595.8 ± 123.6	479.1 ± 41.9
Tridecylic acid	11.0 ± 1.1	14.2 ± 2.4	25.5 ± 3.7*****	14.6 ± 1.4	25.7 ± 7.9*****	16.8 ± 3.6
Malic acid	132.7 ± 17.8	120.8 ± 15.1	285.2 ± 105.2****	129.0 ± 17.4	118.9 ± 12.2	110.6 ± 13.3
Phosphoric acid	199.9 ± 46.3	285.2 ± 89.5	283.2 ± 40.9	430.1 ± 79.9*****	218.9 ± 22.0	182.9 ± 43.8
Methyl malonic acid	2.4 ± 0.7	2.6 ± 0.5	4.1 ± 0.6*****	1.6 ± 0.3	2.2 ± 0.2	1.6 ± 0.8
Maleic acid	3.1 ± 0.6	2.7 ± 0.5	5.5 ± 1.3*****	4.2 ± 0.8	3.0 ± 0.3	2.2 ± 0.9
Threonic acid	5.6 ± 1.1	5.6 ± 1.0	15.0 ± 4.6*****	6.3 ± 0.8	8.3 ± 1.6	4.3 ± 0.9
Behenic acid	6.0 ± 0.9*****	1.9 ± 1.2	6.0 ± 1.9*****	1.0 ± 1.0	3.5 ± 1.5	0.0 ± 0.0*****
Ferulic acid	3.3 ± 0.5*****	4.2 ± 0.5	4.7 ± 0.3	4.4 ± 0.3	3.9 ± 0.4	5.2 ± 0,2
Nicotinic acid	3.3 ± 0.5*****	4.2 ± 0.5	4.7 ± 0.3	4.4 ± 0.3	3.9 ± 0.4	5.2 ± 0.2

Note: * – Russian varieties; ** – French varieties, *** – arithmetic mean, **** – "±" – standard error of the arithmetic mean, ***** – metabolite content with statistically significant differences

Примечание: * – русские сорта; ** – французские сорта, *** – среднее арифметическое, **** – «±» – стандартная ошибка среднего арифметического, ***** – содержание метаболитов со статистически значимыми различиями

Table 4. Structure of canonical variables

Таблица 4. Структура канонических переменных

Effect	Function 1	Function 2	Function 3	Function 4	Function 5
3-Hydroxypropionic acid	0.938	–0.402	–0.924	–0.033	0.996
Valine	–0.650	–1.913	–0.082	0.487	–0.005
Behenic acid	–0.330	1.390	–0.390	–0.081	0.387
Hydroxydecanoic acid	–2.054	–1.060	1.098	0.246	–0.447
Xylitol	0.252	0.060	0.870	0.660	0.422
Fucosterol	–3.242	–0.065	–0.138	–0.057	–0.196
Sorbose	–0.688	1.519	–0.228	0.428	–0.610
Maltose	2.803	0.376	0.312	–0.252	0.433
Percentage of explained variance	**79.4**	**13.2**	**5.3**	**1.4**	**0.7**

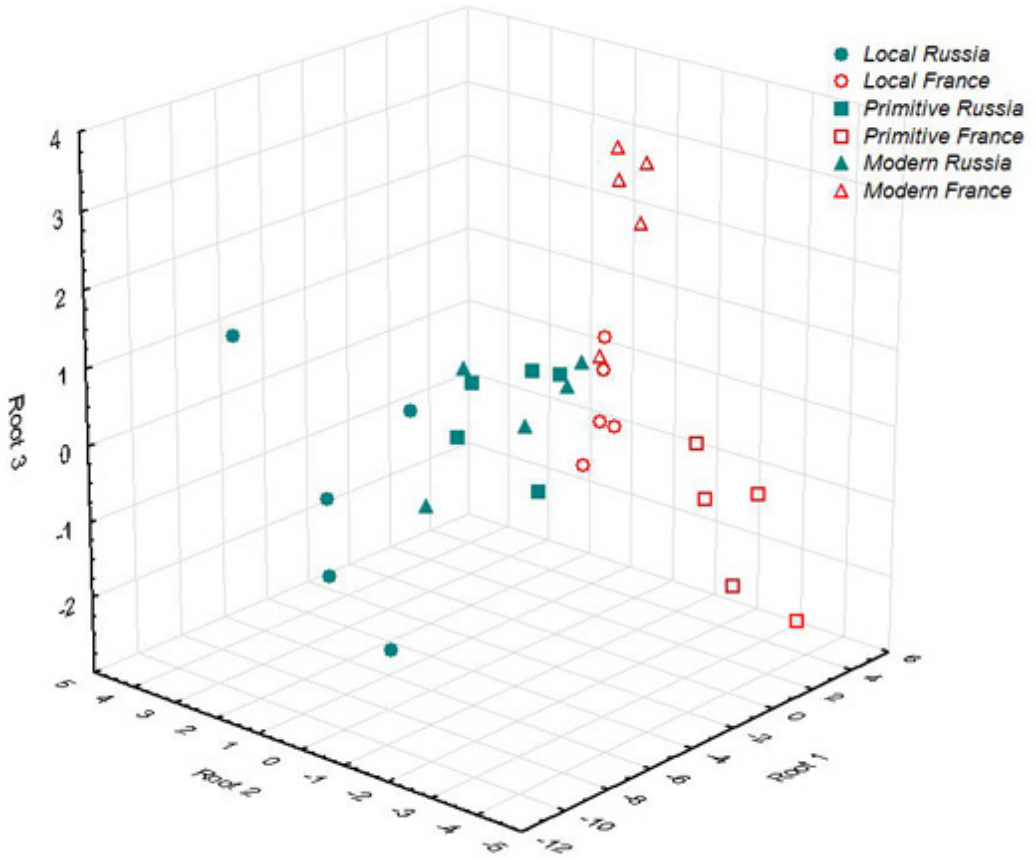

Figure. Scatterplot of the studied accessions in the space of the first three canonical axes:
circle – Local (landraces), square – Primitive (primitive cultigens), triangle – Modern varieties (modern improved cultivars); colored geometric figures – Russian origin, colorless – French

Рисунок. Диаграмма распределения изученных образцов в пространстве первых трех канонических осей:
круг – местные (ландрасы), квадрат – примитивные селекционные (сорта примитивной селекции), треугольник – современные селекционные сорта (современные улучшенные сорта); окрашенные геометрические фигуры – российское происхождение, неокрашенные – французское

Discussion

The investigation of biodiversity of the main cereal crops, including those that are part of the world genetic collections of plant resources in different countries, has been carried out unceasingly. An in-depth study of plant resources makes it possible to identify changes arising in the course of breeding work as well as to understand the features of approaches in the process of obtaining new cultivars with improved agronomic characteristics in various regions of the world. Unfortunately, programs for the conservation, studying and use of plant biodiversity are high-priced activities (Leišová et al., 2007), so any information on this topic is invaluable. Leišová et al. (2007) assessed the biodiversity of 330 oat varieties from the Research Institute of Crop Production Gene Bank (Czech Republic) collection using microsatellite analysis. Ninety-four oat accessions from the Albert Atterberg collection and genebanks mainly from Nordic countries and Germany were investigated covering different breeding periods by He and Bjørnstad (2012) using three different molecular maker techniques (SSR and DArT markers, and AFLP assay). These studies showed the influence of the degree of breeding refinement and geographic location of origin on the differences among oat varieties. The study by Winkler et al. (2016), encompassing 1000 oat landraces and accessions of uncertain improvement status from the USDA National Small Grains Collection, confirmed the effect of origin on the differences among oat accessions. Montilla-Bascón et al. analyzed the genetic diversity among 177 oat accessions, including both white and red oat landraces, and 36 commercial cultivars provided by the Plant Genetic Resources Center (CRF-INIA, Madrid, Spain) and the Andalusian Network of Agriculture Experimentation (RAEA), using simple sequence repeat (SSR) loci, found significant differences between commercial cultivars, red and white oat landraces (Montilla-Bascón et al., 2013). Leišová et al. (2007) showed negative impacts of oat breeding on the genetic diversity of oat varieties, previously observed by Fu et al. (2003). Boczkowska et al. (2016), with their estimation of the genetic diversity of the 91 oat landraces stored in the Polish gene bank, confirmed that oat landraces were characterized by high genetic diversity. Almost all the above-mentioned studies confirm the decrease in the genetic diversity of modern oat cultivars compared to landraces. This phenomenon can be explained by the methodological features of the ongoing breeding work targeted at the development of oat cultivars with a certain set of useful agronomic traits, as well as by the fact that different populations may exhibit different diversity trends due to local breeding strategies and germplasm conservation efforts, and genetic erosion (van de Wouw et al., 2010).

The differences disclosed in this study between the accessions of oat landraces, primitive cultigens and modern improved cultivars of Russian and French origin from the VIR collection using metabolomic profiling confirmed the data obtained earlier for analogous groups of varieties (Leišová et al., 2007; He, Bjørnstad, 2012; Montilla-Bascón et al., 2013; Boczkowska et al., 2016; Winkler et al., 2016). The results of our research show that such methodological approach makes it possible to identify variations in biochemical components of oat grain, which were induced by different levels of breeding refinement in the studied oat accessions. Comparing differentiations between landraces, primitive cultigens, and modern improved cultivars provides an opportunity to assess the practical significance of contemporary breeding trends using biochemical parameters and correct them when necessary.

Conclusion

In the process of studying, the most informative indicators were identified, making it possible to effectuate statistically significant differentiation among the studied oat accessions with different levels of breeding refinement and of different origin. The group of Russian primitive cultigens significantly differed from the other groups in having the highest number of biochemical indicators. Russian landraces and French primitive cultigens were also distinguished by the group of traits. Comparing metabolomic profiles of the studied oat variety groups – landraces, primitive cultigens, and improved cultivars of Russian and French origin – highlighted the breeding trends followed by different schools of oat breeders, with their specific methodological approaches, intensities of breeding efforts, and individual principles of genotype selection that depended in many ways on the techniques of their identification.

Thus, the obtained results show that further breeding efforts targeted at the improvement of biochemical parameters in oat grain would be more effective if they employ the genetic diversity of landraces and primitive cultigens collected or developed in the 1920–1930s, which have been preserved and maintained in the VIR global collection until now.

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