9. Garipov R.R., Shtyrlin V.G., Safin D.A., Zyavkina Y.I., Sokolov F.D., Konkin A.L., Aganov A.V., Zakharov A.V. Combined EPR and DFT study of the copper(II) complexes with N-phosphoryl thioureas // Chemical Physics. 2006. V. 320. P. 59–74.

10. Fokina A.I., Lyalina E.I., Ashikhmina T.Ya., Zhavoronkov V.I., Petrash V.V., Danilov D.N. Study of the composition, stability and toxicity of copper-containing glutathione compounds in aqueous solution // Fundamentalnye issledovaniya. 2014. No. 9. P. 757–762 (in Russian).

11. Shtyrlin V.G., Khafizyanova R.Kh., Zalyalyutdinova L.N., Mokrinskaya I.S., Zakharov A.V., Nazmutdinova G.A., Garayev R.S. Composition of amino acids with microelements, possessing antitumor and antihypoxic activity // Pat. RU 2125874. Application 04.07.1994. Date of publication: 10.02.1999. Bull. 4 (in Russian).

12. Lingtian X., Flippin J.L., Deighton N., Funk D.H., Dickey D.A., Buchwalter D.B. Mercury(II) bioaccumulation and antioxidant physiology in four aquatic insects // Environ. Sci. Technol. 2009. V. 43 (3). P. 934–940.

13. Maryon E.B., Molloy S.A., Kaplan J.H. Cellular glutathione plays a key role in copper uptake mediated by human copper transporter 1 // Am. J. Physiol. Cell Physiol. 2013. V. 304 (8). P. 768–779.

14. Fokina A.I., Lyalina E.I., Olkova A.S., Ashikhina T.Ya. Investigation of the protective properties of reduced glutathione for test organisms in a solution containing copper // Water: chemistry and ecology. 2016. No. 2. P. 64–70.

15. Sokolova M.L. Metrological characteristics of the method for determining reduced glutathione by spectrophotometry // Modern scientific research and development. 2017. No. 4. (12). P. 487–489 (in Russian).

16. Vladykina V.E., Porina N.V., Sokolova M.L., Elkina Yu.S., Katargina V.S., Sivkova S.A., Lyalina E.I., Fokina A.I. The chemical basis of the mechanism of formation of reactive oxygen species in glutathione-containing solutions of copper(II) sulphate // Ecology of the native land: problems and solutions: Materialy Vserossiyskoy nauchno-prakticheskoy konferencii s mezhdunarodnym uchastiem. 2016. P. 170–173 (in Russian).

17. Fokina A.I., Ogorodnikova S.Y., Lyalina E.I., Gornostaeva E.A., Ashikhmina T.Ya., Kondakova L.V., Domracheva L.I. Cyanobacteria as test organisms and biosorbents // Eurasian Soil Science. 2017. V. 50. No. 1. P. 70–77.

18. Fokina A.I., Ogorodnikova S.Yu., Domracheva L.I., Gornostaeva E.A., Ashikhmina T.Ya., Kondakova L.V., Lyalina E.I. Cyanobacteria as test organisms and biosorbents // Eurasian Soil Science. 2017. V. 50. No. 1. P. 70–77.

19. Collection of methods for measuring the mass concentration of copper, lead, cadmium, zinc, bismuth, manganese, nickel, and cobalt ions by the voltammetry method on the voltammetric analyzer “Ecotest-VA”. Moskva: OOO “Ekoniks-Ekspert”. 2004. 61 p. (in Russian).

20. Vasilieva S.G., Tambiev A.Kh., Lukianov A.A., Sedykh E.M., Bannykh L.N. The investigation of the accumulation of vanadium and lithium by *Spirulina platensis* and *Spirulina maxima* cyanobacteria’s cells // Trace Elements in Medicine. 2010. V. 11. No. 2. P. 48–49.

21. Voeikov V.L. Reactive oxygen species, water, photons, and life // Rivista di biologia: Biology Forum. 2001. V. 94. P. 193–214.

22. Stepanova M.A. Complexes of palladium and copper in the reactions of thiol oxidation with hydrogen peroxide. Avtoref. ... cand. khim. nauk. Sankt-Peterburg, 2012. 21 p. (in Russian).

UDC 550.47:631/416.9 **doi: 10.25750/1995-4301-2018-2-107/2-112**

Some aspects of aluminum detoxifying in plants: phytotoxic and genotoxic effects

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The separate and combined impacts of aluminum, manganese and silver ions on onion (*Allium cepa* L.) have been studied. The experiments have been performed in several series with different solutions of metal salts: $AlCl_3 \cdot 6H_2O$, $KMnO_4$, $MnCl_2 \cdot 4H_2O$ for the first and second series and $Al(NO_3)_3$ and $AgNO_3$ – in third series. The ion concentrations of all studied metals amounted to 1 MPC according to the Russian health legislation and were 0.5 mg/L for Al, 0.1 mg/L for Mn and 50 mg/L for Ag. The phytotoxic effect and genotoxic effect (such as mitotic index and the frequency of chromosome aberrations) were estimated. It was showed that aluminum ions promote negative processes in all our experiments. We found that manganese in combined presence in solution with aluminum reduced the phytotoxic and genotoxic effects aluminum on *Allium cepa*: the coefficients of antagonism calculated for frequency of aberrant cells and mitotic index are equal to 0.2. We have the same tendency for the silver ions. Taking into account our previously obtained data (the reducing of genotoxic effect of aluminum ions by iron ions) it is possible to conclude about similar mechanism for manganese (regardless of valency) and silver. Thus our results demonstrated this unique and at the same time universal mechanism of interaction between two metals (aluminum and other) and their detoxification effect in plant. We anticipate our assay to be a new starting point in investigation of detoxification mechanisms for heavy metals in plants: it is found that a combination of several metals reduces the negative action of each of them.

Keywords: aluminum, manganese ions, silver ions, barley, separate and combined action, phytotoxicity and cytogenotoxicity of aluminum, antagonism indicies.

It is known that the well-being of the world around is provided by harmonic combination of all components and appeared deviations should be compensated. Heavy metal contaminations of agricultural lands provide negative effect at all stage of plant growth as well as induce the genotoxic effects [1]. An important role is played by the impact of elevated concentrations of biologically important metals and another metal ions existing in the environment [2]. It has been shown that ions of Cu, Zn or Ni which present separately in the solution for germination of onion (*Allium cepa* test) inhibited onion root meristem cell division in varying degrees. On the other hand, the combine presence of these metals ions in solution for germination of onion reduces the level of genotoxic effect which was obtained in the case of the separate metal ions action. In addition, this effect was associated with the chemical characteristics of metal and its concentration in solution.

Generally, the model objects *Allium cepa* L. are used in many experimental studies for the investigations of genotoxic effects of various harmful and dangerous substances [3–6]. At the same time the presence of iron ions together with aluminum ions contributes to the removal of the negative influence of the latter, which is most pronounced on varieties of barley sensitive to the action of aluminum. It was suggested that a decrease in the phytotoxic effect of aluminum ions due to iron ions is associated with the induction of synthesis of proteins same as transferrin or lactoferrin in animals, organic acids or phytochelatin proteins that inactivate aluminum ions [7]. The influence of Ni and Zn on the synthesis of metallothioneins was noted in [8].

The main mechanisms of toxic effect of heavy metals are discussed in [1] but in most cases they concern the action of one particular metal. Data on the combined action of metals at concentrations actually existing in the environment are practically nonexistent, which prevents the development of standards to limit their impact on ecosystems and components of agrobiocenoses.

For plants it means that the entry of ions of any chemical element in quantities which adversely affect an organism should activate the mechanisms preventing negative reactions. This is also true for essential metals and also metal ions which are found in the same medium but have the capacity for neutralizing adverse effect. Our main aim was to study the phytotoxic and genotoxic effects of some ions of metals in plants and estimate the antagonistic interactions between them.

Objects and Methods

The separate and combined impacts of aluminum, manganese and silver ions have been studied using the *Allium* test recommended by the World Health Organization to assess mutagenic substances in the environment and to estimate 1) general toxicity from the root length inhibition and 2) genotoxicity from changes in the mitotic index value (MI), the frequency of aberrant cells (FAC) and the spectrum of chromosome aberrations (the type of chromosome anomalies).

The object of studies was Stuttgarter Riezen bulb onion (*Allium cepa* L.). This onion has 16 large well-karyotyped chromosomes. The experiments have been performed in several series in a quadruple number of replications. Ten seed onion bulbs of the same size (1.5–1.7 cm) were selected in a replication. The bulbs were preliminary watered in cold distilled water (4 °C) for more uniform germinating. Then the bulbs were being germinated during 72 hours in a germinator at 24.0 ± 0.5 °C: in the reference test – in distilled water, in the experiments – in aluminum and manganese salt solutions ($KMnO_4$, $MnCl_2 \cdot 4H_2O$ and $AlCl_3 \cdot 6H_2O$). In studying a combined impact of silver and aluminum ions the salts $AgNO_3$ and $Al(NO_3)_3$ were used. The ion concentrations of all studied metals amounted to 1 MPC according to the Russian health legislation and were 0.5 mg/L for Al, 0.1 mg/L for Mn and 50 μg/L for Ag, respectively. The hydrogen ion concentration (pH) for all the studied and reference solutions was 4.5 (due to better solubility of aluminum salts at this pH value). The presence of manganese ions (and cations of relevant metals) in a solution did not result in chemical sedimentation of aluminum compounds: the pH value of a solution for germinating onion bulbs was retained by adding small amounts of concentrated HCl at pH = 4.5, whereby aluminum is in a form of Al^{3+}.

During the incubation in distilled water (reference) the length of bulb roots reached 15–20 mm and during the incubation in salt solutions it was close to these values or below them. The roots of about 10 mm in length in the experiment and in the reference test were cut off and preserved in the mixture of alcohol with glacial acetic acid in a 3:1 ratio during 24 hours, later the fixer was drawn off and the specimens were washed first in 80% and then in 70% ethanol. The pressed specimens were stained with hot aceto-orceine by 1–2 min heating of the glasses with an alcoholic lamp. The dividing cells were counted by Laboval's microscope with a 400X magnification. The mitotic index (MI) was found from the following equation:

$$MI = [(F + M + A + T) / (F + M + A + T + I)] \cdot 100\ (\%),$$

where MI is the mitotic index, F is the fraction of cells in prophase, M is the fraction of cells in metaphase, A is the fraction of cells in anaphase, T is the fraction of cells in telophase, I is the fraction of cells in interphase (in fractions of 1).

The frequency of chromosome aberrations (FCA) was found by comparing the number of anaphases with aberrations and the total number of anaphases (not less than 500 per each experiment variant) in the division zone. The chromatid (single), chromosomal (double) and three-lane mitoses were counted. In assessing such aberrations as chromosome retardation, calculated were the chromosomes spaced by a fully two times larger distance from the divided chromatin "caps" than the chromosome depth. The following types of aberrations (mutations) have been considered: 1) a chromatid bridge (single) – the fusion of two chromatids, after an isolocus break; 2) a chromosome bridge (double) – the fusion of two chromosomes, after an isolocus break; 3) a fragment – the chromatid detachment from a chromosome, after an isolocus break; 4) retardation of the entire chromosome; 5) tripolar mitosis – the formation of three strands of a division spindle and the chromosome disjunction to three poles.

The coefficient of antagonism (C_{ant}) in a combined impact of two metals on onion roots was calculated from $C_{ant} = S_{1+2} / (S_1 + S_2)$, where S_{1+2} is the parameter value determined in a combined impact of two chemical elements minus the reference value; S_1, S_2 is the parameter value determined in a separate impact of every chemical element minus the reference value.

The phytotoxic effect (PE) from degradation of the onion root length was calculated using:

$$PE = [(L_0 - L_x) / L_0] \cdot 100\%,$$

where L_0 is the length of onion roots after germinating in distilled water, mm; L_x is the length of onion roots after germinating in metal salt solutions.

The experimental results have been statistically processed with the Excel 2000 software. The reliability of differences was assessed by the Student's test. The differences at $p \leq 0.05$ were considered statistically significant.

Results and discussion

The problem of aluminum toxicity for plants is being considered by many research centers [9–11], the reason of aluminum toxicity is the ability to induce oxide radicals [12–14]. The modulation of toxic aluminum impacts in *Cassia tora* roots by salicylic acid is an indirect evidence of the fact that Al induces the oxidation stress for plants [15]. Cytogenetic effects of metal ions on apical meristem cells of *Allium cepa* L. seeding roots were discussed in [16]. In our experiment the toxic effect of aluminum ions (salt solution of $AlCl_3 \cdot 6H_2O$, ion concentration of Al was 0.5 mg/L) appeared in the degradation of growth processes and the changes in cytogenetic indices. The biochemical and molecular implications of metals on seeds and their significance for seeds germination were discussed in [17]. In the present investigation the degradation of onion roots length as the value of phytotoxic effect (PE) amounted to (39.0±4.6)% ($p < 0.05$ against the blank variant). On the contrary, onion germination in a potassium permanganate solution ($KMnO_4$, ion concentration of Mn was 0.1 mg/L) had stimulated the growth of onion roots. This effect can be explained by both the essential role of manganese (a vital microelement for plant growth) and the presence of potassium ions also important for the plant growth [18]. In germinating onion bulbs in aluminum and manganese salt solutions the growth of roots was inhibited: the PE value practically corresponded to that observed under the impact of Al ions.

It is found that Al and Mn ions in quantities coinciding with their typical concentrations in acid soil solutions [18] have a profound impact on the onion root meristem cells: the reduction in a mitotic index (MI) against reference values and the increased frequency of aberrant cells (FAC) are noted (Table 1, the first series of experiments).

However, in their combined impact on the root meristem cells of onion the cytogenetic effect is not summarized, and on the contrary, there is antagonism: the coefficients of antagonism calculated for FAC and MI are equal to 0.2 in both cases. Thus, the fractions of dividing cells and cells with aberrations in the presence of these two metal ions are practically not different as compared to the blank.

In a type of chromosome aberrations, genome mutations (tripolar mitosis) are found only for the onion root meristem cells exposed to Al ions (separately or in combination with Mn ions) (Table 2). In this case Mn ions reduce their levels only partly. Single bridges and single fragments prevailed among other aberrations. A fraction of single (chromatid) bridges in the reference test (blank) is greater than in other variants of experiment and, on the contrary, a fraction of single fragments is less. The tendency to increase a fraction of single fragments is typical of Mn ions.

The experiment with concentration of Mn ions has demonstrated no impact of manganese (along with potassium) valency on cytogenetic reactions (MI, FAC) proceeding in the onion root meristem (Table 1, the second series of experiments) that may be stipulated by instability of seven-valent manganese compounds and changes in the valency of metal in a solution.

Early we established that not only oxidants diminish the toxic Al impact on plants: iron (III) ions reduced the genotoxic effect of Al ions in the root meristem cells of barley sprouts [19]. The different response of various cultivars of spring barley to the modulating effect of Fe is the validation of genetically determined mechanisms of aluminum toxicity [20]. This and other results highlight the existence of a series of mechanisms of Al-tolerance.

One of physiological responses of plants to heavy and toxic metals as known is protein-phytochelatin synthesis. At the same time, it was showed that Al ions do not provoke phytochelatin synthesis in plants [21]. If we take into account that monovalent silver at 100 μM concentration turned out to be the first in the ranked metals promoting phytochelatin synthesis it will be interested to estimate the effects of aluminum and silver ions separately or together. Based on the new information about the capacity of aluminum to induce oxide radicals [12–14], it can be expected that silver ions would indirectly reduce the genotoxic effect of Al ions.

In our experiment were showed that PE determined from the length of onion roots was 55.0±2.6%. The effect of silver ions on the root meristem cells of onion is also manifested in reducing the MI index value (approximately two fold) as well as in increasing the fraction of aberrant cells

Table 1

Cytogenetics effects of ions Al and Mn (VII and II valency) or Ag (separately and combined effects)

Variant	MI, %	FAC, %
I series of experiments		
Blank	8.7±0.8	0.9±0.7
Al ($AlCl_3$)	4.6±0.7*	7.1±2.5*
Mn ($KMnO_4$) (VII valency)	4.9±0.3	2.8±1.6
Al + Mn	6.9±0.6	2.4±1.1
II series of experiments		
Blank	8.2±0.6	1.4±0.8
Al ($AlCl_3$)	5.1±0.5*	4.1±1.4
Mn ($KMnO_4$) (VII valency)	7.0±0.9	2.2±0.4
Mn ($MnCl_2$) (II valency)	6.2±0.7	1.3±0.6
Al + Mn ($KMnO_4$) (VII valency)	6.9±0.6	2.4±1.1
Al + Mn ($MnCl_2$) (II valency)	7.4±0.7	1.9±0.9
III series of experiments		
Blank	10.1±0.9	1.2±0.8
Al ($Al(NO_3)_3$)	5.9±0.5*	4.0±1.9
Ag ($AgNO_3$)	6.6±0.9	3.5±1.2*
Ag + Al	7.0±0.6	2.2±1.1

*Note: * – differences are significant at $p < 0.05$ compared with blank variant. The degree of MI and FAC in the onion root meristem on exposure to Al ions is more pronounced as compared to blank ($p < 0.05$) than on exposure to Mn ions (VII valency) ($p < 0.1$).*

Table 2

Types of aberrations and their quantitative relations under the action of Al, Mn and Ag ions (separately or in combination) at the root meristem cells of onion

Variant	Type of aberrations*, %				
	m1	m2	f1	f2	g
Blank	51.85	7.41	37.04	3.70	–
Al	31.71	7.32	41.46	13.41	6.1
Mn(VII)	45.10	3.92	47.06	3.92	–
Ag	72.22	–	27.78	–	–
Al + Mn(VII)	33.33	4.77	47.62	9.52	4.76
Al + Ag	64.29	–	35.71	–	–

*Note: * m1 – chromatid bridge (single); m2 – chromosomal bridge (double); f1 – fragment; f2 – retardation of the entire chromosome; g – tripolar mitosis; "–" – that type of aberration is missing.*

($p < 0.05$ in comparison with blank, Table 1, the third series of experiments).

In a combined impact of Ag + Al ions the PE has gone down to 12.5±3.2%. It gives evidence of an obvious antagonism of silver ions relative to aluminum ions (the coefficient of antagonism for MI is 0.4, for FAC it is 0.2).

In a type of chromosome aberrations the impact of silver ions on the root meristem cells of onion was much different from that of aluminum ions (Table 2): only aluminum ions cause genomic violations. The silver ions has contributed only to the formation of single bridges and fragments in the ratio of 72.2:27.8 and 64.3:35.7 for Ag and Al + Ag variants respectively.

Conclusion

Thus among ecological problems the studying of the mechanisms ensuring plant resistance to the impact of aluminum are very important [22, 23]. When we investigating the impact of aluminum on plants, it is found that in a soil solution with which the root system comes into contact in the growth, there are not only Al ions, but also ions of other metals and nonmetals. And all the elements present in the environment can have a cross impact and due to this modify the toxic response of plants to aluminum impact. Particularly, the ions of Fe are capable of reducing both the phytotoxic and the genotoxic effect of Al ions [20]. It can be also expected that ions of other metals available in the rhizosphere are up to modify (and, perhaps, inhibit as Fe) the impact of aluminum.

The present studies of phytotoxic and cytogenotoxic effects of Al and Mn ions on the onion roots have shown that Mn ions (irrespective of valency) stimulate the process of onion root cell stretching and practically do not govern the rate of cell division. On the contrary, aluminum inhibits the processes of growth and causes genetic deviations. The effect of silver ions manifests itself in some reduction of the cell division activity and does not cause a reliable increase of chromosome aberrations.

The simultaneous presence of Al and Mn ions in a solution for germinating onion bulbs reduces the cytotoxic impact of aluminum (reduction of MI) and its genotoxic effect (reduction of FAC and changes in the aberration spectrum – the reduction of genome aberrations most harmful for cells). The presence of manganese ions (and cations of relevant metals) in a solution did not result in chemical sedimentation of aluminum compounds: the pH value of a solution for germinating onion bulbs is retained by adding small amounts of concentrated HCl at pH = 4.5, whereby aluminum is in a form of Al^{3+}. Therefore it can be supposed that reduction of the phytotoxic Al impact on plants takes place at the level of metabolic reactions. The mechanisms of these reactions are in part known [11, 13, 22, 24] and the others are to be found [25].

Considering molecular aspects of the antagonistic interaction found between manganese and aluminum ions and silver and aluminum ions, it can be expected that the impact of manganese ions as well as silver ions results in the synthesis of phytochelatin proteins [21] binding aluminum ions in a complex. The alternative mechanisms of aluminum detoxication are also known [25]. As to manganese, it possesses a pronounced antagonistic (relative to aluminum) impact both in the septivalent and the bivalent states. In the first state manganese is a strong oxidizer, very unstable and therefore can change the valency in a solution.

The performed studies allow one to conclude:

– the simultaneous presence of manganese (valency VII) and aluminum ions in a solution for germinating onion bulbs favors the reduction of an adverse aluminum impact: the fraction of aberrant cells decreases and the MI value of root meristem cells increases; the coefficient of antagonism from these indices is similar and equal to 0.2;

– the ions of silver which are present simultaneously with aluminum ions in a solution for germinating onion bulbs reduce an adverse impact of aluminum ions on meristem cells: the antagonism coefficients are 0.4 for the MI and 0.2 for FAC, respectively.

References

1. Skugoreva S.G., Ashikhmina T.Ya., Fokina A.I., Lyalina E.I. Chemical grounds of toxic effect of heavy metals (review) // Teoreticheskaya и prikladnaya ekologiya. 2016. No. 1. P. 4–13 (in Russian).

2. Ulyanenko L.N., Reva E.V., Synzynys B.I. Cytogenetic effects in *Allium cepa* in the separate and combined effect of copper, zinc and nickel // Sel'skokhozyaistvennaya biologiya. 2017. V. 52. No. 1. P. 183–190 (in Russian).

3. Lerda D., Biagi Bistoni M., Pelliccioni P., Litterio N. *Allium cepa* as a biomonitor of ochratochin A and genotoxicity // Plant Biology. 2010. No. 12. P. 685–688.

4. Olorunfemi D., Iogieseri U.M., Akinboro A. Genotoxicity screening of industrial effluents using onion bulbs (*Allium cepa* L.) // Journal of Applied Sciences and Environmental Management. 2011. V. 15. No. 1. P. 211–216.

5. Leme D.M., Marin-Morales M.A. Chromosome aberration and micronucleus frequencies in *Allium cepa* cells exposed to petroleum polluted water – a case study // Mutation Research. 2008. V. 650. No. 1. P. 80–86.

6. Versienen L., Evers S., Smolder E., De Schamphelaere K., Blust R. Mixture toxicity and interactions of cooper, nickel, cadmium and zink to barley at low effect levels: something from nothing? // Environmental Toxicology and Chemistry. 2016. V. 35. No. 10. P. 2485–2492.

7. Amosova N.V., Synzynys B.I. About complex action by aluminum and iron ions on barley and wheat seedlings// Sel'skokhozyaistvennaya biologiya. 2005. No. 1. P. 85–87 (in Russian).

8. Carpene E., Andreani G., Isani G. Metallothionein functions and structural characteristics // Journal of Trace Elements in Medicine and Biology. 2007. V. 21. Suppl. 1. P. 35–39.

9. Klimashevsky E.E. Genetic aspect of mineral nutrition of plants. Moskva: Agropromizdat, 1991. P. 138–150 (in Russian).

10. Bulanova N.V., Synzynys B.I., Koz'min G.V. Aluminum induces chromosomal aberrations in root meristem cells of wheat // Russian Journal of Genetics. 2001. V. 37. No. 12. P. 1455–1458.

11. Kochian L.V. Cellular mechanism of aluminum toxicity and resistance in plants // Annual Revier of Plant Physiology and Plant Molekular Biology. 1995. No. 46. P. 237–260.

12. Boscolo P.R.S., Menossi M., Torge R.A. Aluminum-induced oxidative stress in maize // Phytochemistry. 2003. No. 62. P. 181–189.

13. Exley C. The pro-oxidant activity of aluminum // Free Radical Biology and Medicine. 2004. No. 36. P. 380–387.

14. Richards K.D., Schott E.J., Sharma Y.K., Davis K.R., Gardner R.C. Aluminum induced oxidative stress genes in Arabidopsis thaliana // Plant Physiology. 1998. V. 116. No. 3. P. 409–418.

15. Wang Y.-Sh., Wang J., Yang Z.-M., Wang Q.-Y. Salicylic acid modulates aluminum-induced oxidative stress of *Cassia tora* // Acta Botanica Sinica. 2004. V. 46. No. 7. P. 819–828.

16. Dovgaluk A.I., Kalinyak T.B., Blume Ya.G. Cytogenetic effects of toxic metal salts on apical meristem cells of *Allium cepa* L. seeding roots // Tsitologiya i genetika. 2001. No. 2. P. 3–10 (in Russian).

17. Kranner I., Colville L. Metal and seeds: biochemical and molecular implications and their significance for seeds germination // Environmental and Experimental Botany. 2011. V. 72. P. 93–105.

18. Orlov D.S., Vasilevska V.D. Soil and environmental monitoring and protection of soils. Moskva: Izdatel'stvo Moskovskogo gosudarstvennogo universiteta, 1994. P. 32–64 (in Russian).

19. Synzynys B.I., Amosova N.V., Reva E.V., Polyakova I.V., Simakova I.M., Necvet N.V. 100 anniversity of E.A. Mitcherlich low for combined action of ecological factors: principles of combined action of essencial and toxical metals and radiation on a plants on the cytogenetical level // Biological effects of low doses of ionizing radiation and radioactive contamination: Materialy mezhdunarodnoy konferentsii . Syktyvkar, 2009. P. 371–373 (in Russian).

20. Synzynys B.I., Amosova N.V., Ulyanenko L.N. Sensitivity of barley varieties to aluminum ions: separately effects and combine with iron ions // American Journal of Plant Science. 2013. V. 4. No. 12A. P. 49–52.

21. Grill E., Winnacker E.-L., Zenk M.N. Phytochelatins, a class of heavy-metal-binding peptides from plants, are functionally analogous to metallothioneins // Proceedings of the National Academy of Sciences of the United States of America. 1987. No. 84. P. 439–443.

22. Amosova N.V., Nikolaeva O.N., Synzynys B.I. Mechanisms of aluminum tolerantce in cultivated plants // Sel'skokhozyaistvennaya biologiya. 2007. No. 11. P. 36–42 (in Russian).

23. Ryan P.R., Bei D., Watt M., Kataoka T., Delhaize M. Strategies to isolate transporters that facilitate organic anion efflux from plant roots // Plant and Soil. 2003. No. 248. P. 61–69.

24. Grill E., Löffler S., Winnacker E.-L., Zenk M.H. Phytochelatins, the heavy-metal-binding peptides of plants, arsynthesized from glutatione by a specific glutamylcysteine dipeptidyl transpeptidase (phytochelatin synthase) // Proceedings of the National Academy of Sciences of the United States of America. 1989. No. 86. P. 6838–6842.

25. Peter W., Patino G.M., Chaves A.L., Mayer J.E., Idupulapati M.R. The high level of aluminum resistance in signalgrass is not associated with known mechanisms of external aluminum detoxification in root apices // Plant Physiology. 2001. V. 125. No. 3. P. 1473–1484.