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# Aluminum tolerance and micronutrient content in the grain of oat cultivars with different levels of breeding improvement from the VIR collection

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**Background**. Soil toxicity of Al is associated with severe changes in plant root morphology that limit the uptake of water and mineral nutrients. Long-term exposure to Al results in deficiencies in some important nutrients, such as phosphorus, calcium, magnesium, potassium, and iron. Thus, the joint study of plant resistance to the effects of Al and the accumulation of micronutrients in the oat grain is relevant.

**Materials and methods**. Thirty oat accessions of Russian and French origin from the VIR collection served as the research material. They were represented by cultivars with different levels of breeding improvement: landraces (early 1920s), cultivars developed by primitive breeding (1920–1930s), and modern improved cultivars.

**Results**. Oat cultivars with different breeding improvement levels demonstrated significant differences in the content of micronutrients and aluminum tolerance. Among the studied accessions, landraces and modern improved cultivars showed a tendency towards medium or high Al tolerance, the group of primitive cultivars from Russia had the lowest Al tolerance, while primitive cultivars from France demonstrated the highest average resistance (0.5–1.9).

**Conclusion.** The content of Fe and Zn was influenced by the geographic origin of genotypes. The concentrations of different micronutrients positively correlated with each other. Strong correlations were recorded between the contents of Zn and Fe (r = 0.81), and between Zn and Mg (r = 0.75). There was a positive correlation between the content of micronutrients and the resistance to crown rust (0.38 to 0.50). High content of the studied set of micronutrients was registered in such improved cultivars from France as the naked 'Avoine Nue Renne', 'Chantilly', 'Negrita' and 'Noire de Michamps', plus the Russian improved naked cultivar 'Gavrosh'. Among them, 'Chantilly' was distinguished for its yield, and the naked 'Gavrosh 'for its high tolerance to aluminum.

Keywords: Avena L., landraces, varieties, aluminum toxicity, Zn, Cu, Fe and Mg, micronutrients

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Научная статья

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# Алюмотолерантность и микроэлементный состав зерновки сортов овса из коллекции ВИР с различной степенью селекционной проработки

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**Актуальность.** Почвенная токсичность Al связана с серьезными изменениями в морфологии корней у растений, которая ограничивает поглощение воды и минеральных питательных веществ. Длительное воздействие Al приводит к дефициту некоторых важных питательных веществ, таких как фосфор, кальций, магний, калий и железо. Таким образом, совместное изучение устойчивости растений к воздействию Al и накопления микроэлементов в зерновке овса являются актуальными.

**Материалы и методы**. Материалом для исследований послужили 30 образцов овса российского и французского происхождения из коллекции ВИР. Они были представлены сортами с разным уровнем селекционной проработки: стародавними сортами (начало 1920-х гг.), сортами, полученными методом примитивной селекции (1920–1930-е гг.), и современными улучшенными сортами.

**Результаты**. Сорта овса с разным уровнем селекционной проработки показали существенные различия по содержанию микроэлементов и толерантности к алюминию. Среди изученных образцов стародавние сорта и современные улучшенные сорта проявляли тенденцию к средней или высокой устойчивости к Al, самая низкая устойчивость к Al была у группы примитивных сортов из России, а самая высокая средняя устойчивость (0,5–1,9) проявлялась у примитивных сортов из Франции.

Заключение. На содержание Fe и Zn повлияло географическое происхождение генотипов. Концентрации различных микроэлементов положительно коррелировали между собой. Сильные корреляции зафиксированы между содержаниями Zn и Fe (r = 0.81), а также между Zn и Mg (r = 0.75). Выявлена положительная корреляция между содержанием микроэлементов и устойчивостью к корончатой ржавчине (0.38-0.50). Высокое содержание изучаемого набора микроэлементов отмечено у таких улучшенных сортов из Франции, как голозерные 'Avoine Nue Renne', 'Chantilly', 'Negrita' и 'Noire de Michamps', а также у российского селекционного голозерного сорта 'Гаврош'. Среди них 'Chantilly' отличался урожайностью, а голозерный сорт 'Гаврош' – высокой устойчивостью к алюминию.

Ключевые слова: Avena L., местные сорта, селекционные сорта, устойчивость к Al, Zn, Cu, Fe и Mg, микроэлементы

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#### Introduction

An increased concentration of mobile aluminum ions in the soil solution (67% of the total acidic soil area) is the principal factor that determines the phytotoxicity of acidic soils. Aluminum toxicity in acidic soils reduces the yield of food crops, especially cereals, being the main obstacle to crop production (Pérez-Clemente et al., 2013).

Higher concentrations of protons in soil solutions lead, *per se*, to an abrupt decrease in the supply of nutrients in the cationic form to plants, inhibit the activity of many microorganisms, and, as a result, retard the release of nitrogen, phosphorus, sulfur and many trace elements from plant residues. The content of a number of chemical elements in the soil solution can grow to levels toxic for plants, especially in technologically polluted soils. An increase in the concentration of such components in the soil solution means that these compounds become involved in significant amounts in food chains, provoking all the ensuing negative consequences (Gupta et al., 2013).

The negative effect of aluminum primarily afflicts the roots. Plant roots become short and brittle, change their color, and the growth of root hairs is inhibited. At the cellular level, the arrest of root growth is caused by the suppression of cell division and enlargement of the meristem. Aluminum interacts with the cell wall, plasma membrane, and cytoplasm of plant cells; such interaction forms Al complexes (Gupta et al., 2013).

Thus, the toxicity of Al is associated with serious changes in root morphology, limiting the absorption of water and mineral nutrients. Prolonged exposure to Al leads to shortages in some important nutrients, such as phosphorus, calcium, magnesium, potassium and iron, which are easily traced in plants as deficiency symptoms. All this ultimately induces a decrease in biomass or plant death.

As a consequence, many authors noted the loss of agronomic qualities in crops. The effect of high Al concentrations deteriorates the quality of plant products, reducing the content of monosaccharides, sucrose and total sugars as well as protein forms of nitrogen in them (White, Broadley, 2005).

There were many reports on nutritional imbalances caused by exposure to Al in several plant species. Aluminum prevents the absorption, transport and utilization of most minerals. The Al stress inhibits the uptake of many cations, including  $\rm Ca_2+$  (69%),  $\rm Mg_2+$ , K+ (13%) and NH<sub>4</sub>+ (40%), but enhances the influx of nitrate (44%) and phosphate (17%) anions (Olivares et al. 2009; Gupta et al. 2013). Both sensitive and tolerant wheat genotypes showed a decrease in the K and Mg content in their roots, while the content of Ca, Al, and Si in them increased (Silva et al., 2010).

Aluminum interfered with the binding of cations in the cell wall by the same order of magnitude as their influx, whereas the binding of phosphate was strongly enhanced. The results are consistent with the mechanism of binding Al to the plasma membrane phospholipids, thus forming a positively charged layer that affects the movement of ions to the binding sites of transport proteins. A positive charge layer would retard the movement of cations and increase the movement of anions to the plasma membrane proportionally to the charges carried by these ions (Nichol et al., 1993).

Differences in acid resistance between cultivars of the same crop were found to overlap interspecies differentiation in resistance to ionic toxicity (Loskutov, 2007; Loskutov, Rines 2011).

Resistance of plant forms to aluminum toxicity is the result of their long-term growth on soils with high Al content,

i. e., it is a genetically determined trait. Different plant genotypes show different resistances to aluminum exposure (Loskutov et al., 2017; Pukhal'skaya, 2005).

One of the ways to solve the problem of acidic soils is the development of acid-resistant cultivars, facilitated by the significant intraspecific variability in aluminum tolerance and relatively simple screening and breeding schemes (Batalova, 2000). Laboratory screening techniques are most frequently used to assess a gene pool for aluminum tolerance; they are based on seed germination in nutrient solutions with toxic Al concentrations. Plants are most vulnerable to a mobile Al excess in the soil at early stages of their ontogenesis, which makes it possible to diagnose Al resistance in seedlings. A fairly high correlation was observed between the results of early diagnosis and the data of field trials (Kosareva, 2013).

Micronutrients are an important component in the mineral nutrition of plants. They are vital because they perform various catalytic and regulatory functions in metabolic processes: absorption, transport, redox and biosynthesis of organic compounds, and transfer of genetic information. Each element has its own range of safe concentration, ensuring normal functioning of an organism. When it is disturbed, various pathological disorders in metabolic processes are observed: a shortage leads to deficiency, while an excess provokes toxicity (Rebrov, 2008).

The content of micronutrients in the generative parts (seeds or fruits) of the reproductive organs, where the elemental chemical composition is under strict genetic control, is little changed under the influence of environmental stressors. Therefore, the reproductive organs (seeds or fruits) are believed to manifest barrier-type accumulation of micronutrients. At the same time, there is evidence of significant variability in the content of micronutrients in plant seeds under the impact of environmental factors (Ermakov, 2018).

Zinc, iron and copper play an important role not only in seed formation and germination processes but also in the protective mechanisms of aluminum-induced oxidative stress responses and the restoration of tissues damaged by toxic effects.

It is known that, after treatment of plants with  $Al^3+$ , the exudation of organic acids can occur either immediately or after a delay. Pretreatment with  $Mg^2+$  was noted to increase citrate secretion within an hour, compared to seedlings without  $Mg^2+$  pretreatment. The activity of  $Mg^2+$  inside the cytoplasm is directly involved in the regulation of ATPase H+ activity, sending directing H+ from the cytoplasm either to the apoplasm or to the vacuole.

Thus, high physiological activity of the studied elements was observed in many studies, including their participation in the protective mechanisms formed under exposure to toxic aluminum

There is enough evidence that normal vital functions of a plant organism are possible only if it is fully supplied with micronutrients. With a deficit in one or another chemical element in the soil, plants suffer serious metabolic disorders and may die. A number of micronutrients are coenzymes of many enzymes: iron, copper, molybdenum, manganese, zinc, magnesium, and cobalt. Grain and products of its processing are among important sources of minerals (first of all, phosphorus, potassium, magnesium, calcium, sulfur and iron) absorbed by a human organism with food (Panasenko, 2018).

Despite the abundance of the required chemical elements in most soils, the availability of Fe, Zn and Mn for plants is often limited, especially in limestone soils. Low bioavailability of such trace elements as Fe, Zn or Mn leads to their deficiency in plants and results in significant decreases of crop yields worldwide (Alloway, 2008).

Humans require a variety of micronutrients, including iron (Fe), zinc (Zn), manganese (Mn) and other trace elements, and plants are sources of their supply (White, Broadley, 2005; Frossard et al., 2000; Gómez-Galera et al., 2010). Grain is the most important source of calories; meanwhile, the food produced from cereals has low concentrations of micronutrients but is rich in nutrients (such as phytic acid and phenols) that limit the absorption of many minerals in the intestine (Grusak, DellaPenna, 1999; Mendoza, 2002).

Besides, grain is polished or ground when processed. Since the concentration of some trace elements is highest in the bran, the processed grain can lose large amount of minerals during polishing or grinding on the way to the end product (Doesthale et al., 1979; Gregorio et al., 2000). The deficiency in micronutrients is a serious global problem provoked by various nutrition patterns (for example, insufficient consumption of vegetables and fruits, animal and fish products; or low total levels and poor bioavailability of micronutrients in plant foods), which may lead to serious health problems or lethality among consumers, especially women and children (Bhullar, Gruissem, 2013).

Iron deficiency anemia is one of the most common micronutrient deficiencies in the world (WHO 2002). Zinc deficiency affects, on average, one third of the world's population (International Zinc Nutrition Consultative Group et al., 2004). In industrialized countries, the daily intake of Mn in the diet is higher than the estimated daily requirement, and Mn deficiency appears to be a rare effect of malnutrition (Bornhorst et al., 2010).

The problem of micronutrient deficiencies can be solved by enriching crop cultivars or enhancing their nutritional properties through either agronomic intervention or breeding practice (Graham et al., 2001; Kutman et al., 2010; Sperotto et al., 2012). It is possible, however, that such efforts will result in increasing the concentration of micronutrients in leaves but not in seed or grain (Frossard et al., 2000). Similar concentrations of micronutrients (for example, Zn) in fruits or seeds are strongly restricted by the low mobility of trace elements in the phloem. Combined techniques were therefore proposed, joining together breeding and agrochemical approaches: they made it possible to accumulate trace elements from the soil in edible parts of plants (White, Broadley, 2005). There are significant genetic differences in the concentration of micronutrients in the edible parts of most crops. Genetic variability in micronutrient concentrations is often lower in seeds than in leaves. Nevertheless, studying large collections of major cereal crops showed a wide variety of micronutrient concentrations in their kernels (White, Broadley, 2005).

Common oat has been found to possess, along with useful agronomic traits, good grain quality characteristics. High values of both biochemical and agronomic indicators combined in one cultivar have been the goal of oat breeders in recent years. Grain quality indicators in oat are varietal characters: that is why their further improvement is possible. Depending on the cultivar, the content of crude ash in whole grain is reported to range from 2.0 to 5.7%; in naked oat cultivars it is lower (1.6%) than in hulled ones (Korenev et al., 2015).

There is considerable genetic potential for the development of barley and oat cultivars with higher levels of micronutrients (Fe, Zn and Mn). Among the studied barley genotypes, the content of Fe, Zn and Mn exhibited a 3- to 5.5-fold variation. Different oat cultivars showed a 7.0-fold variation

in zinc content and an almost 3-fold variation in manganese content (Bityutskii et al., 2017). The genetic diversity of the studied characteristics in oat cultivars can be significant, with a 2.7- to 10.5-fold difference between the maximum and minimum values, which implies a search for promising sources of a high content of important micronutrients in grain to serve as a basis for the development of new high-quality oat cultivars (Bityutskii et al., 2020). Wide differences between cultivars of the same crop can be effectively used in breeding programs to increase the content of micronutrients in grain (Loskutov, Khlestkina, 2021; Shelenga et al., 2021).

The objective of this work was to identify oat genotypes contrasting in their resistance to aluminum and composition of micronutrients, and find correlations between acid resistance, useful agronomic traits and micronutrients in the grain of oat accessions, The findings can serve as a basis for research and development of methods for studying the acid resistance mechanisms in common oat (*Avena sativa* L.) and using the identified diversity of accessions from the VIR collection as promising source material for breeding.

#### Research materials and methods

#### Materials

Thirty oat accessions of Russian and French origin from the VIR collection served as the research material. They were represented by cultivars with different levels of breeding improvement: landraces (early 1920s), cultivars developed by primitive breeding (1920–1930s), and modern improved cultivars. It should be mentioned that Russia and France are the countries where the history of oat breeding dates back to the late 19th century, scientific breeding achieved significant progress in the 1920–1930s, and modern improved cultivars are diverse and high-yielding. The selected set included hulled (27 cultivars) and naked (3) oat genotypes. Cv. 'Privet' (VIR-14787, Moscow Province), approved for cultivation in Leningrad Province, was chosen as the reference for the study: it was planted after every 20 plots in the sowing pattern. Research objects are presented in Table 1.

## Field experiment

The selected oat accessions were tested for useful agronomic traits at Pushkin and Pavlovsk Laboratories of VIR (St. Petersburg, 59°42' N, 30°25' E) in 2017-2019 according to VIR's guidelines for studying and maintaining barley and oat collections (Loskutov et al. 2012). The parameters covered by the study included duration of the germination-heading and germination-harvest periods; plant height, lodging resistance, panicle length, number of spikelets per panicle, 1000 grain weight, yield per plot, field resistance to crown and stem rusts. The soils in the experimental field are sodpodzolic, light loamy, sandy loam, well or moderately cultivated, with a neutral or slightly acidic reaction, low moisture capacity, and good air permeability. The climate in the region is transitional from the maritime climate to a more continental one. The sum of active temperatures is 1600-2000°C. The mean annual precipitation is 500-600 mm, with 65-75% falling in the warm season. Sowing was carried out at the optimal time for the area on 1 m<sup>2</sup> plots. The experiment was performed in two replications.

## Acid resistance assessment technique

Aluminum tolerance (AT) was assessed in 2017 and 2019 for 28 oat varieties (30 grains per each of them). The experiments were carried out in a controlled environment (climate chamber) at Pushkin and Pavlovsk Laboratories of VIR.

Table 1. Evaluated oat accessions from the VIR collection Таблица 1. Изученные образцы овса из коллекции ВИР

VIR catalogue No.	Cultivar name	Botanical varieties	Origin	Year acquisition	
1461	Local	var. aurea	Russia, Penza Prov.	1919	
1512	Local	var. aurea	Russia, Saratov Prov.	1919	
1539	Local	var. aurea	Russia, Tyumen Prov.	1919	
1711	Local	var. ligulata	Russia, Smolensk Prov.	1919	
1733	Local	var. brunnea	Russia, Irkutsk Prov.	1920	
1670	Local	var. brunnea	France	1919	
1722	Local	var. <i>pugnax</i>	France	1919	
5336	Local	var. culta	France	1927	
5337	Local	var. culta	France	1927	
5338	Local	var. mutica	France	1927	
2219	Smolenets	var. mutica, aurea	Russia, Arkhangelsk Prov.	1922	
2306	Selektsionny 33	var. mutica	Russia, Orel Prov.	1922	
2896	Chervonny	var. segetalis	Russia, Kirov Prov.	1922	
2919	Shatilovsky	var. mutica	Russia, Tula Prov.	1923	
2938	Zhelanny	var. mutica	Russia, Kursk Prov.	1923	
2108	Avoine jaune de Ardennes	var. ligulata	France	1921	
2122	Avoine nue grosse	var .inermis	France	1921	
2113	Avoine d'hiver	var. cinerea	France	1921	
7795	Avoine noire inversable	var. montana	France	1929	
11145	Trophee Vilmorin	var. aristata	France	1930	
14787	Privet	var. aurea	Russia, Moscow Prov.	2000	
15276	Borrav 2	var. mutica	Russia, Leningrad Prov.	2010	
15439	Gavrosh	var .inermis	Russia, Kemerovo Prov.	2013	
15494	Medved	var. mutica	Russia, Kirov Prov.	2014	
15495	Vsadnik	var. mutica	Russia, Ulyanovsk Prov.	2014	
14516	Negrita	var. brunnea	France	1995	
14641	Criniere	var. mutica, aristata	France	1997	
14712	Noire de Michamps	var. montana	France	1998	
15399	Avoine nue Rennes	var. inermis	France	1995	
15401	Chantilly	var. aristata	France	2012	

The technique employing the eriochrome cyanine dye for visual assessment of Al resistance in cereals was used in the work. This method was developed by A. Aniol (Aniol, 1991) and modified by the Department of Plant Resistance and Development Physiology at VIR (Kosareva et al., 1995).

The earliest symptoms of toxicity are associated with roots, so inhibition of root growth can be used as a tool to measure Al toxicity.

The method is based on the assessment of mitotic activity restoration in roots after exposure to the Al stress. The area of root tissue damaged by aluminum is stained with Eriochrome cyanine R. This dye is widely used for intraspecific screening and forms a violet-colored complex with aluminum.

The degree of color intensity depends on the Al content in plant tissues. However, this is not a reliable indicator, since the toxicant can accumulate both in the cells of plants sensitive to aluminum and in resistant accessions. Plant resistance to aluminum was assessed by the length of the root tip growth after exposure to the toxicant.

Materials and equipment: climatic chamber with a day-time temperature of 19–21°C and a nighttime temperature of 14–16°C, the length of the light period of 14 hours, and the illumination of 5 klx; thermostat with a temperature of 22–25°C; Petri dishes; filter paper; germinators with cells and mesh bottoms; containers for solutions; distilled water; pH meter; nutrient solution with pH = 4.0, containing CaCl $_2$  = 177.584 mg, KNO $_3$  = 262.888 mg, MgCl $_2$ ·6H $_2$ O = 203.312 mg, (NH $_4$ ) $_2$ SO $_4$  = 5.28 mg, NH $_4$ NO $_3$  = 12.8 mg; 1% aqueous solution of Eriochrome cyanine R; salt AlCl $_3$ ·6H $_2$ O.

Seeds were placed on moistened filter paper in Petri dishes, and the latter were put into a thermostat at +22°C for 48 hours for germination. After culling, the remaining sprouted high-quality seeds were transferred to germinators with mesh bottoms, which were inserted into plastic containers with a nutrient solution for three days. Then the meshes with seedlings were returned to the same nutrient solution but with added aluminum chloride (concentration 0.25 mM). The pH of the solution was adjusted to 4.2. After 24 hours, the seedlings on the meshes were washed with running water, their roots were quickly dried with filter paper, and the plants were transferred on the meshes to a fresh aluminum-free nutrient solution for 48 hours. Then the roots of the seedlings were stained with a 0.1% solution of Eriochrome cyanine R. For this purpose, the roots were immersed into a dye solution for 10 min, and the solution was slightly stirred. Excess dye at the root tips was washed off with running tapwater, and the roots were dried with filter paper. Seedlings with root meristems damaged by aluminum had intensely colored root tips, while intact ones manifested a colored section followed by a regrown white root tip. The regrown part of the root was measured, and the average root growth after the stressor's impact was calculated. Depending on the length of the root growth after the impact of the Al stressor, the accessions were ranked into groups.

#### Assessment of micronutrient composition

The composition of micronutrients in  $30\,\text{oat}$  accessions was studied on the harvests of 2017 and 2019. A sample of each accession contained  $100\,\text{grains}.$ 

Micronutrient composition in oat grains was assessed at the Center for Collective Use of St. Petersburg State University.

Ash mineralization was performed using the "wet ashing" technique on a microwave digestion autoclave (CEM, USA). Chemically pure nitric acid and hydrogen peroxide were used. The composition and content of micronutrients were analyzed in the laboratory.

The total content of micronutrients in the tested genotypes was measured using inductively coupled plasma atomic emission spectrometry (ICP-AES) with preliminary sample preparation though acid mineralization.

The essence of the method was to register the electromagnetic radiation emitted by excited-state atoms. The excitation source was the Ar plasma initiated by an electric discharge and supported by an HF field. Since the energy of such radiation is individual, a characteristic spectrum was detected for each trace element.

The work was done using the ICPE-9000 device. The data were registered and processed with the ICPEsolution software, and later exported to MC Excel 2016 for further processing.

This method is applicable to liquid samples. Acid mineralization is effective for converting solid samples into a liquid solution.

Sample preparation started with grinding and homogenization. For this purpose, a small fraction of a sample was ground in a coffee grinder (fine grinding). Samples of about 100 mg were selected, and 4 ml of concentrated  $\mathrm{H}_2\mathrm{O}_2$  were added to them as oxidizing agents. As soon as the violent chemical reaction had abated, the samples were decomposed in a microwave oven. Blank samples were prepared to deduct the errors introduced by the reagents. The samples were adjusted to the volume of 30 ml

Thus, the samples reached homogenization, the matrix effect was averted, and strong dilution was done to avoid errors caused by the difference in rheological characteristics of fluids and self-absorption. As a consequence, aqueous solutions with salts of the studied elements may be used as references.

Reference samples are solutions with a precisely fixed concentration of the chemical elements to be measured. Eleven calibration solutions containing the studied Cu, Zn, Fe and Mg in the range of 0.0001–0 mg/L were prepared from the standard solution (stock solution with a certified concentration) with a concentration of 50.0 mg/L to serve as references. A series of working solutions were prepared from the stock solution with such range of concentrations that harbored the analyzed samples for all the tested chemical elements. Additionally, a "zero reference" was prepared, i. e., a blank sample for reference solutions (an empty flask was filled to the  $\mathrm{HNO}_3$  mark, 1:100), in order to subtract the analytical signal contained in the solvent and auxiliary reagents.

The measured elements and wavelengths corresponding to spectral lines with the lowest detection limit (higher sensitivity):  $\lambda Cu = 224.700 \text{ nm}$ ;  $\lambda Zn = 202.548 \text{ nm}$ ;  $\lambda Fe = 259.940 \text{ nm}$ ;  $\lambda Mg = 285.213 \text{ nm}$ .

The spectra were registered in the following sequence: "zero standard"  $\rightarrow$  reference samples in the ascending order of their concentrations  $\rightarrow$  analyzed samples. All parallel measurements were performed automatically. To establish the calibration dependence, the software used the following formula describing how the concentration of elements in the solution affects the radiation intensity:

$$C = aI^3 + bI^2 + cI + d$$

where C is the concentration of a chemical element in the chosen units of measurement; I is the intensity of a spectral line; a, b, c and d are the experimentally determined parameters of the equation.

The resulting volumetric concentration (mg/dm<sup>3</sup>) was recalculated into the mass concentration ( $\mu$ g/g) in the oat grain:

$$\omega = \frac{(\text{Csamp-Cblank})*V}{m} *10^6,$$

where Csamp is the concentration in a sample; Cblank is the concentration in the blank sample; V is the volume of a sample; m is the mass of a sample.

## Data processing technique

Replications were compared using Student's *t*-test for dependent samples. The groups of cultivars differentiated according to their level of breeding improvement and the countries of their origin were compared using the two-way analysis of variance. Fisher's least significant difference (LSD) test was used for a *post hoc* analysis. Pearson correlation coeffi-

cients were calculated. The principal component analysis (PCA) was applied to select accessions according to a set of indicators.

#### Results and discussion

**Aluminum tolerance.** Student's dependent sample t-test confirmed the absence of differences in Al tolerance (AT) among oat genotypes between the 2017 and 2019 years of research (p = 0.116, for the initial data see Table 3, which suggests that the method used for identifying the genetic diversity of the accessions is reliable and has good convergence of data regardless of the place and year of seed growing. The

analysis that follows is associated with the two-year average indices of root growth (IRG) in centimeters after the Al stress in the studied oat accessions (Table 2, Fig. 1). AT (IRG, cm) varied from 0.4 to 1.9. The reference 'Privet' had AT of 1.7. The two-way ANOVA showed that there was no effect of either the country of origin (p = 0.129) or the degree of breeding improvement (p = 0.307); however, the effect size of their interaction (p = 0.042) was significant (see Fig. 1, Table 3). The post hoc analysis using Fisher's LSD test showed that, on average, the group of primitive cultivars from Russia had the lowest AT (0.4–1.5): it was significantly lower than in all other groups. Primitive cultivars from France had the highest average Al resistance (0.5–1.9).

Table 2. Indices of root growth (IRG) in oat seedlings after the Al stress recorded for two years of reproduction, cm (Pushkin, 2017 and 2019)

Таблица 2. Показатели прироста корней проростков овса после Al-стресса образцов двух лет репродукции, см (Пушкин, 2017 г., 2019 г.)

(Пушкин, 2017 г., 2019 г.)									
VIR catalogue No.	Cultivar name	Origin	Level of	(AT) IRG, cm					
			breeding improvement	Mean	Min	Max			
Highly resistant									
7795	Av. noire Interesable	France	primitive	1.90	1.87	1.94			
5336	Local	France	landrace	1.89	1.82	1.98			
11145	Trophee Vilmorin	France	primitive	1.86	1.78	1.93			
2122	Av. nue Crosse	France	primitive	1.84	1.73	1.95			
14712	Noire de Michamps	France	improved	1.78	1.72	1.83			
1733	Local	Russia	landrace	1.65	1.57	1.70			
14787	Privet	Russia	improved	1.65	1.58	1.74			
15495	Vsadnik	Russia	improved	1.60	1.52	1.70			
15276	Borrav 2	Russia	improved	1.58	1.55	1.61			
1722	Local	France	landrace	1.56	1.52	1.63			
2919	Shatilovsky	Russia	primitive	1.54	1.52	1.59			
1670	Local	France	landrace	1.53	0.99	1.73			
15439	Gavrosh	Russia	improved	1.42	1.26	1.61			
	Medium resistant								
1461	Local	Russia	landrace	1.33	1.31	1.36			
1512	Local	Russia	landrace	1.30	1.30	1.31			
1711	Local	Russia	landrace	1.27	1.22	1.30			
15399	Av. nue Renne	France	improved	1.25	1.19	1.29			
1539	Local	Russia	landrace	1.23	0.98	1.34			
5337	Local	France	landrace	1.23	1.14	1.29			
14516	Negrita	France	improved	1.13	1.07	1.21			
15494	Medved	Russia	improved	1.12	1.04	1.29			
5338	Local	France	landrace	1.11	1.05	1.17			
15401	Chantilly	France	improved	0.99	0.95	1.02			

Table 2. The end Таблица 3. Окончание

VIR catalogue No.	Cultivar name	Origin	Level of	(AT) IRG, cm				
			breeding improvement	Mean	Min	Max		
	Nonresistant							
2306	Selektsionny 33	Russia	primitive	0.78	0.75	0.80		
2938	Zhelanny	Russia	primitive	0.67	0.66	0.68		
2108	Av. Jeune de Ardennes	France	primitive	0.55	0.39	0.70		
2219	Smolenets	Russia	primitive	0.49	0.43	0.56		
2896	Chervonny	Russia	primitive	0.39	0.27	0.47		
	LSD <sub>0.05</sub>							

The highest Al resistance (1.78–1.90 mm) was recorded for a set of 5 accessions (see Table 2) from France: Avoine Noire Interesable (primitive, k-7795), Avoine Nue Grosse (primitive naked, k-2122), Trophee Vilmorin (primitive, k-11145), Local (landrace, k-5336), and 'Noire de Michamps' (improved, k-14712). The lowest resistance (0.39-0.78) was identified in the group of primitive cultivars: 'Chervonny' (k-2896), 'Smolenets' (k-2219), 'Zhelanny' (k-2938) and 'Selektsionny 33' (k-2306) from Russia, and 'Avoine Jeune de Ardennes' (k-2108) from France.

The observed range of resistance (0.4–1.9 mm) was subdivided into 3 intervals with a step of 0.5: accessions with AT < 0.9 were classified as nonresistant; those with  $0.9 \le AT < 1.4$ , as medium resistant; and those with AT  $\ge 1.4$ , as highly resistant.

Landraces and modern improved cultivars from the studied set showed a tendency towards medium and high levels of Al resistance; the lowest resistance for landraces was 1.1, and for improved cultivars 1.0. The wide range of variability

among primitive cultivars from both countries shows that cultivars developed by primitive breeding were not the results of targeted improvement for this trait, while landraces and modern improved cultivars were purposefully selected for this indicator.

**Micronutrient composition in the grain of oat genotypes.** The initial data are presented in Table 3. Student's dependent sample t-test did not identify significant differences between replications in the content of Cu (p = 0.445), Fe (p = 0.802), Mg (p = 0.502) or Zn (p = 0.471), which attests to the reproducibility of the method.

The three-year average values of the Cu, Fe, Mg and Zn content, Al tolerance, and field yield of 30 oat cultivars are shown in Table 3. The analysis of variance proved that there were differences among the cultivars in all the indicators.

The effect of the country of origin and the level of breeding improvement on the studied indicators was analyzed (Fig. 2).

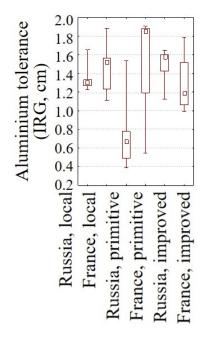


Fig. 1. Aluminum tolerance of oat accessions with different levels of breeding improvement from Russia and France Рис. 1. Алюмотолерантность образцов овса разного уровня селекционной проработки из России и Франции

Table 3. Micronutrient content values in the grain of oat cultivars (Pushkin, 2017–2019)

Таблица 3. Характеристика микроэлементного состава зерновок сортов овса (Пушкин, 2017–2019 гг.)

VIR		Origin	Content in the grain, µg/g						
catalogue No.	catalogue Cultivar name No.		Cu	Fe	Mg	Zn	Yield, g/m <sup>2</sup>	IRG, cm,	
Landraces									
1461	Local	Russia	14.6	52.5	1295.4	31.2	341.0	1.33	
1512	Local	Russia	14.9	49.6	1616.0	42.5	403.0	1.30	
1539	Local	Russia	13.7	50.9	1622.2	36.7	388.0	1.23	
1711	Local	Russia	13.2	41.2	1594.8	36.4	402.0	1.27	
1733	Local	Russia	13.1	45.2	1641.4	38.7	414.0	1.65	
1670	Local	France	13.1	43.8	1319.3	37.5	347.0	1.53	
1722	Local	France	13.6	33.0	1659.2	37.8	282.0	1.56	
5336	Local	France	13.5	38.7	1502.9	36.8	320.0	1.89	
5337	Local	France	14.0	71.9	1801.9	61.1	103.0	1.23	
5338	Local	France		47.8	1669.8	41.9	370.0	1.11	
		(	Cultivars of p	primitive br	eeding				
2219	Smolenets	Russia	13.7	42.5	1748.9	30.6	419.0	0.49	
2306	Selektsionny 33	Russia	13.1	59.7	1726.6	47.1	350.0	0.78	
2896	Chervonny	Russia	12.8	44.3	1784.1	38.0	408.0	0.39	
2919	Shatilovsky	Russia	12.9	43.8	1680.2	42.5	368.0	1.54	
2938	Zhelanny	Russia	12.8	55.2	1796.7	46.0	400.0	0.67	
2108	Av. Jeune de Ardennes	France	14.9	54.5	1910.3	41.7	342.0	0.55	
2113	Av. de Hiver	France	13.8	52.5	1561.3	39.0	122.0	_	
2122	Av. nue Crosse	France	13.8	47.9	1944.8	43.4	164.0	1.84	
7795	Av. noire Interesable	France	13.9	48.6	1784.0	38.4	416.0	1.90	
11145	Trophee Vilmorin	France	12.8	43.1	1660.5	32.3	450.0	1.86	
			Modern im	proved cult	ivars				
14787	Privet	Russia	16.7	58.7	1745.8	35.2	495.0	1.65	
15276	Borrav 2	Russia	17.9	52.5	1614.6	33.2	226.0	1.58	
15439	Gavrosh	Russia	20.3	70.5	2091.6	56.4	190.0	1.42	
15494	Medved	Russia	16.0	60.8	1575.8	36.3	525.0	1.12	
15495	Vsadnik	Russia	14.8	52.4	1497.8	33.3	619.0	1.60	
14516	Negrita	France	16.5	79.1	1798.4	48.9	538.0	1.13	
14641	Criniere	France	14.9	89.0	1728.8	49.1	286.0	_	
14712	Noire de Michamps	France	17.4	98.8	1969.4	58.6	519.0	1.78	
15399	Av. nue Renne	France	16.8	102.2	2414.5	69.4	282.0	1.25	
15401	Chantilly	France	15.6	79.8	2151.8	47.9	683.0	0.99	
LSD <sub>0.05</sub>			2.5	31.7	269.1	10.0	139.1	0.19	

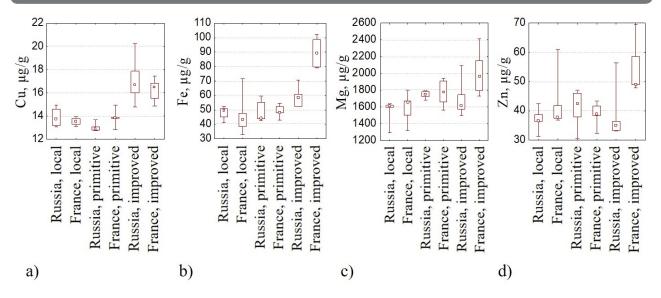


Fig. 2. The range of micronutrient content variability in the grain of oat cultivars with different levels of breeding improvement from Russia and France

Рис. 2. Диапазон изменчивости микроэлементов в зерновке сортов овса различной степени селекционной проработки из России и Франции

Cu. The content of copper (see Fig. 2a) in the grain of the studied accessions ranged from 12.8 to 20.3 µg/g. The reference cultivar Privet contained 16.7 µg/g of Cu. The two-way analysis of variance showed that the principal component of breeding improvement (p=0.000) had a significant effect on the Cu content, while the country of origin (p=0.722) and the interaction between the principal components (p=0.227) showed no effect. The highest Cu content was observed in the modern improved cultivars, both Russian and French, without any significant difference between them. The Cu content in improved cultivars was 14.8–20.3 µg/g, which is significantly higher than that in landraces or primitive cultivars. The highest amounts were found in the Russian improved cultivars. The maximum of 20.3 µg/g was recorded for the naked oat cultivar 'Gavrosh' (k-15439).

Fe. The iron content (Fig. 2b) in the grain of the studied accessions varied from 33.0 to 102.2 µg/g. The reference Privet had 58.7 µg/g of iron. The Fe content was influenced by both principal components: the country of origin (p = 0.006) and breeding improvement level (p = 0.000), as well as by their interaction (p = 0.001). The highest values (79–102 µg/mg) were recorded in the group of modern improved cultivars from France, including the maximum value of 102.2 µg/g in the naked cultivar 'Avoine Nue Renne' (k-15399). The smallest amount (33.0 µg/g) was observed in the French landrace k-1722.

Mg. The magnesium content (see Fig. 2c) in the set of the studied accessions varied from 1295.4 to 2414.5  $\mu$ g/g. The reference showed 1745.8  $\mu$ g/g. The level of breeding improvement had a significant effect (p = 0.008). Neither the country of origin (p = 0.089) nor the interaction of the principal components (p = 0.191) had any influence. The group of improved cultivars of French origin demonstrated a high Mg content (1728.8–2414.5  $\mu$ g/g), significantly exceeding the landraces but not differing reliably from the French cultivars developed by primitive breeding. The highest value (2414.5  $\mu$ g/g) was registered for the naked cv. 'Avoine Nue Renne'. The smallest amount (1295.4  $\mu$ g/g) was found in the Russian landrace k-1461.

**Zn.** The zinc content (see Fig. 2d) in the grain of the studied accessions ranged from 30.6 to 69.4  $\mu g/g$ , while the reference Privet contained 35.2  $\mu g/g$  of Zn. This indicator was af-

fected by the principal component of the geographic origin (p = 0.030), while the level of breeding improvement and the interaction between the principal components did not influence the Zn level (p = 0.099 and p = 0.057, respectively). Accessions from France were characterized by a higher Zn content (on average, 45.6 µg/g) than the Russian genotypes (38.9 µg/g). The group of improved French cultivars showed a high content of Zn (47.9–69.4 µg/g). The highest levels were recorded for two improved cultivars from France, 'Noire de Michamps' and the naked 'Avoine Nue Renne': 58.6 and 69.4 µg/g, respectively, as well as for the French landrace k-5337 (61.1 µg/g). The lowest content was observed in the Russian accessions: 30.6 µg/g in the primitive cultivar 'Smolenets' and 31.6 in the landrace k-1461.

The **yield** varied from 103 to 683 g (Fig. 3). Neither the country of origin (p = 0.321) nor the level of breeding improvement (p = 0.185) nor their interaction (p = 0.353) had any effect on the yield. The highest yields (over 600 g) were observed in the improved cultivars: 'Vsadnik' (k-15495) from Russia (619 g), and 'Chantilly' (k-15401) from France (683 g). The lowest yields (103–226 g) were recorded for French genotypes: landrace k-5337, primitive Avoine de Hiver (k-2113), and primitive naked Avoine Nue Crosse (k-2122).

The **analysis of variance** showed that, among the field characteristics, there was a statistically significant difference between the groups of oat cultivars with different breeding improvement levels in their resistance to crown rust (p = 0.019). Modern improved cultivars had the highest average score (4.9) and significantly exceeded the landraces with their lowest score (2.3). Cultivars of primitive breeding had intermediate resistance (3.2). Russian and French cultivars differed in their resistance to crown rust (p = 0.042): Russian cultivars scored 2.7, and French ones scored 4.3. The accessions from two countries did not differ in other field characteristics.

**Correlation analysis** showed that micronutrients are closely related to each other (correlation coefficients are 0.42–0.81, all are significant); they practically do not depend on the yield or AT. There was a positive correlation between the content of micronutrients and crown rust resistance: correlation coefficients varied from 0.38 to 0.50. Strong correlations were recorded between the content of Zn and Fe

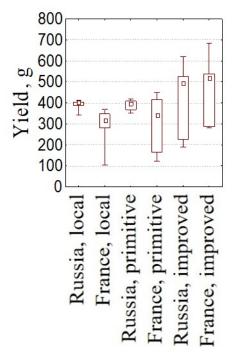


Fig. 3. The yield in the groups of oat accessions with different levels of breeding improvement from Russia and France

Рис. 3. Урожайность групп образцов различной степени селекционной проработки из России и Франции

(r = 0.81), and between Zn and Mg (r = 0.75). Correlations of Al tolerance with all the studied characteristics were insignificant. The yield significantly correlated neither with the content of micronutrients nor with AT. The yield is associated only with agronomic characters: it negatively correlated with the duration of the periods from germination to heading (r = -0.62) and from germination to harvest (r = -0.48), and positively with lodging resistance (r = 0.52) and 1000 grain weight (r = 0.42).

# Comparison of micronutrient compositions in the groups contrasting in Al tolerance

ANOVA (Fig. 4) showed the absence of statistically significant differences in micronutrient composition between the groups with different AT (p > 0.220).

The group of nonresistant accessions demonstrated the lowest variability in the content of all micronutrients. The group with medium resistance had an intermediate range of variability in the content of Cu, and the highest variability in other micronutrients. The group of highly resistant accessions was characterized by the greatest variability in the content of Cu and Fe, and in the rest of the micronutrients it had an intermediate variability span.

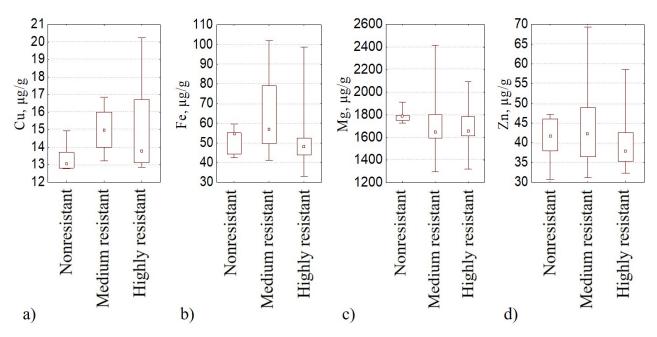


Fig. 4. Micronutrient composition in the groups with different aluminum tolerance Рис. 4. Микроэлементный состав групп с разной алюмотолерантностью

# Polymorphism of oat accessions assessed for a set of characters by means of PCA

PCA was carried out for 6 indicators: the content of 4 micronutrients, yield, and aluminum tolerance. According to the scree plot criterion, it is sufficient to leave two principal components explaining 67.0% of the variance. The first principal

component (PC1 – 47.9%) is associated with the content of 4 trace elements, and the second (PC2 – 19.1%) with the yield and AT (Fig. 5).

As far as PC1 is concerned, the set of micronutrients demonstrates higher amounts than the average level in improved cultivars from France (Fig. 6): the naked 'Avoine Nue Renne',

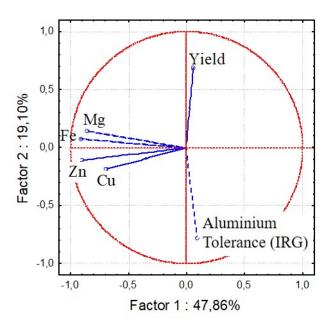


Fig. 5. Plot coordinates of variables in the space of the first two principal components Рис. 5. Координаты переменных в пространстве первых двух факторов

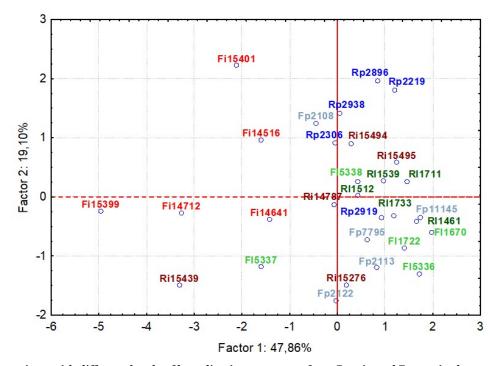


Fig. 6. Oat accessions with different levels of breeding improvement from Russia and France in the space of the first two factors according to PCA. Designations: RI – Russia, landraces (dark-green), FI – France, landraces (green), Rp – Russia, primitive (blue), Fp – France, primitive (light-blue), Ri – Russia, improved (brown), Fi – France, improved (red).

Designations also contain accession numbers according to the VIR catalogue

Рис. б. Образцов различной селекционной проработки из России и Франции в пространстве первых двух факторов. Обозначения: RI – Россия, местные (темно-зеленый цвет), FI – Франция, местные (зеленый), Rp – Россия, примитивные (синий), Fp – Франция, примитивные (голубой), Ri – Россия, селекционные (коричневый цвет), Fi – Франция, селекционные сорта (красный). Обозначение содержит также номер сорта по каталогу ВИР

'Chantilly', 'Negrita' (k-14516), and 'Noire de Michamps', plus the Russian improved naked cultivar 'Gavrosh'. Among them, 'Chantilly' was distinguished for its yield, and the naked 'Gavrosh' for its Al tolerance.

#### Conclusion

Oat cultivars with different breeding improvement levels demonstrated significant differences in the content of micronutrients and aluminum tolerance. The case study of Russian and French accessions showed that oat breeding trends differed in the requirements to these indicators across different countries and periods of their plant breeding history.

The content of Cu, Fe and Mg in grain exhibits statistically significant differences between cultivars with different levels of breeding improvement. The highest content of micronutrients is observed in modern improved cultivars, while the lowest amounts are characteristic of landraces and cultivars developed by primitive breeding.

The content of Fe and Zn was influenced by the geographic origin of genotypes; on average, accessions from France were characterized by higher concentrations of these trace elements.

Among the studied accessions, landraces and modern improved cultivars showed a tendency towards medium or high Al tolerance, the group of primitive cultivars from Russia had the lowest Al tolerance, while primitive cultivars from France demonstrated the highest average resistance (0.5–1.9).

The concentrations of different micronutrients positively correlated with each other, which may be associated with the targeted breeding of these cultivars for functional nutrition. Strong correlations were recorded between the contents of Zn and Fe (r = 0.81), and between Zn and Mg (r = 0.75). There was a positive correlation between the content of micronutrients and the resistance to crown rust: the correlation coefficients are statistically significant (0.38 to 0.50).

High content of the studied set of micronutrients was registered in such improved cultivars from France as the naked 'Avoine Nue Renne' (k-15399), 'Chantilly' (k-15401), 'Negrita' (k-14516) and 'Noire de Michamps' (k-14712), plus the Russian improved naked cultivar 'Gavrosh' (k-15439). Among them, 'Chantilly' was distinguished for its yield, and the naked 'Gavrosh' for its high tolerance to aluminum.

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