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EFFECT OF CD ON PHYSIOLOGICAL AND BIOCHEMICAL PROCESSES OF PLANTS

This review focuses on the issue of cadmium contamination in agricultural lands, a significant concern in many developing countries, including Kazakhstan. Such contamination is primarily linked to the growth of heavy industries in mining regions, soil pollution from metallurgical plants, emissions from vehicles, and the widespread use of phosphorus fertilizers and pesticides containing cadmium. Heavy metals tend to accumulate around large industrial hubs, contaminating soil, water, and plants. These metals can then enter the food chain via forage plants, affecting animals and humans. Even small amounts of cadmium in the soil can reduce crop yields, inhibit plant growth, and disrupt physiological and biochemical processes. Therefore, it is essential to study how cadmium impacts plants and explore strategies to enhance plant resistance to this metal. This review examines the effects of heavy metals, particularly cadmium, on plant pollution, its accumulation in plant tissues, and its toxic impact on plant growth, photosynthesis, pigment content, respiration, oxidative stress, and mineral nutrition. Additionally, it discusses the mechanisms through which plants protect themselves against cadmium toxicity, such as the production of metal-binding proteins like metallothioneins and phytochelatins, as well as the activation of antioxidant systems in response to this stress.

Key words: cadmium, heavy metals, plants, toxic effects, protective mechanisms.

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Кадмийдің өсімдіктердің физиологиялық және биохимиялық процестеріне әсері

Көптеген дамушы елдерде, соның ішінде Қазақстанда өзекті болып табылатын кадмий иондарымен ауыл шаруашылығы алқаптарын ластау мәселесін шолуда қарастырады. Бұл кен орындары мен шахталар аймағындағы ауыр өнеркәсіптің дамуына, Металлургия зауыттарының айналасындағы кадмий иондарымен топырақтың ластануына, көліктердің ластануына, сондай-ақ құрамында кадмий бар фосфор тыңайтқыштары мен пестицидтердің кеңінен қолданылуына байланысты. Ірі өндірістік орталықтардың айналасында ауыр металдар топырақта, суда және өсімдіктерде жиналып, азық-түлік тізбегі арқылы жемшөп өсімдіктері арқылы жануарлар ағзасына, демек адам ағзасына беріледі. Тіпті кадмийдің аз мөлшері топырақта жиналып, дақылдардың өнімділігін төмендетеді, өсімдіктердің өсуі мен дамуын тежейді, физиологиялық және биохимиялық процестерді бұзады. Осыған байланысты кадмийдің өсімдіктерге уытты әсер ету механизмдерін және өсімдіктердің кадмий әсеріне төзімділігін арттыру стратегияларын зерттеу өзекті мәселе болып табылады. Бұл шолуда өсімдіктердің ауыр металдармен, атап айтқанда кадмиймен ластануы, өсімдік мүшелерінде кадмийдің жинақталу заңдылықтары, кадмийдің өсу және даму процестеріне уытты әсері, фотосинтез, фотосинтетикалық пигменттердің құрамы, тыныс алу, тотығу стрессінің дамуы, өсімдіктердің минералды қоректенуі қарастырылады, сондай-ақ өсімдіктерді кадмий иондарының өсімдіктерге уытты әсерінен қорғау механизмдері қарастырылады, металлотионеиндер, фитохелатиндер сияқты металды байланыстыратын ақуыздардың синтезі, сондай-ақ, кадмийдің уытты әсеріне жауап ретінде өсімдіктердің қорғаныс реакциясы ретінде антиоксиданттық жүйенің белсенділігін арттыру.

Түйін сөздер: кадмий, ауыр металдар, өсімдіктер, улы әсері, қорғаныс механизмдері.

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Влияние кадмия на физиологические и биохимические процессы растений

В обзоре обсуждается проблема загрязнения сельскохозяйственных угодий ионами кадмия, которая актуальна во многих развивающихся странах, включая Казахстан. Это загрязнение связано с ростом тяжелой промышленности в районах месторождений и шахт, загрязнением почвы вокруг металлургических заводов, выбросами автотранспорта, а также с использованием фосфорных удобрений и пестицидов, содержащих кадмий. В окрестностях крупных промышленных объектов тяжелые металлы накапливаются в почве, воде и растениях, что приводит к их попаданию в пищевую цепочку через кормовые растения, а затем в организм животных и человека. Даже небольшие количества кадмия, накапливаясь в почве, могут снижать урожайность сельскохозяйственных культур, замедлять рост и развитие растений, нарушая их физиологические и биохимические процессы. Поэтому исследование того, как кадмий воздействует на растения и разработка методов повышения их устойчивости к этому элементу являются важными задачами. В этом обзоре рассматриваются закономерности накопления кадмия в частях растений, его токсическое влияние на рост, развитие, фотосинтез, содержание фотосинтетических пигментов, дыхание, развитие окислительного стресса и минеральное питание растений. Также обсуждаются механизмы защиты растений от токсичного воздействия ионов кадмия, такие как синтез металлсвязывающих белков (металлотионеинов, фитохелатинов) и повышение активности антиоксидантной системы, что представляет собой защитную реакцию растений на кадмиевое отравление.

Ключевые слова: кадмий, тяжелые металлы, растения, токсическое действие, защитные механизмы

Introduction

Trace amounts of cadmium (Cd) that accumulate in the soil can lower crop yields, impede plant growth, and disrupt physiological and biochemical processes. Thus, investigating how Cd affects plants and developing methods to enhance plant resistance to Cd is a pressing concern. Soil contamination with cadmium is a significant issue in many developing countries, like Pakistan, India, Bangladesh and the CIS countries, including Kazakhstan. This problem arises from the pollution of extensive areas surrounding metallurgical plants and the widespread use of phosphorus fertilizers and pesticides that contain Cd [1-5].

Pollution of soil and water with heavy metals is a major environmental challenge. Despite heavy metals being naturally present in soil as trace elements, their spread is exacerbated by activities such as agriculture, waste management, metallurgy, and manufacturing. Among these pollutants, cadmium is considered one of the most harmful to plants. Its high solubility in water allows it to be rapidly absorbed by plants, which is the primary way it enters the food chain, posing severe risks to human health. Even at low levels, the uptake of cadmium by plant roots and its transport to other parts of the plant can

adversely affect mineral nutrition and homeostasis during the growth and development of the roots [6-10].

The high mobility of cadmium (Cd) within the soil-plant system can interfere with biochemical processes, leading to damage to the plasma membrane and significant disruptions in physiological functions. These disruptions can impact key processes such as photosynthesis, respiration, water regulation, and the uptake and distribution of macro- and micronutrients. Consequently, this can result in reduced plant growth or even cell death [11-16].

Impact of Cadmium (Cd) on Plant Biochemical and Physiological Functions

Cadmium has a negative effect on plants, disrupting their normal growth and development. An increase in the Cd content in the soil leads to a slowdown in root growth, a reduction in their length, a decrease in the number of lateral roots and the death of root hairs, which, in turn, reduces the total biomass of plants. Similar effects are observed both in cultivated plants and in wild species [17].

It was established that Cd negatively affects the processes of cell division, elongation, decreasing the growth of roots and plants in general. Experiments show that in the presence of Cd in growth medium cell division was inhibited, the number of

cells involved in mitosis decreased, and the mitotic cycle elongated. The reason of this effect would be the strong affinity of Cd for sulfhydryl groups in spindle proteins and enzymes involved in mitotic regulation. Cadmium leads to a violation of the water balance of cells and the permeability of their membranes. As a result of all the negative processes of cadmium action, the growth and development of plants decreases [17-20].

The primary indicators of cadmium (Cd) toxicity in plants include leaf curling, chlorosis, disrupted water absorption, and stomatal closure [20, 21]. Chlorosis, a common symptom of Cd toxicity, affects the photosynthetic apparatus by reducing the content of green pigments in the leaves. Studies have shown that cadmium exposure leads to a decrease in chlorophyll levels (both *a* and *b*) in various wild and cultivated cereal species [22-25]. In addition, the negative effect of Cd on photosynthesis is also observed in a decrease in the amount. Additionally, Cd negatively impacts photosynthesis by reducing carotenoid levels in plants that are not tolerant to cadmium. However, some research suggests that carotenoids in cereal leaves are less affected by cadmium stress compared to green pigments [18, 26-29].

It is believed that cadmium (Cd) inhibits Photosystem II (PS II) by altering the composition of thylakoid membrane lipids. Additionally, evidence suggests that Cd damages the light-harvesting antenna complexes of both Photosystem I (PSI) and Photosystem II (PSII). In response to Cd stress, green bristlegrass and barley exhibit a reduced rate of electron transport, a decline in the photochemical quenching coefficient of chlorophyll, and an increase in non-photochemical quenching. Furthermore, cadmium negatively impacts the dark reactions of photosynthesis by inhibiting the activity and synthesis of Calvin cycle enzymes, including ribulose-1,5-bisphosphate carboxylase/oxygenase and triose phosphate dehydrogenase [17, 21].

At low cadmium (Cd) concentrations, respiration rates increase due to the activation of respiratory enzymes by Cd. However, higher Cd levels inhibit enzyme activity, reducing respiration intensity. This includes decreased activity of key enzymes like hexokinase, malate dehydrogenase, and glucose-6-phosphate dehydrogenase. Enzyme inhibition is linked to structural changes caused by Cd binding to sulfhydryl (SH) groups and disrupted protein synthesis. Additionally, reduced respiratory activity may result from membrane depolarization, H⁺-ATPase inhibition, and lower ATP levels [17].

Cadmium in the soil can affect the uptake of essential elements by both the aboveground and un-

derground parts of plants. High Cd concentrations can alter the levels of various macro- and micro-elements in plants, which can negatively impact plant health [7]. Specifically, Cd has been found to adversely affect nitrogen metabolism, and increasing Cd levels are associated with reduced nitrogen and phosphorus content in plants [15, 30, 31].

Several factors contribute to the negative impact of cadmium (Cd) on nitrogen metabolism:

1) Cd ions compete with ammonium ions (NH₄⁺) for transport through membrane ion channels.

2) Cd reduces the activity of key enzymes such as nitrite reductase, glutamate synthase, and aminotransferase.

Cadmium in the soil can interfere with the uptake of essential elements by both aboveground and belowground plant parts. As Cd levels increase, the concentrations of various macro- and micro-elements in plants may be altered, negatively affecting plant health. Studies have shown that low Cd content in cereals can increase some mineral elements, like phosphorus, potassium, nitrogen calcium, sulfur, magnesium. But higher Cd rate negatively affects on content of mineral elements [7,8, 15, 30].

Cadmium also disrupts sulfur metabolism by lowering enzyme activity, such as ATP-sulfurylase in corn and oats, while increasing O-acetylserine lyase activity, which raises cysteine levels, a precursor to glutathione and phytochelatin [31].

The studies show a decrease in magnesium in the shoots and roots of oats and corn due to inhibited absorption. But in some cases in wheat and barley leaves, magnesium levels may increase at lower Cd concentrations, possibly due to redistribution to photosynthetic tissues

Iron deficiency under cadmium stress causes chlorosis of leaves, and it is also affecting roots size, disrupts membranes of root cells, and decrease of activity of Fe reductase, which responsible for reduction of Fe³⁺ to Fe²⁺. Cd also competes with zinc, reducing its levels and causing potential zinc deficiency, as Cd cannot replace Zn's biochemical functions [17, 18].

Researchers have utilized transcriptomic, proteomic, and metabolomic platforms to investigate Cd's effects. For instance, a comparative study of *Brassica chinensis* varieties with differing Cd uptake showed that the timing of specific transcriptional responses varies by variety. In cotton, Cd stress triggers an increase in enzymes that neutralize reactive oxygen species (ROS). A combined transcriptomic, proteomic, and metabolomic analysis of radish roots exposed to Cd highlighted Cd's influence on amino acid metabolism and oxidative phosphorylation.

Phosphorylation is the most extensively studied due to its stability, abundance, and crucial role in cellular function. It primarily affects the hydroxyl group in threonine, serine, and tyrosine. A substantial number of signaling pathways in rice's response to Cd are regulated by phosphorylation/dephosphorylation events, though current understanding is limited by the typical focus on single phosphoproteins [32].

An excess of reactive oxygen substances is harmful as it reacts with lipids, proteins, and nucleic acids, causing membrane damage, enzyme inactivation, and DNA mutations that may jeopardize cell viability [33-35].

Mechanisms of Plant Defense Against Heavy Metals

Plants have complex defense mechanisms to reduce the toxicity of heavy metals. The first line of defense includes physical barriers like thick cuticles, trichomes, cell walls, and mycorrhizal symbiosis, which protect against metal stress. Trichomes can store metals for detoxification or release secondary metabolites to counteract toxicity. If metal ions penetrate plant tissues, plants activate biochemical responses to mitigate damage. This involves the production of metal-binding compounds such as glutathione, phytochelatins, metallothioneins, and other secondary metabolites, including flavonoids and phenolic compounds [36, 37]. If these mechanisms are insufficient, the cellular redox balance is altered, resulting in high rate of an oxidative stress. To combat reactive oxygen species (ROS), plants activate antioxidant systems, which include enzymatic antioxidants – superoxide dismutase and catalase, as well as non-enzymatic scavengers of ROS like glutathione and carotenoids. The activity of antioxidant enzymes is influenced by the stage of plant development and may even decrease after short-term exposure to metals. Superoxide dismutase (SOD) plays a crucial role in combating oxidative stress. Other endogenous compounds synthesized within the cell, such as organic acids, thiols, polyphenols, and polyamines, serve as effective mechanisms for neutralizing most metal ions. Heavy metals binds to endogenous compounds and accumulates in vacuoles. It's an effective mechanisms for neutralizing of heavy metals in tolerant plants species [33, 34, 37-39].

Certain detoxification molecules are multifunctional, displaying chelation, radical-scavenging, or antioxidant abilities. The activation of these mechanisms differs based on plant species, metal type, and growth stage. Higher plants have two types of cysteine-rich metal-binding peptides: metallothio-

neins (MT) and phytochelatins. Metallothioneins, first identified in 1957, are low-molecular-weight proteins with high metal-binding capacity, making them essential for metal detoxification. Their concentration increases with heavy metal exposure and decreases when metal levels decline. Metallothioneins are categorized into 3 groups according to their chemical structure [40]:

- Class 1 MT include 20 cysteine residues, similar to mammalian kidneys.

- Class 2 MT also possess cysteine clusters, but these do not have a straightforward comparison with Class 1 MT.

- Class 3 MT include γ -glutamylcysteinyl residues, which are present in the polypeptides of algae, fungi, and plants.

MT genes have been identified in several higher plants, including *Arabidopsis*, where, in addition to Class 1 and Class 2 MT genes, types MT3 and MT4 have also been discovered. Other plant species are believed to contain a large family of MT genes across multiple classes, with expression studies showing tissue-specific patterns. While there is no comprehensive information about the metals that can bind to MT in plants, copper (Cu), zinc (Zn), and cadmium (Cd) have been the most extensively studied. Phytochelatins (PC) are capable of binding to various metals, including Cd, Cu, Zn, and arsenic (As), through sulfhydryl and carboxyl groups. Their synthesis is primarily regulated by metals like Cd or metalloids like As. Glutathione (gamma-glutamylcysteinyl-glycine) plays a key role in this process, with the enzyme PC synthase catalyzing the synthesis. Genes encoding this enzyme, such as CAD1 and PCS1, have been isolated from plants, yeast, and some animals. Studies inhibiting PC synthesis through glutathione have highlighted its crucial role in metal detoxification in yeast, fungi, green algae, some aquatic plants, as well as in suspended cells and intact tissues of higher plants [40].

Differing from enzymatically synthesized phytochelatins, metallothioneins (MT) are formed through mRNA translation. Phytochelatins mainly detoxify Cd, MTs can bind a broader range of metals, like as zinc, copper, arsenic, cadmium. MT properties and functions differ across organisms.

There are multiple MT groups in plants, categorized into 4 subgroups based on cysteine residue location, each showing specific expression patterns in organs and development stages. For instance, MT group 1 is discovered in roots, group 2 – in shoots, group 3- in leaves and fruit maturation, group 4 – in seeds. Each subgroup (MT1–MT4) is further divided into isoforms. All MT groups and isoforms can

bind heavy metals and act as chelators or storage sites. But their metal-binding capacity and tissue localization vary across plant species [40].

In suspension cultures of *Silene cucubalus* cells, an enzyme class was discovered and characterized that produces phytochelatin (PC), peptides composed of repeating units of γ -glutamylcysteine with a glycine carboxyl end. These peptides range from 5 to 17 amino acids in length and are involved in binding heavy metals [40].

Phytochelatin (PCs) can bind to various metals, including Cd, Cu, Zn, and As, through sulfhydryl and carboxyl groups. However, their synthesis is primarily regulated by the presence of metallic Cd or the metalloid As. Glutathione (gamma-glutamyl-cysteinyl-glycine) plays a key role in this process, with its synthesis being catalyzed by the enzyme PC synthase. The genes encoding this enzyme, such as CAD1 and PCS1, have been isolated from plants, yeast, and some animals. Studies inhibiting PC synthesis with glutathione have highlighted its essential role in metal detoxification in yeast, fungi, green algae, certain aquatic plants, and both suspended cells and intact tissues of higher plants. Overexpressing PC synthase genes has been shown to increase Cd tolerance in yeast and bacteria, though this effect is not observed in all higher plants, particularly in metal-accumulating species. [40].

Phytochelatin (PCs) contribute to the detoxification of metal ions through several mechanisms:

- 1) Activation of phytochelatin synthase by a metal ion;
- 2) Formation of Class 3 metallothioneins (MT) with heavy metals;
- 3) Transport of Class 3 MT-metal complexes into the vacuole.

It is important to note that type 3 MTs with a low molecular weight, aid in the transport of Cd into the vacuole. There it stores as a high-molecular-weight complex. Additionally, any disruption in these detoxification mechanisms can decrease the plant's resistance to heavy metals. For example, mutations in the gene encoding PC-synthase lead to increased sensitivity to Cd. Comparable mutants have been discovered in *Vigna angularis*, *Arabidopsis thaliana*, *Schizosaccharomyces pombe*. With the development of the understanding of MT in plants, it becomes obvious that due to the diverse molecular traits and structural modifications, they probably execute a greater variety of tasks relative to different organisms. In plants, MT plays a key role in neutralizing the toxicity of heavy metals by binding them in cells, regulating intracellular metal homeostasis and the transport of these elements.

For plants MT plays a key role in mitigating heavy metal poisoning by binding these metals within cells, controlling their intracellular balance, and regulating their transport [40].

In addition to detoxification, MT is involved in various cellular processes such as the removal of ROS, preservation of redox homeostasis, restoration of membrane, cell growth support and correction of impaired DNA. MT production and expression are also influenced by various internal and external factors, like as drought, osmotic stress, nutrient deficiencies, extreme temperatures, viral diseases, hormonal emissions, damages, tissue senescence [40].

Conclusion

Impact of even relatively low concentrations of cadmium (Cd) in the roots is sufficient to impair enzyme activity, suppress photosynthesis, block stomatal movement, and disrupt transpiration, resulting in leaf curling, growth inhibition, and chlorosis. As cadmium is a non-essential element for plants, it is readily absorbed by the roots through transporters that typically import essential micro- and macronutrients. This interference reduces the plant's ability to take up, transport, and utilize these vital trace elements.

Cd ions also disrupt the plant's water balance, inhibit mitochondrial oxidative phosphorylation, they disrupt the normal metabolism of H^+/K^+ , inhibit the activity of the P-type ATPase and raise the level of ROS indirectly. In reaction, the plants triggered various defense mechanisms, such as metallothioneins and phytochelatin. In response, plants have developed several defense mechanisms, including metallothioneins and phytochelatin.

The known mechanisms of plant resistance to heavy metals have important practical applications in various fields. It can be used for phytoremediation technology. The use of plants to clean polluted lands and reservoirs of heavy metals. Some plants are able to accumulate metals from the soil, which makes it possible to clean the environment. This can be used to restore polluted areas such as mining areas or industrial zones.

The study of mechanisms of resistance to heavy metals helps in the creation of new crop varieties that can successfully grow in polluted soils. This is especially important for ensuring food security in regions where soil contamination with heavy metals is a problem.

In environmental monitoring – plants that can accumulate heavy metals are used as bioindicators

to monitor the state of the environment. They help to identify and assess levels of heavy metal pollution in ecosystems.

In agriculture and agronomy – applying knowledge about metal resistance mechanisms to increase yields in regions with high levels of metals in the soil, which reduces the negative impact of pollution on crops.

These mechanisms can significantly contribute to improving the quality of the environment and ag-

ricultural production, as well as ensuring ecosystem resilience to pollution.

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