International Journal of Biology and Chemistry 13, № 1, 109 (2020)

IRSTI 633.16:581.1 https://doi.org/10.26577/ijbch.2020.v13.i1.11

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Response of plants to cadmium stress

Abstract. In this article we discuss cadmium pollution in the environment and the various ways plants take up cadmium and respond to its accumulation. The increased development of metallurgical and mining industries is primarily responsible for the increases in cadmium pollution in the environment. Another significant source of cadmium contamination of agricultural plants is the widespread use of phosphorus fertilizers, which contain cadmium. Cadmium reduces the growth and development of plants. Cadmium in the soil also competes with the basic essential mineral elements thereby reducing their uptake by plants. This article reviews the published data on the cellular and molecular mechanisms of cadmium uptake by plants, its metabolic transformations, effects on nutrient status of plants, modulation of cadmium response by polyamines and amino acids, and the growth of plants. Strategies to reduce cadmium uptake and accumulation are also discussed.

Key words: Cadmium, plants, crops, growth, toxic effect.

Introduction

The expansion of industry and agriculture to cope with increasing world population leads to an increase in the number of heavy metals in the environment. Often this increase is several orders of magnitude greater than background concentrations. The primary sources of anthropogenic contributions of heavy metals are industrial emissions associated with mining, and metallurgical and chemical industries. There is a constantly growing volume of industrial waste from new technological landscapes which have become a source of contaminated dust that extends long distances from the source, polluting the environment and posing a threat to public health and biodiversity of the region.

Contamination of soil, plants and water with heavy metals in the vicinity of large industrial centers has become one of the most pressing environmental problems. Cadmium (Cd) in unpolluted soils is present in trace amounts (0.05- 0.15 mg/kg) [1]. Nevertheless, human industrial activities and agricultural practices increase the level of Cd in the soil. The operations of metallurgical enterprises and the use of Cd containing phosphorus fertilizers and pesticides, contributes to high Cd accumulation in soil [2]. The degree of contamination of soil Cd fertilized with phosphorus fertilizers can reach 300 mg/kg dry weight [3].

Cadmium enters human body through the food chain, and it remains in the body for many years. Cadmium-contaminated food can induce chronic toxicity. Cadmium is a calcium (Ca) antagonist. Increased accumulation of Cd in the human body is responsible for diseases like Itai-Itai, which translates into reducing the content of Ca in the bones, which causes their softening [4]. The World Health Organization (WHO) has set a maximum limit of Cd in human diet to about 60-70 mg per day, and the Codex Alimentarius Commission of the US (usda.gov/codex) and the Food and Agriculture Organization (FAO) (http://www.fao.org/fao-who-codexalimen tarius /en/) has set a limit of 0.1 mg Kg^{-1} for cereals and oilseeds [5]. Because of its high solubility in the soil (~35%), Cd is more readily available than other heavy metals such as Zn, Cu, Pb, which have a higher absorption coefficients [6].

Toxic effect of cadmium on plants

The mechanism of interaction of heavy metals, including Cd, in plants is exceedingly complicated, and can be schematically represented in the following way: heavy metals → cell membranes → cell → organ → system of organs → organism → return to the ecosystem after decomposition of plants residues. Heavy metals cause inhibition of growth and a decrease in crop yields due to disruption of physiological and biochemical processes in plant cells and in the plant body as a whole. The fibrous root system of many crops like rice, which increases the absorbing surface of plants for Cd uptake [7], chelating agents, such as organic acids of rhizosphere microorganisms, and phytosiderophores, all contribute to the absorption of Cd by cereal plants [8]. It has been suggested that because of the low diffusion coefficients and generally lower concentrations of Cd in soil solution, its uptake by plant roots is mainly controlled by transpiration. Both Lux et al. [9] and Yamaguchi et al. [10] reported that abscisic acid promotes the closure of stomata leading to a decrease in transpiration, ultimately lowering the rate of transport of Cd to the aerial organs.

Cadmium-induced chromosomal aberrations including C-mitosis, chromosomal fragmentation, anaphase bridges, and chromosome adherence was observed in *Allium cepa*, which indicate a genotoxic effect [11]. Cadmium reduced the mitotic index in root cells, which correlated with the degree of decrease in root growth. C-mitosis, was the main type of chromosomal aberration, with a high degree of compaction that occurred at the root tips of barley from exposure to low concentrations (1 and 10 μM) of Cd [12].

Reduced biomass was observed in various rice varieties grown in a medium containing varying amounts of Cd [13]. In our studies, under the action of cadmium, the content of photosynthetic pigments in the studied wheat varieties was significantly reduced [14]. The content of chlorophyll *a* at a relatively low cadmium concentration (0.15 mM) decreased to the greatest extent in the variety Kazakhstanskaya rannaya (by 34%) (Figure 1).

In the varieties Kazakhstanskaya -3 and Shagala, this indicator decreased by 19 and 18%, respectively. With a doubling of the cadmium concentration, the content of chlorophyll a decreased to the greatest degree in the varieties Shagala and Kazakhstanskaya rannaya – by 34 and 43%, accordingly. To the least extent, this indicator decreased in the variety Kazakhstanskaya-3 – by 21% relative to the control. According to the content of chlorophyll a, the varieties can be arranged as follows: Kazakhstanskaya -3 (79%) > Shagala (66%) > Kazakhstanskaya rannaya (57%).The content of chlorophyll *b* in the presence of cadmium decreased almost to the same extent as the content of chlorophyll a in all the studied wheat varieties. At 0.15 mM $CdSO_4$, the chlorophyll *b* content decreased by 35, 18, and 17% in the Kazakhstanskaya rannaya, Kazakhstanskaya-3, and Shagala varieties (Figure 2). With an increase in the concentration of cadmium (0.3 mM $CdSO_4$), the content of chlorophyll *b* in the Kazakhstanskaya rannaya variety decreased the most (by 44%). In the least degree, this indicator decreased in the Kazakhstanskaya-3 variety – by 23%, in Shagala variety – by 32%.

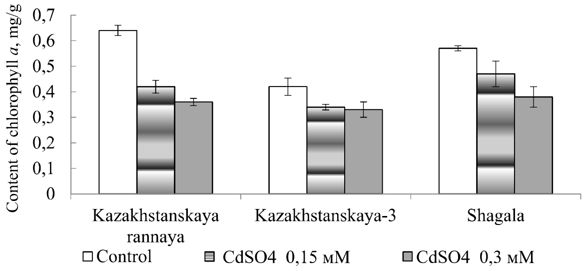

Figure 1 – Effect of cadmium on chlorophyll *a* content in leaves of wheat varieties

The amount of chlorophylls (*a*+*b*) in the presence of cadmium in soils also decreased (Figure 3). For this indicator, with a high concentration of cadmium, the varieties were arranged as follows: Kazakhstanskaya -3 (79%) > Shagala (68%) > Kazakhstanskaya rannaya (52%).

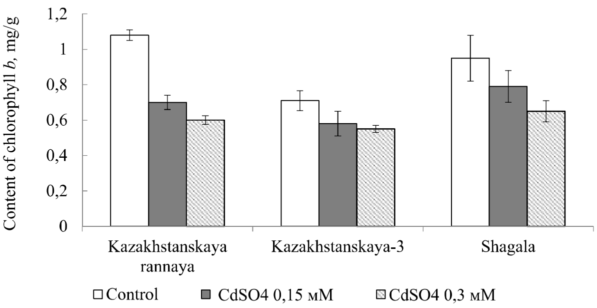

Figure 2 – Effect of cadmium on chlorophyll *b* content in leaves of wheat varieties

The content of carotenoids at a relatively low concentration of cadmium (0.15 mM) decreased the most in the Shagala variety – by 61%, and the least in the Kazakhstanskaya-3 variety (by 30%) (Figure 4). In the Kazakhstanskaya rannaya variety, the content of carotenoids at a low concentration of cadmium decreased by 50%. According to the content of carotenoids at a high concentration of cadmium (0.3 mM), wheat varieties can be arranged as follows: Kazakhstanskaya -3 (63%) > Kazakhstanskaya rannaya (47%) > Shagala (19%).

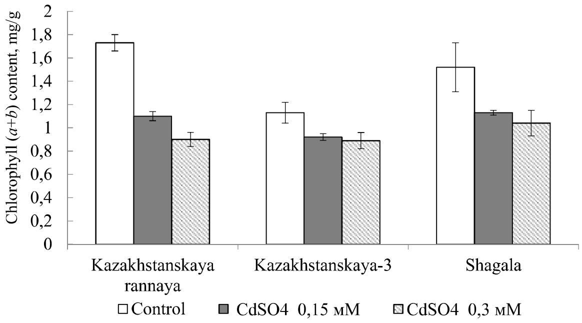

Figure 3 – Effect of cadmium on chlorophylls (a+b) content in leaves of wheat varieties

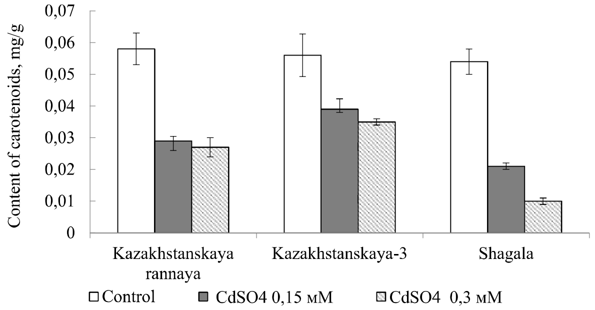

Figure 4 – Effect of cadmium on carotenoids content in leaves of wheat varieties

According to other researchers, cadmium causes disorganization of the leaf structure, reduces the intercellular space, and leads to structural changes in thylakoids in chloroplasts [15].

Under the effect of cadmium, changes in the ultrastructure of chloroplasts were observed as a result of oxidative stress [16]. Cadmium causes disorganization of the thylacoid and stroma systems and a decrease in starch grains [17]. Structural changes in chloroplasts lead to a decrease in photosynthetic activity [18].

Plants respond to environmental stresses by controlling the level and activity of various hormones. Cadmium ions have been found to reduce the content of free forms of auxin in poplar plants and increase the activity of peroxidase, which increases lignification of cell walls under stress [19].

In addition to affecting vital processes of cell division and signaling pathways, Cd ions known to cause oxidative stress in plants [20]. Cell membranes are the primary target of the action of heavy metals. Under the influence of heavy metals, including Cd, membrane permeability changes, leading to increased rates of membrane lipid peroxidation and K^+ leakage, and a decrease in chlorophyll content. The physiological and biochemical processes that control photosynthesis, water consumption efficiency, mineral nutrition, and sugar metabolism are disrupted by Cd, thus the yield of plant biomass decreases [20]. Free radicals can directly destroy proteins, amino acids and nucleic acids, and induce lipid peroxidation [21].

Cadmium, along with other heavy metals, increases the products of reactions with thiobarbituric acid (TBA), which are an index of lipid peroxidation and oxidative stress. Lipid peroxidation of membranes has a negative effect on their function and integrity and can produce irreversible damage in the function of cells. In our studies, the level of lipid peroxidation in wheat varieties increased with Cd in the growth medium [14]. In resistant varieties of wheat, lipid peroxidation increased to a lesser degree than that of non-tolerant wheat varieties.

Cadmium is not a redox metal and does not participate in Fenton-type reactions, but it can also produce oxidative stress indirectly, causing damage in chloroplasts, the formatin of reactive oxidized substances such as superoxide radicals ($O^{2-\cdot}$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($^\cdot OH$) [21].

According to the degree of increase in the lipid peroxidation under the action of 0.3 mM $CdSO_4$, the varieties can be arranged as follows: Shagala (159) > Kazakhstanskaya-3 (139) > Kazakhstanskaya rannaya (107) (Figure 5).

In relatively resistant varieties to these stressors, the content of malonic dialdehyde increased to a lesser extent than in Shagala variety.

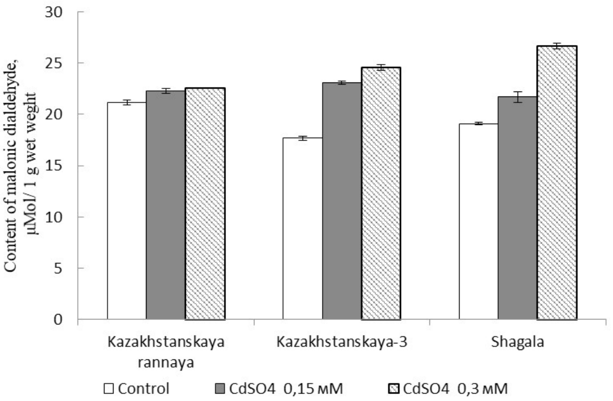

Figure 5 – Effect of cadmium on lipid peroxidation level in several wheat varieties (*Triticum aestivum* L.)

With the increase in the overall ionic strength of the soil solution, the adsorption of Cd by soil particles decreases. Zinc (Zn) in phosphate fertilizers competes with Cd for adsorption to soil particles, which increases the concentration of Cd in the soil solution [22]. Consequently, the amount of accumulated Cd depends on various factors, such as its content in the soil, its bioavailability, genetic characteristics of the plant, the nature of the soil and its total ionic strength, and finally, the rhizosphere microbiome [23].

Cadmium especially competes with zinc, copper and iron. Silicon (Si) has been reported to decrease Cd accumulation within shoots. This effect is attributed to shoot Si-mediated down-regulation of transporter genes involved in Cd uptake and translocation [24].

The mechanisms of Cd absorption by plant roots are the key to its accumulation. One can ask the question "if Cd is not an essential metal, why would cells have Cd transporters?" Indeed, plants do not have any specific Cd-specific transporters. However, transporters of Zn^{2+} like OsZIP1, and Fe^{2+} like OsIRT1 and OsIRT2 have been shown to transport Cd ions in the roots [25].

In countries where rice is the staple food, there is generally a deficiency of micronutrients in the soil [26]. The presence of Cd ions in the soil aggravates micronutrient deficiencies in rice grains.

In our previous study, the effects of Cd on the content of minerals were determined in three varieties of rice namely: Madina, Bakanaskyi and Chapsari [27]. Plants were grown in pots containing 2 mM kg^{-1} of $CdSO_4$. Although Cd was not found in grains of these rice varieties under investigation it caused a decrease in the content of mineral nutrients like Mg, Cu, Mn, Zn in variety-specific manner (Table 1).

It has been reported that the sensitivity to Cd increases in transgenic Arabidopsis expressing the genes for AtNramp1, AtNramp3 and AtNramp4 transporters from the Nramp (natural resistance-associated macrophage protein) family, which transport Zn, Mn, Fe, Co and Ni [28]. The OsLCT1 (Low-affinity Cation Transporter1) transporter of rice participates in the transport of Cd to the phloem, and it is a homolog of the wheat gene LCT1, which presumably regulates Cd release in the plasma membrane. Expression of the OsLCT1 gene was higher in leaf blades and nodes during the reproductive period, especially at node 1; i.e., the highest node. The expression of OsLCT1 was seen in diffuse vascular bundles in the panicles [29].

Table 1 – Content of mineral elements in rice grain [27].

Rice varieties	$CdSO_4$, mMol/kg	Mg, mg/kg	Mn, mg/kg	Fe, mg/kg	Cu, mg/kg	Zn, mg/kg	Cd mg/kg
Madina	0	1363.0 ±32.3	174.2±6.2	19.3±0.63	5.8±0.19	24.9±1.1	0.0
	2	1267.0±44.6	125.7±5.5	17.1±0.58	5.3±0.21	23.2±0.9	0.0
Bakanas	0	1480.3±51.7	161.0±8.7	17.2±0.7	7.2±0.3	26.4±1.3	0.0
	2	1456.1±72.3	120.3±6.1	12.4±0.49	6.3±0.26	22.9±1.4	0.0
Barakat	0	1311.0±39.8	133.1±4.7	15.7±0.58	5.0±0.22	19.4±0.81	0.0
	2	1105.4±51.3	84.6±3.4	7.46±0.7	4.4±0.15	16.4±0.52	0.0
Chapsari	0	1403.7±80.5	170.0±7.3	12.4±0.62	6.0±0.19	21.3±0.8	0.0
	2	1212.0±44.9	121.6±5.1	7.1±0.26	5.4±0.23	18.6±1.0	0.0
	P	ns	$P < 0.01$	$P < 0.05$	$P < 0.01$	$P < 0.01$	

Clemens [30] has also suggested that there are other genes whose products participate in the subcellular transport of Cd from the cytoplasm to the apoplast, and in its compartmentalization in the vacuole as a mechanism of tolerance by the plant.

Thus the antagonistic effects of these ions are an important factor to consider when estimating net accumulation of Cd ions in a living organism [31]. Thus, biofortification, either through plant breeding and/or transgenic approaches to the development of new varieties that accumulate high concentrations of certain nutrients [26], is one possible solution to the problem of harmful Cd effects in humans. Efforts to biofortify seeds with Fe and Zn in rice were focused on increasing the content of the ferritin protein [32], the overexpression of Zn-transporter *ZIP1* gene [33], the expression of the phytosiderophore synthesis genes (*NAS*) [34], and the increase of Fe-reductase in the roots [35]. Thus, increased accumulation of Fe^{+2} and Ca^{+2} may be one of the effective ways to decrease Cd uptake by crop plants.

Mechanisms of plant resistance to cadmium

Plants have several mechanisms in place for providing resistance to heavy metals, including Cd. These mechanisms can be divided into two groups: 1) restriction of the entry of metals into most of the plant through its accumulation mainly in the root system and isolation in the vacuole; 2) changes in the metabolism of cells, aimed at reducing the toxic effect of metals. Biochemically bonded metal ions can be deposited in organs such as cell wall and vacuoles, which limits their transport as well as their deleterious effects on the plant [36]. Dai et al. [37] suggested that root cell walls were the first and the main barrier against Cd, with intracellular Cd being mainly stored in the vacuoles.

Seregin and Ivanov [36] have proposed that the ratio of the concentration of a toxic ion present in the plant in a tightly bound vs. mobile state determines not only the degree of influence of this ion on metabolism, but also determines the cellular structures and the processes associated with its functions. The reason for greater resistance or sensitivity of certain plants to Cd (and Pb) may be related to their ability to safely compartmentalize these metals in cellular organelles. The content of metals in plant cells does not necessarily reflect their content in their cytoplasm because of their ability to effectively exclude metals from the cytoplasm by binding with chelating agents and insulating them in vacuoles and cell walls.

Another effective mechanism for detoxification of most toxic metal ions in plants is their binding by organic acids and thiols in the cytoplasm, followed by the sequestration of these complexes in vacuoles. Glutathione (GT) plays an important role in the antioxidant defense of plants. Glutathione is also a precursor to phytohelatins (PCs) that are capable of binding heavy metals [38]. The determination of SH-groups in plant cells serves as one of the integral indicators of plant responses to the action of heavy metals [39, 40].

It is known that a common response of living organisms to the accumulation of Cd (and other heavy metals) is the induction/promotion of the biosynthesis of low molecular weight, cysteine-rich proteins called metallothioneins (MTs) or peptides called phytochelatins (PCs). Chemical bonding of Cd^{+2} with organic ligands is much stronger than that of other metal ions. At high concentrations, Cd-PC complexes are transported and localized in vacuoles; at low concentrations, 86-100% of Cd was found in the cytoplasm in *Datura inoxia* [41]. At high concentrations, Cd also binds with organic acids, and at low concentrations, with GT in the cytosol.

Phytochelatins, cadastins, glutamyl-peptides, found in some algae, higher plants and fungi containing γ-glutamylcysteinyl residues, differ from the mts by the fact that they are synthesized enzymatically and not by ribosomes. Phytochelatins are compounds with the general formula $[(\gamma\text{-Glu-Cis})_n\text{-Gly}$, where n is at most 11, but more often varies from 2 to 5. The ratio of pcs and their derivatives depends on the plant species, as well as on the ratios of metals in the soil or nutrient solution [42]. For example, in *rice,* resistance to Cd is provided by hydroxymethyl-PC $[(\gamma\text{-Glu-Cis})_n\text{-Ser}]$ and cadastines, but with increasing metal concentration the ratio shifts towards the latter [43].

Modulation of cadmium response by polyamines and amino acids

Several studies have reported the role of common polyamines [PAs – putrescine (Put), spermidine (Spd) and spermine (Spm)] in the modulation of plant responses to Cd and/or other heavy metals. Nahar *et al.* [44] hypothesized that exogenous additions of 0.2 mM Put and/or nitric oxide could improve physiological processes to enhance tolerance to Cd-toxicity for up to 2.0 mM in mung bean plants via coordinated effects on antioxidant and glyoxalase systems. Pretreatment with Put caused an increase in endogenous PA content and a decrease in protection from Cd stress, which was accompanied by a decrease in PCs and GS levels and PCS enzyme in rice plants [45]. These authors suggested that Put pre-treatment may inhibit the expression of the PCS gene or may decrease PCS activity, probably due to the depletion of GS by increased PA metabolism. It is conceivable that the added Cd may have bound to PAs used for pre-treatment, thus reducing the amount of free Cd to below the level required for the induction of PCS activity. Thangavel et al. (2007) reported a trend in the increase of Put in response to an increased concentration of Cd (12.5 µM-200 µM) in red spruce suspension cultures but this change was not statistically significant. Exogenous PAs were not supplied to these cultures and concentrations of Cd may not have been high enough to trigger a response in the PA pathway. Another study reported a decrease in Put and Spd in discs of sunflower leaves when treated with 0.5 mM Cd [46]. However, these authors reported that in 0.5 mM Cd-treated wheat leaves there was an increase in Put that was accompanied by increases in the activities of orthinithine decarboxylase and arginine decarboxylase, the two enzymes responsible for Put biosynthesis in plants. These authors concluded that differences in the effects of Cd on PAs in these two studies may be attributed to environmental conditions and the species-specificity of responses.

Although not yet tested with Cd, the exogenous application of 1 mM Spd was shown to improve the growth of Cr-stressed seedlings of *Raphanus sativus* L., perhaps through effects on the endogenous levels of PAs, amino acids, antioxidants such as GT, ascorbic acid, proline, glycine betaine, and total phenols, along with the activities of antioxidant enzymes [47]. These observations were accompanied by increases in PCs, photosynthetic pigments, H_2O_2, and total soluble sugars in seedlings treated with Spd and Cr – all indicating better adaptation to Cr-stress. Groppa *et al.* [46] showed that the exogenous addition of Spm resulted in a partial reversal of the effects of Cd on certain antioxidant enzymes, and an increase in the levels of endogenous PAs. Differences observed in the effects of treatment with Put or higher PAs (SPD and SPM) could be explained by the possibility that the exogenous application of higher PAs may not induce the synthesis of dcSAM from SAM, while after Put treatment, its conversion to higher PAs (Spd and Spm) would involve SAM utilization [48]. Since amino acids, PAs and PCs share common metabolites in the nitrogen pathway, cellular amino acids concentrations also change under Cd toxicity [39, 48]. Zhu *et al.* [49] also hypothesized that higher adaption of *Noccaea praecox* than *N. caerulescens* to Cd-induced stress was partially due to differences in the cellular accumulation of glycine, sarcosine and ornithine; both glycine and ornithine are precursor metabolites for the synthesis of PCs.

Higher Cd tolerance and Cd accumulation was associated with greater accumulation of free amino acids Gln and Asn, in *Crassocephalum crepidioides* (Cd hyperaccumulator) as compared to *Ageratum conyzoides* L.. Thangavel *et al.* [39] reported an increase in glutamine and arginine along with a concurrent decrease in cystine + cysteine in Cd-treated red spruce cell cultures.

The effect of cadmium on plants can be presented as in the following figure (Figure 6):

Conclusion

The degree of negative impact of Cd on plant health is the result of the interaction of many factors such as the degree of Cd pollution from the environment, changes in physiological and biochemical processes in response to Cd exposure, antagonistic relationships among other anions, the functioning of transport systems and metal transporters, and the activation of protective reactions of the plant. Because of the ubiquitous presence of Cd ions in the soil as a result of active human industrial activity, there is a danger of contamination by this metal in agricultural crops. It is worth emphasizing that even though low concentrations of Cd in the soil do not lead to the accumulation of Cd in the fruits or grain of most crops, they do negatively impact the growth and development of most plants. The strengthening of oxidative stress, decrease of antioxydative enzyme activities, changing in membrane permeability and other negative alterations lead to inhibition of growth and biomass accumulation and mechanisms of homeostasis provide the plants tolerance to cadmium. Studies are needed to identify Cd-resistant crops, taking into account endogenous and exogenous factors that determine the degree of Cd toxicity for each plant species.

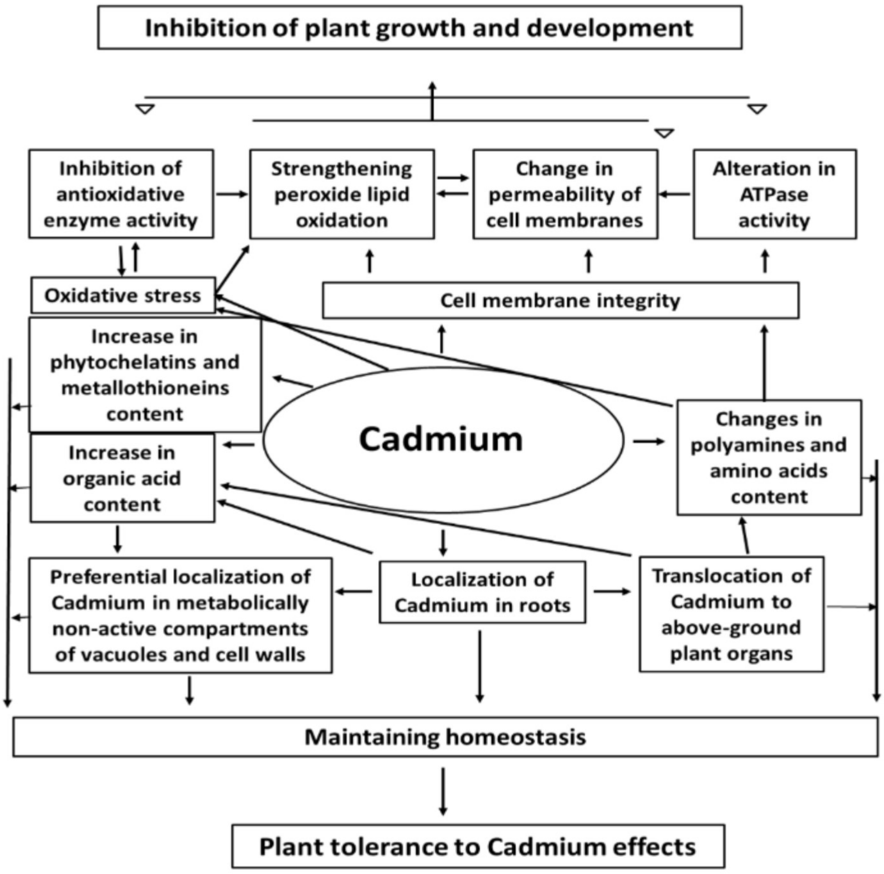

Figure 6 – Toxic effect of cadmium on plant and mechanisms of cadmium detoxification

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