UDC 581.191.143.6
DOI 10.31654/2786-8478-2025-BN-4-42-52

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HEAVY METAL IONS – ECOLOGICAL AND PHYSIOLOGYCAL BENEFITS AND HARMFUL EFFECTS ON PLANT ORGANISM

Heavy metals include a number of the most toxic xenobiotics, which cause general and specific damage to organisms. This applies to heavy metal ions. The reaction of plants to the type and concentration of HMI is extremely diverse. Absorbing HMIs leads to reduced productivity or death. During the study of the effect of ten types of HMI, which were part of cations and anions in concentrations of 10-1 – 10-5 M.

Plants growing in conditions exposed to heavy metal ions accumulate toxic cations. Hyperaccumulators are capable of accumulating HMI in large quantities. Most plants absorb HMI through two types of absorption systems. HMI affect the electrochemical status of membranes and electrical potential. Also, depending on their concentration, they cause a series of interrelated stress reactions in plants. The severity of stress damage is reflected in integral indicators – growth, morphogenesis, productivity. Sensitivity to stressors is determined in each specific case, since the characteristics depend on the plant genotype.

Studies of the effect of heavy metal ions on plant growth and development have shown that all pathological changes begin at the cellular level. Cell culture is a convenient and promising system for studying the stress effect of the stressor itself and the mechanisms of resistance. The protective reactions of the whole organism, aimed at reducing the toxic effect, are separated from the cellular detoxification reactions.

Key words: *heavy metal ions, toxicity, abiotic factors, plants, harmful effect.*

Among the most aggressive environmental pollutants that have a detrimental effect on the biosphere are heavy metal ions (HMI) [1, 61, 67]. The systemic harmful effect of heavy metal ions is increasing from year to year, as they can significantly reduce the natural resistance of biological objects to biotic and abiotic environmental factors and as a result of the expansion of economic activity and increased anthropogenic pressure [2, 63, 64].

In the natural state, 90 elements can exist, of which 21 are nonmetals, 16 are light metals, and the remaining 53 (excluding As) are heavy metals [8, 66]. Heavy metals are elements whose density exceeds 5 g\cm3. They are transitional elements from V (but not Sc or Ti) to the semi-metal As, from Zn (but not Y) to Sb, from La to Po. Lanthanides and actinoids can also be classified as heavy metals. Most heavy metal atoms have incomplete d-orbitals, which is why IVMs are able to form complex compounds. The latter can be characterised by redox activity. Some HMI (in trace amounts) play a role in biochemical reactions. However, they are toxic in large quantities. In particular, such IRMs include Zn^{2+}, Cu^{2+}, Mn^{2+}, Co^{2+}, Ni^{2+}, Fe^{2+}, $Mo6^{+}$. The widespread occurrence and toxicity of IVMs are of interest to a wide range of researchers.

At the same time, there are heavy metals whose concentration in nature varies between 10 and 1 nM, such as V, Cd, Cr, W, Ga, Zr, Th, Pb, Hg [20, 47, 66]. Some of them, in particular Cd^{2+}, Hg^{2+}, Pb^{2+}, are actively studied. Some HMI are the objects of research solely because of their special properties [11, 19, 45, 66].

The natural content of their clusters is considered to be the starting point for changes in the concentration of HMI in soils [1, 6, 7, 23]. HMI (with the exception of mercury) mainly enter the atmosphere in the form of aerosols and fall out as a component of precipitation. The composition of pollutants depends on the industrial and energy sectors. A significant amount of them is deposited in the soil. The transition of mobile HMI to a sedentary state is possible due to isomorphic substitution and ion exchange in mineral particles and exchange and chelation reactions. When pollutants enter the soil in anionic form, the absorption role of the soil is less effective. This is due to the low adsorption capacity of clay minerals for anions, as they contain few particles that carry a positive charge [1, 13].

The reaction of plants to the type and concentration of HMI is extremely diverse. When studying the effect of ten types of HMI, which were part of cations and anions in concentrations of 10^{-1} – 10^{-5} M, on the germination of seeds of 20 plant species of different taxonomic groups, species-specificity of the reaction was established, depending on the nature of the pollutant and its concentration [14, 18, 66]. The pathway of HMI absorption by plants can also vary.

When studying the accumulation of copper and nickel ions in the tissues of *Vaccinium angustifolium* L. plants growing near a steel mill in Ontario, Canada, a logarithmic dependence of the decrease in the concentration of pollutants with increasing distance from the production was found. The metals were distributed in the tissues as follows: root > stem > leaves > fruits. Root tissues were the primary site of accumulation of these elements [26, 44]. The predominant accumulation of Cu^{2+} ions in the roots of various plants has been reported in other publications [1, 6, 19, 49, 55].

Cadmium ions are absorbed by plant roots and deposited in them, as well as in the aboveground part. Thus, in the seedlings of *Nicotiana tabacum* L., HMI were deposited in equal amounts in the dry matter of leaves and roots, and in *N. rustica*, the concentration of Cd^{2+} in leaves was half that in root tissues [14, 44], and in young seedling tissues cadmium was in soluble form (80% represented by Cd-peptides), while in adult plants soluble and insoluble cadmium compounds were represented in equal amounts. The study of Cd^{2+} distribution between cellular compartments in *Athyrium yokoscence* plants showed that 80% of cadmium was deposited on cell membranes and this amount increased with increasing concentration in the medium. The rest of the cadmium was distributed in cells almost equally between the fractions of nuclei, mitochondria and plastids [24, 66].

Significant accumulation of cadmium ions in root tissues has been reported for a number of plants [4, 67]. Cadmium can bind to proteins. For example, in the protein fractions from rice and wheat grains, the Cd-bound part of proteins was 54,5 and 55 kD, respectively. Other Pb, Pb^{2+}, Zn^{2+}, and Mn^{2+} are also accumulated by plants [57, 66]. The Pb-accumulating ecotype of stonecrop (Sedum alfredii Hanse) accumulates the element in the root system and transports it to the stem and leaf tissues. The stem cell wall fraction contained 50%, and the same fractions of roots and leaves contained 80 % of the lead accumulated by the cell. A mutant of Arabidopsis grown on soil with an excess of manganese accumulates 7,5 times more manganese, and when grown in hydroponics, 5,4 times more than wild-type plants [3, 61].

All plants growing under the influence of heavy metal ions accumulate toxic cations. In this case, hyperaccumulators are able to accumulate HMI in quantities that significantly exceed their content in the soil [63]. The accumulation of heavy metal anions, similar to the accumulation of cations, is usually not observed, because in this case the toxicity of the metal is higher. For example, hexavalent chromium is more active and toxic than trivalent chromium [45]. Vanadium can be absorbed by living organisms in two forms: vanadate (V(V) and vanadyl (V(IV); the spectrum of toxic effects of vanadate is much wider. However, it should be noted that vanadyl can self-oxidise to form vanadate. At the same time, vanadate is reduced by reducing agents such as glutathione, ascorbate, and NADPH. During the study of corn seedlings and fodder beans grown on artificial solutions containing various forms of vanadium in concentrations of 2 – 200 μM, the absorption activity and distribution of this element were determined. Regardless of the species, plants absorbed vanadyl more actively than vanadate. The relative amount of vanadium transported to the ground parts was 0,9 – 2,6% of the consumed amount and did not depend on the form and concentration of this element in the medium [25, 41, 42, 43].

In the case of the uptake of HMI by the root system, the availability of the element (proportion of the total content) and the ability of the plant to transport ions from the exogenous system to the substrate – the roots – play an important role. HMI can also be absorbed by leaves from the air. Elements associated with small (< 2 μm) particles of ash and smoke are easily dissolved in acidified rainwater and enter leaf tissues [12, 37, 62, 66]. Once inside the cell, HMI interact with its structural and metabolic components.

In contrast to biotic stress, which is controlled by a monogenic trait, tolerance to abiotic stress is a genetically constitutive characteristic (a dynamic process). It includes numerous components of signalling chains that are multigenic in nature. Moreover, the links between individual links can be direct, reverse, or crossed. TF families, differential expression of stress-induced genes ensures the stability of vital activity in the event of changes in cultivation conditions. Adaptation to a specific situation is manifested in the specialisation of metabolism: synthesis/accumulation of protective compounds of different composition. Methodologies for obtaining plants using HMI should be linked to studies of the expression of gene(s), product(s) involved in signalling pathways or the synthesis of functional or structural proteins and metabolites. Planning of prospective studies based on a systematic approach using transcriptomics, metabolomics, proteomics, etc. is a guaranteed strategy for improving plant resistance to HMI and other abiotic stresses [44].

Systems for the absorption of heavy metal ions. In general, plants absorb HMICs in two ways (through two types of absorption systems). The first method is fast, nonspecific, and involves the use of vectors of different species. The second method is slow and requires high substrate specificity of the vector and energy source (ATP). In microorganisms, Ni^{2+}, Co^{2+}, Zn^{2+}, and Mn^{2+} ions are absorbed by the reactive method with the use of inorganic transporters. Chromates and arsenates are also transported rapidly: the former by the phosphate transport system, the latter by the sulfate transport system [28, 42]. Vanadate, which is structurally similar to phosphate, can enter plants via phosphate uptake systems [33, 41, 43].

While the transport of HMI in microorganisms has been studied extensively and systematically (highly specific chemiosmotic transporters or ATP-bound cassette transporters have been identified for a number of ions), in plants, only a few publications have been devoted to this problem, despite the fact that many hyperaccumulative mutants have been obtained. Thlaspi caerulescens and Arabidopsis halleri are hyperaccumulators of zinc and cadmium. It was found that plants of the first species use the *ZNT1* transport system, which is highly affinity for Zn^{2+} ions, to obtain Zn^{2+} uptake. The presence of a similar mechanism is not excluded in the second species. Cd^{2+} ions can also move with the participation of the *ZNT1* transporter, which in this case is an indirect low-affinity transporter [28, 31, 64, 66]. The manganese hyperaccumulator mutant of Arabidopsis thaliana also accumulates other elements. The amount of Cu^{2+}, Zn^{2+}, and Mg^{2+} ions in the leaves of this family is 4.6, 2.8, and 1.8 times higher than in the leaves of wild-type plants, respectively. It is believed that this total ion transport is mediated by ferric chelate reductase. Ferric oxalate reductase activity is quite widespread among plants and is considered to be crucial in the regulation of iron ion uptake. Some authors note that other ions can also be transported through root cell membranes with the participation of this enzyme [5, 24, 25, 31].

The effect of copper ions (1, 5, 50 μM) on the cell culture of sharp-leaved maple (*Acer pseudoplatanus*) was studied. A linear dependence between the concentration of Cu^{2+} in the culture medium and the content of these ions in the cell was found. Thus, the possibility of cation transport by common channels on cytoplasmic membranes is not excluded [48, 62]. In general, the rate of ion penetration into the cell depends on the sensitivity of metabolic sites to a particular ion. Such parameters of the plasma membrane as redox potential and pH barrier are external mechanisms that regulate the penetration of HMI into the plant.

HMI affect not only the electrochemical status of membranes, but also the electrical potential. After the addition of 0.1 or 1 mM Cd^{2+} to the experimental solution containing rice root cell membranes, a sharp depolarisation of the membranes was observed within a few minutes. The initial membrane potential was restored only after 6 to 8 hours of Cd^{2+} The fact that these cations are absorbed even at 00C, when the metabolism is very slow, also indicates significant changes in the properties of plant cell membranes under the influence of Cd^{2+} ions [7, 11, 26, 48].

Antagonism of cations affects the absorption of HMI. The ions of alkali and alkaline earth metals can be placed in the following order according to the degree of their inhibitory effect on the absorption of Cd^{2+}: $Na^+ < K^+ < Mg^{2+} < Ca^{2+}$ [23, 47]. Zn^{2+} and Cu^{2+} ions and even elements of the same group can be antagonists of Cd^{2+} uptake [24, 50, 65]. This is the nature of the accumulation of Na^+ cations and its chemical analogue, Cs^+. A study of the dynamics of radionuclide uptake by young (2-day-old) wheat (*Triticum aestivum* L.) seedlings showed that ^{134}Cs gradually accumulated in young leaves over 20 days, while ^{22}Na accumulated only temporarily and then was released through the roots. Thus, even within the same chemical subgroup (alkali metals), the processes of uptake, distribution and translocation of HMI by plants differ significantly.

Once inside the cell, HMI cause various harmful effects. The phytotoxicity of a particular type of ion is determined, on the one hand, by the chemical properties of the element, and, on the other hand, by the sensitivity or resistance of the plant organism, depending on the genotype.

Toxicity of heavy metal ions. Absorbing HMI, plants undergo pathological changes at all levels – from subcellular to organismal, which ultimately leads to reduced productivity or death. The interaction of IPM with the cytoplasmic membrane activates lipid peroxidation. [24, 54, 57]. Oxygen radicals precede the peroxidation of polyunsaturated fatty acids on the membrane, which leads to membrane damage and cellular decompartmentation. The toxic effect can be enhanced by poly phenols, which are products of lipid peroxidation [24]. In response to the oxidative process, the activity of catalase, peroxidase, and SOD increases [20, 40, 62]. Thus, the treatment of sugarcane seedlings with 2 mM CdCl2 caused the appearance of 7 isozyme forms of Cu/Zn-SOD. It is believed that activation of lipid peroxidation (the result of oxidative catabolism) is a common metabolic link in the plant response to stress. The interaction between the IBM and the membrane is the primary site of action.

If the stress caused by the toxicity of IRMs is not removed, physiological processes, the direction of biochemical reactions and, as a result, cell homeostasis begin to change.

HMI significantly affect photosynthesis, chloroplast structure, and pigments. Cd^{2+} and Pb^{2+} ions cause changes in the lipid state of thylakoid membranes. A typical phenomenon is a decrease in the chlorophyll content, with the content of chlorophyll b decreasing more than chlorophyll a [9]. A similar effect is caused by Cu^{2+}, Ba^{2+}, Zn^{2+}, Mn^{2+}, Hg^{2+} ions [10, 22, 60]. Usually, the processes of respiration and ATP synthesis are studied simultaneously with photosynthesis [15, 16, 31].

It has been established that as a result of the toxic effects of HMI, mitochondria lose their native structure, and proton and electron transport is disrupted. A decrease in H+-secretion under the influence of vanadate in the segments of petioles of *Regnellidium diphyllum* and *Nymphoides peltarta* (S. G. Gmel.) O. Kuntze was observed already 1 hour after the pollutant application. This decrease lasted for 6 hours, despite the fact that the direct effect of the stressor ceased after 3 hours. In addition to V^{5+}, Cd^{2+} and Pb^{2+} ions have a toxic effect on the electrotransport chain, disrupting its integrity [36, 41, 42].

Once in the cell in large quantities, HMI disrupts the mineral nutrition of plants, inhibits the absorption of the necessary cations K^{+}, Ca^{2+}, Mg^{2+}, Mn^{2+} [2, 26, 64, 66]. There are two mechanisms of HMI influence on absorption. The first one is caused by the proximity of the ionic radii of the IVMs and is determined by physical and chemical reasons. For example, Cd^{2+} (1,03 Å) reduces the absorption of Zn^{2+} (0,83 Å) and Ca^{2+} (1,06 Å). The second is related to the disturbance of cell metabolism caused by the IMI, which results in membrane restructuring. Along with the change in cation uptake, anion transport decreases. The latter is determined by a decrease in the content of nitrogen, phosphorus, and sulfur in plant cells [38, 39]. Phosphorus deficiency especially affects the sensitivity/resistance of plants to HMI. Phosphorus is used for the formation of polyphosphates, which are synthesised by poly-P kinases, which reversibly transfer the phosphate residue from the macroergic donor to the poly-P chain. There is strong evidence that poly-Ps provide binding of HMI and resistance to them in plants. Three possible mechanisms have been proposed: cells use poly-Ps to scavenge heavy metals; poly-Ps associated with the cell surface may be involved in binding HMI on the surface; and poly-Ps are degraded during growth in the presence of HMI [64]. Limiting plant phosphorus uptake can inhibit DNA synthesis [4, 30, 52, 53].

HMI affect the content and structure of nucleic acids in plants. Cd^{2+} and Zn^{2+} ions in concentrations exceeding 250 μM dramatically reduce DNA synthesis. At the same time, cadmium ions at a concentration of 50 μM can stimulate RNA synthesis. The level of ATP-sulfurylase mRNA increased almost 3-fold during the day of exposure to IVM [21, 67]. In plants exposed to ever-increasing doses of Cd^{2+} (up to 20 μM), the amount of mRNA increased linearly. A similar phenomenon was observed for Cu^{2+}, Pb^{2+}, Zn^{2+}, and Hg^{2+}. Despite the fact that the level of nucleic acid increased, the activity of the enzyme ATP-sulfurylase was inhibited by the toxic effect of Cd^{2+}.

The inhibitory effect of HMI on other enzymes was also established. For example, nitrate reductase (the first enzyme of the nitrogen assimilation chain) can be inhibited by V^{5+}, Hg^{2+}, Cd^{2+}, Pb^{2+} ions [32, 34]. The effect of tungsten oxyanion on nitrate reductase is characteristic. Tungsten is a well-known antagonist of molybdenum, capable of competing with the latter for the active site of Mo, the restraining enzyme. By replacing molybdenum in the cofactor, tungsten inactivates the enzyme, since tungsten analogues of Mo enzymes are usually inactive, except for formate dehydrogenase of some anaerobes [25, 29, 35, 42, 43].

HMI not only affects the coordination of nitrogen and carbon metabolism. In the leaves and roots of beans, Cd^{2+} ions increase the activity of glutamate dehydrogenase (GDH) due to an increase in ammonia levels. The stressful effect of cadmium is also manifested in an increase in the activity of phosphoenolpyruvate carboxylase and $NADPH^{+}$ isocitrate dehydrogenase in the leaves. The study of the sensitivity of PEPC to pH showed that the increase in activity is due to the synthesis of the enzyme and its modification during phosphorylation [27, 32, 67].

As noted, the lipid composition of membranes changes under the influence of IPM, which can affect the activity of ATPases. The ATPase isolated from a suspension culture of maple cells was inhibited by vanadate, which inhibited its activity in a non-competitive way, by more than 50% [34, 67]. In addition, vanadate and tungstate are known inhibitors of protein kinases and protein phosphotases [53, 55]. Changes in phosphorus concentration can occur by increasing the activity of acid phosphatase. A decrease in phosphorus content in the tissues of *Hyptis suaveolens* (L.) Poit and *Helianthus annus* L. under the influence of Ni^{2+} ions may be a signal of regulation of acid phosphatase and ATPase activity [40, 49, 53, 67].

Fluctuations in the activity of key enzymes cause qualitative and quantitative changes in the chemical composition of the cell. Under the influence of Ni2+, the content of soluble nitrogen and HMI protein are arranged in a series: Cd > Pb > Ni > Mo [17, 38, 39, 45]. Polyamines play an important role among stress metabolites of the nitrogen chain. There is a high correlation between the concentration of Cd^{2+} ions and the content of polyamines (spermine, putrescine, spermine din). The clearest correlation was observed for putrescine (correlation coefficient 0,94). At the same time, polyamines are known indicators of water stress. Cadmium ions significantly reduced the tolerance of plants to drought and caused a loss of turgor [24, 51, 58, 59].

Thus, HMI, depending on their concentration, cause a number of interrelated stress responses in plants. The depth of stress damage is manifested in integral indicators – growth, morphogenesis, productivity. The sensitivity to HMI is determined on a case-by-case basis, as this characteristic varies depending on the plant genotype. Seeds and seedlings are the most resistant to the stressful effects of HMI, as the latter are mostly fed by endogenous endosperm reserves at the beginning of ontogeny. However, in this case, stressful, detrimental concentrations of HMI have been established.

For example, the germination of *Vigna ambacensis* seeds germinated in solutions of cadmium, mercury, and lead salts of different concentrations decreased even at the lowest concentration.

Studies of the impact of HMI on plant growth and development have shown that all pathological changes begin at the cellular level. Cell culture is the most convenient and promising system for studying the stress effect of HMI and resistance mechanisms. In this case, the protective reactions of the whole organism aimed at reducing the toxic effect are separated from the cellular detoxification reactions.

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ІОНИ ВАЖКИХ МЕТАЛІВ – ЕКОЛОГІЧНА ТА ФІЗІОЛОГІЧНА КОРИСТЬ ТА ШКОДОЧИННИЙ ВПЛИВ ДЛЯ РОСЛИННОГО ОРГАНІЗМУ

Серед важких металів знаходяться ряд найбільш токсичних ксенобіотиків, які спричиняють загальні та специфічні ураження організмів. Це стосується іонів важких металів. Реакція рослин на вид та концентрацію ІВМ надзвичайно різноманітна. Поглинаючи ІВМ, Це призводить до зменшення продуктивності або загибелі. Під час вивчення впливу десяти видів ІВМ, що входили до складу катіонів і аніонів у концентраціях 10^{-1} – 10^{-5} М.

Рослини, які ростуть в умовах дії іонів важких металів, акумулюють токсичні катіони. Гіперакумулянти здатні нагромаджувати ІВМ у кількостях. Здебільшого рослини поглинають ІВМ за рахунок двох типів поглинальних систем. ІВМ впливають на електрохімічний статус мембран та електричний потенціал. Також залежно від концентрації вони спричиняють низку взаємозумовлених стресових реакцій рослин. Глибина стресового ураження виявляється в інтегральних показниках – рості, морфогенезі, продуктивності. Чутливість до стресора визначається в кожному конкретному випадку, оскільки характеристика звлежить від генотипу рослин.

Дослідження впливу іонів важких металів на ріст та розвиток рослин показали, що всі патологічні зміни починаються з клітинного рівня. Культура клітин є зручною і перспективною системою вивчення стресової дії самого стресора та механізмів стійкості. Захисні реакції цілісного організму, спрямовані на зменшення токсичного впливу, відокремлюються від клітинних реакцій детоксикації.

Ключові слова: *іони важких металів, токсичність, абіотичні фактори, рослини, шкодочинна дія.*

Стаття до редакції надійшла 04.12.2025 року
Рецензія на статтю надійшла 19.12.2025 року