Innovations

Role of Calcium in Mitigating Cadmium-Induced Stress in Plants: A Review

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Abstract: *The pollution of agricultural soils caused by cadmium (Cd) has started being a topical problem because of its adverse effect on the health of plants, the yield of the crops, and, finally food safety. Cd is readily transported to the root of plants once in the soil and may build up in plants such as leaves, fruit and seeds thus finding its way into the food chain, with severe health hazards to humans and animals. Exposure to Cd disrupts seed germination, inhibitroot and shoot growth, reduce the absorption of water and nutrients, and affect the photosynthesis process. More so, it initiates harmful reactive oxygen species (ROS) formation, thus presenting oxidative stress which destroys cellular structures. Some of the techniques that have been in active research by the researchers to counter this problem are soil treatment, the use of phytoremediation, and even the use of genetically modified plants. Calcium (Ca), being one of the necessary plant nutrients, is very important in the structural integrity and the regulation of the cellular activities. More to the point, it reduces the harmfulness of Cd, enhancing zinc (Zn) absorption, supporting cell walls, and triggering the antioxidant shield system of the plant, namely the enzymes, such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). Ca also plays a role in signaling that enables plants to detect and react to stress, and this increases the level of resistance towards heavy metal toxicity. This review focuses on the adverse effect of Cd on the plant systems and highlights positive role of Ca in enhancing tolerance of plants and sustaining agriculture production, under the contaminated environment.*

Keywords: *Agriculture, Cadmium toxicity, Calcium signaling, Antioxidant defense, Phytoremediation, Stress tolerance*

1. Introduction

1.1Background on Heavy Metal Pollution in Agriculture

The issue of heavy metals contamination in the agricultural sector has advanced as one of the common and urgent issues in the sector majorly attributed to human activities. There are industrial waste products, polluted water used to irrigate, as well as over application of chemical fertilizers that have led to a concentration of toxic metals in soil and water bodies. However, unlike organic pollutants, heavy metals such as Cd cannot be degraded by microbial activity and can persist in theenvironment for decades, gradually accumulating to harmful levels. Over time, this accumulation can disrupt both plant and animal ecosystems. Among these metals, Cd has received special attention due to its high mobility in the soil-plant system and its toxicity even at trace concentrations. When present in agricultural soils, cadmium(Cd) can impair seed germination, restrict root growth, suppress photosynthesis, and interfere with nutrient absorption and hormone regulation (Herrroway, 2022). Despite offering no nutritional benefit to plants or animals, Cd often enters farmlands through the continued use of phosphate fertilizers, which are naturally contaminated with this metal (Alloway, 2012). Cd tends to be quite mobile in soil, especially when certain environmental factors—such as low pH, high moisture, or limited organic matter-are present. This mobility increases its likelihood of being taken up by plants. Cd is absorbed by the roots through channels built for helpful substances such as zinc(Zn) or calcium(Ca) (DalCorso et al., 2010). First, Cd enters plants by the roots, then moves to the stems and leaves and fruit which increases its level in edible food (Jarup andAkesson, 2009).

1.2. Significance of Understanding Cd Toxicity and the Role of Ca in Mitigation

Understanding how Cd affects plant systems is essential for developing effective strategies to combat its toxicity in agriculture. Cd has no beneficial role in plant growth or development, yet it severely disrupts numerous physiological, biochemical, and molecular processes (Benavides et al., 2005). The development of roots and shoots is usually inhibited when there is exposure to Cd and this affects cell division and the transportation of nutrients in plant tissues (Lux et al., 2011). Among the others that are most apparent, there is a reduction in photosynthetic efficiency-plants in contact with Cd tend to have their chlorophyll break down, damaged structures of the chloroplast, and gas exchanges become compromised all of which have an effect on shortened growth due to weakened yield. A thorough knowledge of the Cd toxicological effects is needed to develop mitigation measures that are specific to address the problem. The studies have now focused on genetic engineering methods of increasing Cd tolerance in crops, as well as the production of better soil amendments and more efficient nutrient management procedures.

Bolstering of antioxidant protection in plants is also promising as one means of limiting the harm wrought by Cd-induced oxidative stress (DalCorso et al., 2008). Ca is critical to many areas of plant physiology which include maintenance of structural integrity to the regulation of the development and even the stress-responsive processes. In addition to its role as part of cell walls and membranes, Ca is a major secondary messenger in the plant signaling network. In response to environmental stresses like drought, pathogen invasion or encountering toxic metals like Cd, cytosolic Ca-referred to as Ca transients-rise rapidly and locally and trigger downstream signaling cascades which contribute to plant responses and adaptation. It has been found out that Ca prevents the harmful impact of Cd by limiting its uptake and its movement on the plant tissues. It also promotes the expression of antioxidant enzymes which include superoxide dismutase (SOD), catalase (CAT) and other peroxidases that combine to counteract the reactive oxygen species (ROS) produced upon Cd stress. Also, Ca plays a regulatory role in gene expression by Ca-dependent protein kinases (CDPKs) and calmodulin-signaling pathway that influences the hormonal balance and homeostasis in cells in stressful environments (Schulz et al., 2013; Kudla et al., 2018). Due to the wide range of effects, Ca becomes a promising agent not only to decrease the toxic effect of Cd, but also strengthen the health of plants. Its application promotes more viable and environmentally friendly methods of controlling heavy metal contamination of agricultural soils.

2. Cd Uptake, Transport, and Accumulation in Plants

2.1. Mechanisms of Root Uptake and Xylem Transport

Cd enters the roots of plants mainly by absorption, so the rhizosphere is the first point of contact of this heavy metal. Cd does not enter the plant through a unique or dedicated transporter; rather, it exploits the existing transport pathways designed for essential divalent cations. Due to its chemical similarity to these nutrients (Clemens,2006). Among the key transporter families involved, the Zinc-regulated transporter/Iron-regulated transporter-like proteins (ZIP) transporters-play a central role. These proteins facilitate the movement of Cd ions from the soil solution into the cytoplasm of root cells alongside essential metals (Guerinot, 2000). Once inside the root, Cd can follow two main paths: sequestration in vacuoles to limit systemic toxicity or upward translocation to the shoot via the xylem. The driving force behind Cd transport through the xylem is transpirational pull-an upward flow of water created by evaporation at the leaf surface. This negative pressure effectively draws Cd ions dissolved in the xylem sap toward the aerial parts of the plant (Lux et al., 2011). Cd mobility is influenced not solely by rate of transpiration but also by expression and function of xylem-loading transporters and metal-chelating ligands. Plants have developed strategies of regulating excess Cd within their bodies such as sequestration in plant storage vacuoles and binding to organic acids or peptides such as phytochelatins (PCs) which can inhibit transfer of Cd to consumable parts of a plants body. These transporters are the high-affinity ones that can promote, or inhibit this movement and are of great importance in regulating Cd sensitivity of a plant or tolerance of the same (Song et al., 2010). Agriculturally, it is important to have knowledge on these uptake and transport mechanisms in order to establish an efficient remediation approach to land contamination and in securing food safety. Genetic modification of transporter expression or use of crop varieties in which Cd does not move to the edible portions of plants in great quantities through xylem may enable reduction of Cd accumulation in edible plant tissue thus limiting its exposure to humans through the food chain (DalCorso et al., 2008).

2.2. Factors Affecting Cd Accumulation

Table 1: Soil Factors Affecting Cd Availability

Soil Factor	**Influence on Cd Availability**	**References**
pH	High in acidic soils.	Adriano (2001)
Organic Matter	Can bind Cd and reduce uptake	Xiong et al. (2009)
Clay Content	High content immobilizes Cd	Xiong et al.(2009)

A complex interaction of soil properties and physiography of the crop plants determines the concentration of Cd that accumulates in crop plants. Soil pH is one of these most important factors affecting Cd mobility and bioavailability. Cd is mostly present in soluble forms in acidic soils and this factor drastically elevates the Cd intake by the root system of crops and the possibility of its entrance to the food chain (Xiong et al., 2009). The presence and concentration of competing cations-such as Zn^{2+}, Ca^{2+}, and Mg^{2+} (magnesium)also strongly influence Cd uptake, as these elements share similar ionic radii and chemical properties with Cd making it difficult for plant transport systems to distinguish between them. Beyond pH, the pedogenesis (soil formation processes), cation exchange capacity(CEC), and organic matter content are key determinants of how Cd behaves in soil systems. Clay rich soils and soils that have high CEC are able to bind Cd with more success through electrostatic forces, which would lower its movement and consequent acceleration to plants (Adriano, 2001). In the same manner, increasing contents of organic matter would produce stable complexes with Cd, which reduce its availability to the soil solution. A set of internal processes governs Cd absorption, translocation and accumulation in the plant side.Root structure, depth, and surface area also influence the volume of soil explored, thereby affecting the level of Cd uptake. At the molecular level, metal transporter genes such as the ZIP, Natural Resistance-Associated Macrophage Protein (NRAMP) families etc enhance specificity and effectiveness of Cd transporters across the membranes. Those protective strategies such as plants with deeper root systems and with an effective metal transport system are more likely to exhibit a restricted rate of Cd taking and its distribution to the tissues (Lux et al., 2011). An appreciation of the interface between the soil chemistry and the physiology of plants forms a basis of identifying specific methods that can be developed to curtail the build-up of Cd in crops.

The ability of plants to absorb, translocate and accumulate Cd differs greatly among species and this has major implications in the way the consequences of Cd contamination are evaluated in natural ecosystems and farms (Zhao et al., 2015). These variations are directed by a mixture of physiological, biochemical, and genetic processes that act so that plants can control Cd uptake and develop detoxification tactics in cells (Uraguchi and Fujiwara, 2012). It is observed that there are some species that rise to hyperaccumulation status and thus some manage to absorb and accumulate/deposit very high concentrations such as Cd, frequently hundreds of times above non-accumulatorsseemingly without developing visible signs of toxicity (Yang et al., 2004; Assunçãoet al., 2003). Such plants have highly developed adaptations which make them useful to phytoremediation attempts. Conversely, most of the common crops such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), spinach (*Spinacia oleracea*) is more prone to accumulate Cd in their edible parts thus calling in question the safety of food since such crops have relatively low tolerance to Cd-stress (Grant et al., 2008; Rizwan et al., 2016). Differences in accumulation of Cd among different species can be explained mainly by the alternation of metal transporter proteins expression and activities. The transporters (ZIP and NRAMP) increase Cd binding capability and are usually upregulated in hyperaccumulators than those observed in non-accumulators (Guerinot, 2000). The existence of these transporters enhances increased uptake and transport of Cd in the plants. Protective detoxification of Cd in plants also goes hand in hand with the work of antioxidant protection systems. SOD and CAT are enzymes that are important to neutralize ROS produced at the level of Cd stress. In addition to that the Cd ions are bound by metal-binding ligands such as phytochelatins (PCs), metallothioneins (MTs) to facilitate intracellular compartmentalisation by reducing their toxicity (Hall, 2002; Clemens, 2001). Such detoxification mechanisms are usually more developed in hyperaccumulators to the extent that they can sequester high loads of toxic metals and with minimal cellular stresses. Lastly, the Cd tolerance and accumulation in a plant is simply a combination of factors, including the genetic status of the plant, the architecture of roots as well as the selectivity and activities of the transporters of the metal and the efficiencies of its antioxidant and detoxification mechanisms (Rizwan et al., 2016). To develop new varieties of crops that would store lesser Cd or improved methods of dealing with metal-contaminated soils, one would have to learn more about these processes.

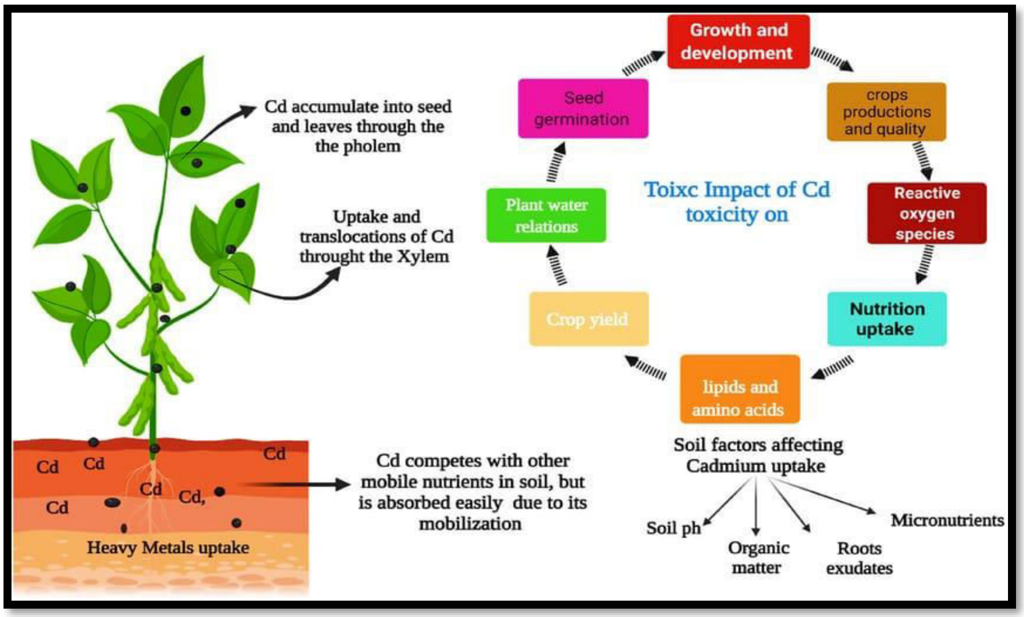


Figure 1. Cdabsorption, transport, accumulation and toxicity in plant species. The level of soil pH, micro-and macronutrients, and soil organic matter are the major variables affecting the Cd intake of plants (Alsafran et al., 2022)

3. Physiological and Biochemical Effects of Cd in Plants

3.1. Growth Inhibition

Root and shoots are primarily damaged by Cd which in turn causes growth arrest of plants and more particularly roots since they receive direct contact with the growth suppressor (Gallego et al., 2012). It interferes with formation of root tips hence leading to short and thick roots (Lux et al., 2011) and impairs zones of cell division and elongation. Cd also impacts on mitochondrion, decreasing the cellular respiration and ATP production, restricting the availability of energy to support the growth (Romero-Puertas et al., 2004). It also imbalances the hormones especially auxins and cytokinins and this disturbs the proper cell division, elongation and differentiation. Cd harms chloroplasts, decreases chlorophyll content, and impairs electron transport, reducing photosynthetic efficiency. These combined effects slow plant development and, in many cases, cause irreversible damage leading to plant death (Clemens, 2006). While some species show tolerance, most crop plants are sensitive and eventually suffer growth inhibition under Cd stress (DalCorso et al., 2008).

3.2. Disruption of Photosynthesis

Cd has a detrimental impact on plant photosynthesis by damaging critical components of the photosynthetic machinery (Kapur and Singh, 2023). Disruption of this process directly impairs plant growth and significantly lowers productivity. One major effect of Cd exposure is a decline in chlorophyll content, leading to chlorosis. It also alters chloroplast structure, interfering with both the light-dependent and light-independent stages of photosynthesis. Among the photosynthetic complexes, Photosystem II (PSII) is particularly sensitive to Cd-induced damage. Additionally, Cd inhibits the activity of Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), the key enzyme in the Calvin cycle responsible for carbon fixation. Damage to chlorophyll and photosystems, along with the generation ROS compromises cellular components, including lipids, proteins, and nucleic acids. Overall, Cd disrupts the efficiency of photosynthesis, leading to weakened plant health, reduced energy production, and ultimately lower crop yield and quality (Benavides et al., 2005).

3.3. Alteration in Nutrient Uptake

The presence of Cd in soil causes plants to take up less Ca, Mg, Zn, K (potassium), Fe (iron) and Cu (copper)(DalCorso et al., 2008; Hasan et al., 2009). Cd replaces Ca and other ions on the transport sites found on membrane proteins (Clemens, 2006). Although Cd does not right away change how Mg and K are absorbed, it leads to less of both being available which then affects chlorophyll production and regulation of water content in cells. Cd sharply limits the absorption of Zn and Fe which are important for many biochemical functions, auxin and chlorophyll production. The presence of Cd also slows the movement of nutrients by roots to shoots and disturbs the spread of nutrients in the plant (Lux et al., 2011). In general, nutritional imbalances caused by Cd damage the physical and physiological function of plants. It disrupts vital activities by lowering the levels of Ca and Mg that are important for protecting membranes, enzyme activity, free-radical defense, photosynthesis and respiration in plants. Because Cd sticks tightly to vital nutrients, it badly affects the growth and health of plants. Contact with Cd can interfere with plant metabolism by breaking vital enzymes (Hussain et al., 2019). The enzyme nitrate reductase is most affected and it plays a key role in turning nitrate into nitrite during nitrogen metabolism (Singh et al., 2013). Cd interferes with how the ATPase system functions which means cells have less energy for critical activities and it also blocks amylase, so there is less starch splitting and less energy provided (Gratão et al., 2005).

Overall, Cd stops enzymes from working correctly in the areas of metabolism, nutrient uptake and protection from oxidative stress which increases the plant's risk and lowers its strength (Yadav, 2010; Ismael et al., 2019).

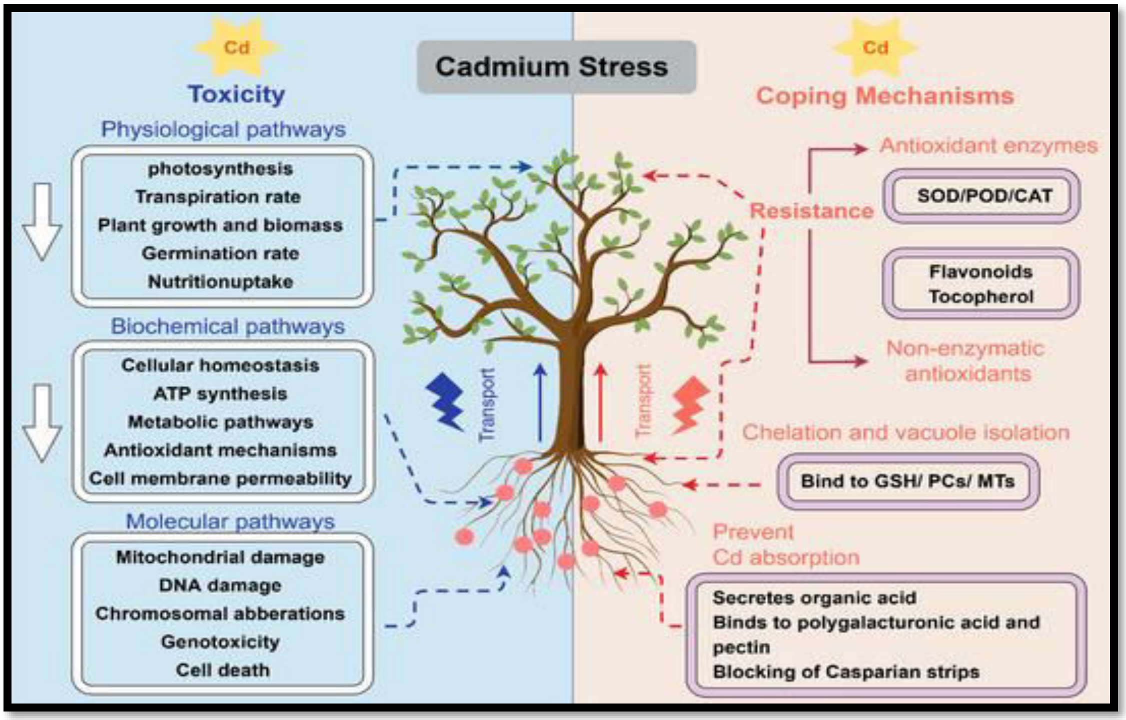


Figure 2. Toxic effects of Cd on plants and plant coping mechanisms(Zhang et al., 2024).

Table 2: Summary of Cd Effects on Plant Physiology

Physiological Aspect	Cd Effect	References
Root Growth	Inhibited elongation, thickened roots	Benavides et al. (2005)
Photosynthesis	Chlorophyll degradation, reduced CO_2 fixation	Gallego et al. (2012)
Nutrient Uptake	Disrupted uptake of Ca, Mg, Zn, Fe	Clemens (2006)
Enzymatic Activity	Reduced activity of NR, ATPase, SOD, CAT	DalCorso et al. (2008)

4. Mechanisms of Cd Detoxification in Plants.

4.1. Chelation by Phytochelatins and Metallothioneins

Plants use chelation to effectively fight against Cd toxicity by binding to the toxic Cd ions. The organic molecules in the chelation process attach to metal ions to make them less harmful by minimizing their biological uptake and chemical activity (DalCorso et al., 2008; Yadav, 2010). Phytochelatins are peptide chains that consist of glutathione units which derive from the glutamate-cysteine-glycine tripeptide. Under heavy metal stress conditions, phytochelatin synthase (PCS) produces PCs through glutathione synthesis from the plant cell (Cobbett and Goldsbrough, 2002). Inside the cytosol, Cd ions reach phytochelatins which secure them through the sulfur (-SH) groups in cysteine residues. The Cd–PC complexes create the basis for transport inside vacuoles to achieve their final solution. The ability of vacuoles to store toxic metals makes them essential cellular compartments because they provide isolation from regular metabolic activities. Among the cysteine-rich proteins that aid metal detoxification processes, metallothioneins (MTs) help to sequester Cd. The small proteins known as metallothioneins show multiple cysteine residues that serve to capture different heavy metals-specifically Cd-through their reactive thiol (-SH) groups (Zhou and Goldsbrough, 1994). MTs have functions which carry applications beyond their role in Cd storage. Plant cells maintain metal ion homeostasis through metallothioneins which also control the levels of Zn and Cu while performing their main role of heavy metal binding including Cd (Guo et al., 2008). PCs and MTs link their chelation calls to work together as duplicate systems. MTs help Cd detoxification by capturing it in the cytosol while PCs specialize in Cd complex formation with subsequent vacuolar transport (Sanità di Toppi and Gabbrielli, 1999). Both chelators function together to stop Cd toxicity through metal binding and storage which reduces cellular damage. Phytochelatins along with metallothioneins enable plants to combat Cd stress by helping them restore normal function. The biosynthesis of phytochelatins happens rapidly following the detection of Cd exposure while being triggered by environmental signals that signify rising Cd levels in the soil or water (Haider et al., 2021).

4.2. Sequestration in Vacuoles

Following chelation by ligands such as phytochelatins, vacuolar sequestration functions as a major detoxification strategy by compartmentalizing Cd away from the cytosol. The Cd ions which have been bound with PCs or other ligands in cytosol are transported to the vacuole by active transport as Cd-PC complexes (Clemens, 2006). Vacuoles in plants act as enclosed chambers and lead to the storage of a variety of compounds of ion and also secondary metabolites and trash items which contain contaminant metals. The transporters that localize in the tonoplast in the vacuolar membrane integrate in the tonoplast to take the Cd-PC complexes into the vacuolar chamber. The major transporter group, that mediates this process, is the ATP-Binding Cassette (ABC) transporter family. The tonoplast transporters translocate the Cd-PC complex into the vacuole and this process uses ATP hydrolysis to provide energy. There are numerous biological advantages of vacuolar sequestration mechanism in the plants. The vacuolar sequestration process decreases cytoplasmic free Cd levels which protects vital cellular processes from disruption (Verbruggen et al., 2009). The plant benefits from vacuolar sequestration because it enables safe Cd accumulation at higher levels, particularly in cells with large vacuoles such as root and leaf cells (Clemens, 2006). The vacuolar sequestration mechanism shows specific patterns of distribution between different plant organs. The Cd accumulation process in roots occurs through vacuolar storage, which prevents the metal from moving to edible plant parts and shoots (Ueno et al., 2008). The selective storage mechanism safeguards photosynthetic tissues and reproductive organs from damage, which helps prevent growth and reproductive impacts (Krämer, 2010).

4.3. Role of Antioxidant Enzymes (SOD, CAT, POD, etc.)

Table 3: Antioxidant Enzyme Response under Cd Stress and Ca Treatment

Enzyme	**Cd Stress Alone**	**Cd + Ca Treatment**	**References**
SOD	Decreased	Increased	Gill and Tuteja (2010); Huang et al. (2021)
CAT	Decreased	Increased	Gill and Tuteja (2010)
APX	Low	Moderate to High	Zhou et al. (2020); Huang et al. (2021)
POD	Suppressed	Stimulated	Gill and Tuteja (2010)

When plants encounter Cd stress their cells develop redox imbalance through excessive formation of ROS that includes superoxide anions ($O_2^{\cdot -}$) hydrogen peroxide (H_2O_2) and hydroxyl radicals (•OH) according to Huang et al. (2021). When plants encounter oxidative hazards, they use a complex group of enzymes to defend their cells against harm. SOD starts the chain of defense against harmful ROS when activated. As an enzyme SOD changes superoxide radicals directly into hydrogen peroxide and molecular oxygen in a single process(Gill and Tuteja, 2010). In plant cells CAT primarily functions by detoxifying H_2O_2 by transforming it into water and oxygen in peroxisomes. Cd exposure usually reduces the activity of catalase which causes an increase in hydrogen peroxide when other enzymes cannot compensate (Kapur and Singh, 2019; Huang et al., 2021). Peroxidase, Phenol oxidase, and Dehydrogenase in Class III use hydrogen peroxide to transform different substances within the cytosol complementing with cell-wall and vacuole membranes. The antioxidant enzymes enhance their work under Cd stress as a way to protect the plant. APX removes H_2O_2 from the plant system by using AsA as an electron donor while protecting the AsA-GSH (glutathione) detoxifying cycle. The enzyme system has enhanced importance in chloroplasts since these organelles generate a lot of ROS during photosynthesis according to Gill and Tuteja (2010). Glutathione Reductase enables GSH maintenance through its conversion of GSSG (oxidized glutathione) back to GSH using Nicotinamide Adenine Dinucleotide Phosphate (NADPH). GSH protects against ROS while helping the plant remove harmful metals through its role in phytochelatin production (Foyer and Noctor 2005). The two enzymes Monodehydroascorbate reductase (MDHAR) and Dehydroascorbate reductase (DHAR) support the recycling of AsA and GSH in the AsA-GSH cycle by converting them back to their reduced state. Non-enzymatic antioxidants such as ascorbate, glutathione, carotenoids, flavonoids, and tocopherols directly remove ROS(Mittler, 2002). Organisms that tolerate Cd experience stronger activity from antioxidant enzymes helping them to survive Cd toxicity, whereassensitive plants experience oxidative damage and diminished health due to their reduced enzyme activity according to Gallego et al. (2012).

5. Ca as a Mitigating Agent Against Cd Toxicity

Cell membranes along with cell walls maintain their stability through structural participation of Ca. Membrane lipids oxidize under Cd stress which results in an increase of membrane permeability and associated ion movement. The uptake channels frequently show competition between Cd and Ca because both elements have identical ionic radii and charges. An antagonistic competition between these elements initiates their biological interaction. Cd interference disrupts the absorption of vital ions including Mg and Fe as well as K from the soil. Through Ca supplementation the nutrient balance becomes stable because the treatment safeguards transportation channels while preserving ionic equilibrium (Hasan et al., 2021). The application of Ca during phytostabilization functions to restrict both Cd movement in soil and plant-based transport of Cd. The application of Ca-based substances like $CaCO_3$ and gypsum in contaminated soils reduces the available Cd content according to He et al. (2020).

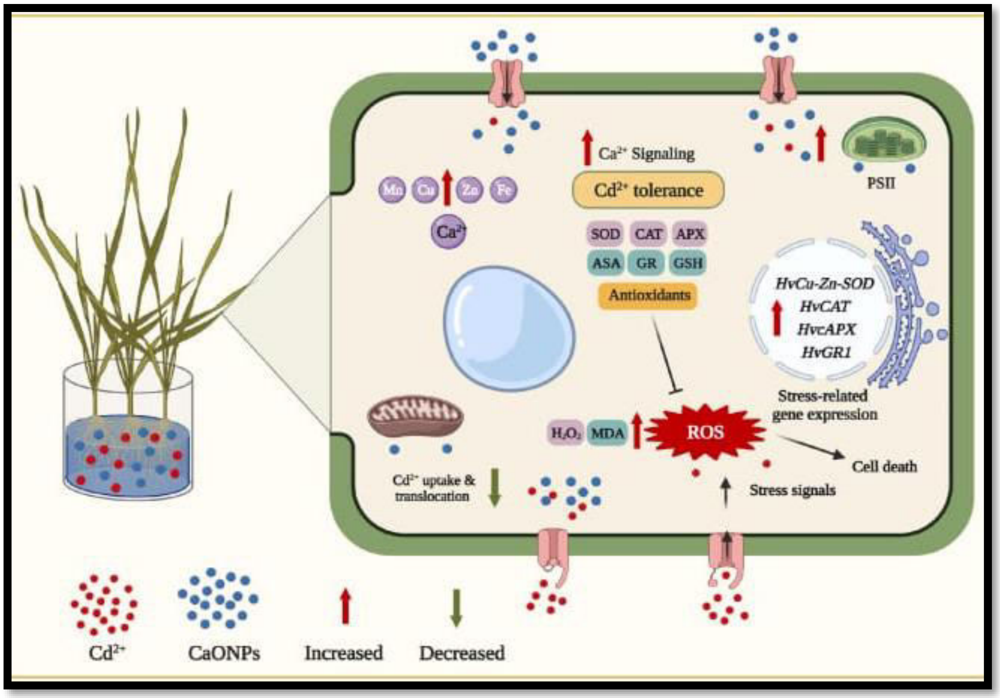
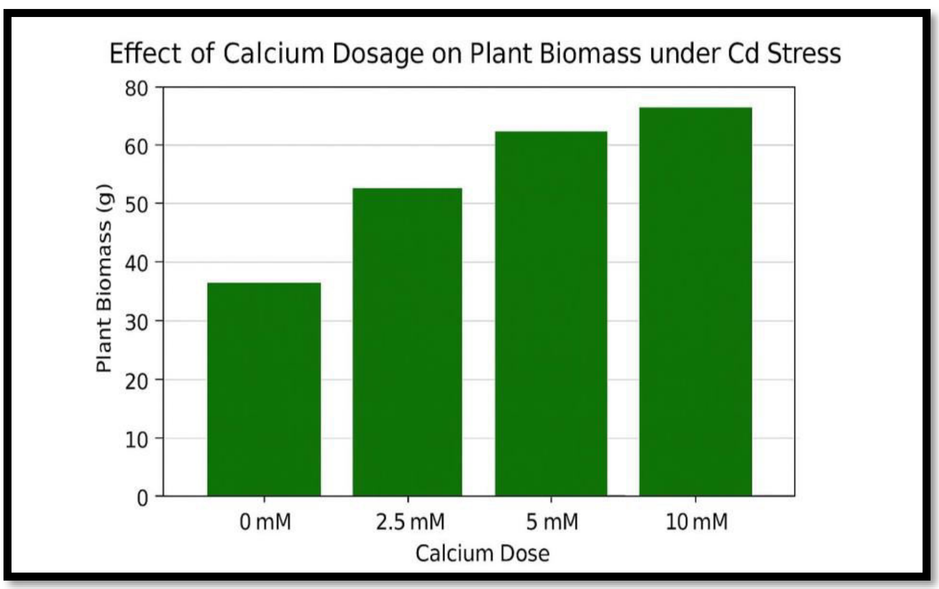


Figure: 3 Role of CaONPs in alleviating Cd toxicity in plants. CaONPs reduce Cd uptake and enhance Ca signaling, boosting antioxidant defenses and stress-related gene expression. (Nazir et al., 2024)



6. Experimental Evidences and Case Studies

Figure 4: Effect of Ca Dosage on Plant Biomass under Cd Stress (Hasan et al., 2021)

The presence of Ca helps to protect the plant by activating ROS-scavenging enzymes SOD as well as CAT and APX through their upregulation (Zhou et al., 2020). Experimental results consistently show that Ca supplementation reduces Cd uptake, enhances plant growth, and improves stress tolerancein a range of plant species. In *Brassica juncea*, for instance, supplementation with 50 mM Ca resulted in increased root and shoot biomass, elevated chlorophyll content, and enhanced activity of antioxidant enzymes such as SOD, APX, GR(Glutathione Reductase), alongside a notable decrease in Cd accumulation within plant tissues. In rice seedlings, externally applied Ca was shown to limit oxidative damage by improving both the antioxidant defence system and the glyoxalase pathway, which together supported membrane integrity and lowered lipid peroxidation under Cd stress (Daud et al., 2015). Likewise, in mungbean seedlings, supplementation of Casignificantly improved biomass by enhancing root-shoot length, restoredpigment content and improved relative leaf water content (RLWC),suggesting that Ca supports water uptake and physiological stability under Cd stress (Katoch and Singh, 2014; Kaur and Singh, 2023). These findings underline the multifaceted role of Ca in mediating stress responses and detoxification, and support its use as a practical approach to mitigate cadmium-induced damage in crops.

Conclusion

Cd being a non-essential heavy metal and of high-level toxicity interferes with vital physiological activities of plants like root growth to photosynthesis and in addition promotes severe oxidative stress in plants. Ca has also risen up to become an encouraging component in reversing the effects of Cd toxicity. It has a busy job, such as competing with Cd to be taken up, stability of the membrane, nutrient balance and activating the antioxidant defense systems. The efficacy of Ca in diminishing Cd accumulation and increasing stress tolerance has been demonstrated by experimental evidence studies performed with several plant species. The concept of the integration of the Ca management with crop improvement strategies can provide opportunity in developing Cd-resilient cultivars. To sum up, Ca is not only a nutrient but a strategic partner in alleviating the Cd stress in plants. Through its considerate use, it can achieve safer crop cultivation, better environmental control, and sustainable and secure farming in the future.

References:

1. *Adriano, D.C. (2001). Trace elements in terrestrial environments: biogeochemistry, bioavailability, and risks of metals. 2nd ed. New York: Springer-Verlag, 1–16.*
2. *Alloway, B.J. (2012). Sources of heavy metals and metalloids in soils. In: Heavy metals in soils: trace metals and metalloids in soils and their bioavailability. Dordrecht: Springer Netherlands, 11–50.*

3. *Alsafran, M., Saleem, M.H., Al Jabri, H., Rizwan, M. and Usman, K. (2022). Principles and applicability of integrated remediation strategies for heavy metal removal/recovery from contaminated environments. Journal of Plant Growth Regulation, 42(6): 3419–3440.*
4. *Assunção, A.G.L., Schat, H. and Aarts, M.G.M. (2003). Thlaspi caerulescens, an attractive model species to study heavy metal hyperaccumulation in plants. New Phytologist, 159(2): 351–360.*
5. *Benavides, M.P., Gallego, S.M. and Tomaro, M.L. (2005). Cadmium toxicity in plants. Brazilian Journal of Plant Physiology, 17(1): 21–34.*
6. *Clemens, S. (2001). Molecular mechanisms of plant metal tolerance and homeostasis. Planta, 212(4): 475–486.*
7. *Clemens, S. (2006). Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. Biochimie, 88(11): 1707–1719.*
8. *Cobbett, C. and Goldsbrough, P. (2002). Phytochelatins and metallothioneins: roles in heavy metal detoxification and homeostasis. Annual Review of Plant Biology, 53: 159–182.*
9. *DalCorso, G., Farinati, S. and Furini, A. (2008). Regulatory networks of cadmium stress in plants. Plant Signaling and Behavior, 3(8): 659–661.*
10. *Daud, M.K., Mei, L., Variath, M.T., Zhu, S.J. and Zhu, Y.G. (2015). Exogenous calcium alleviates cadmium-induced oxidative stress in rice seedlings by regulating the antioxidant defense and glyoxalase systems. Brazilian Journal of Botany, 38: 527–538.*
11. *DalCorso, G., Pesaresi, P., Masiero, S., Arosio, P. and Furini, A. (2010). Cadmium stress triggers the expression of specific transporters and detoxification-related genes in plants. Plant, Cell and Environment, 33(3): 490–504.*
12. *Foyer, C.H. and Noctor, G. (2005). Redox homeostasis and antioxidant signaling: a metabolic interface between stress perception and physiological responses. The Plant Cell, 17(7): 1866–1875.*
13. *Gallego, S.M., Pena, L.B., Barcia, R.A., Azpilicueta, C.E., Iannone, M.F., Rosales, E.P., Zawoznik, M.S., Groppa, M.D. and Benavides, M.P. (2012). Unravelling cadmium toxicity and tolerance in plants: insight into regulatory mechanisms. Environmental and Experimental Botany, 83: 33–46.*
14. *Gill, S.S. and Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48(12): 909–930.*
15. *Grant, C.A., Clarke, J.M., Duguid, S. and Chaney, R.L. (2008). Selection and breeding of plant cultivars to minimize cadmium accumulation. Science of the Total Environment, 390(2–3): 301–310.*

16. *Gratão, P.L., Polle, A., Lea, P.J. and Azevedo, R.A. (2005). Making the life of heavy metal-stressed plants a little easier. Functional Plant Biology, 32(6): 481–494.*
17. *Guo, W.J., Meetam, M. and Goldsbrough, P.B. (2008). Examining the specific contributions of individual Arabidopsis metallothioneins to copper distribution and metal tolerance. Plant Physiology, 146(4): 1697–1706.*
18. *Guerinot, M.L. (2000). The ZIP family of metal transporters. Biochimica et Biophysica Acta - Biomembranes, 1465(1–2): 190–198.*
19. *Hall, J.L. (2002). Cellular mechanisms for heavy metal detoxification and tolerance. Journal of Experimental Botany, 53(366): 1–11.*
20. *Hasan, M.K., Cheng, Y., Kanwar, M.K., Chu, X.Y., Ahammed, G.J. and Qi, Z.Y. (2021). Responses of plant proteins to heavy metal stress—a review. Frontiers in Plant Science, 12: 640196.*
21. *Hasan, S.A., Fariduddin, Q., Ali, B., Hayat, S. and Ahmad, A. (2009). Cadmium: toxicity and tolerance in plants. Journal of Environmental Biology, 30(2): 165–174.*
22. *Haider, F.U., Liqun, C., Coulter, J.A., Cheema, S.A., Wu, J., Zhang, R. and Farooq, M. (2021). Cadmium toxicity in plants: impacts and remediation strategies. Ecotoxicology and Environmental Safety, 211: 111887.*
23. *He, J.Y., Ma, C.Y., Sun, Y., Sun, X.X. and Xu, G. (2020). Mitigation of cadmium toxicity in rice by calcium application. Agricultural Sciences, 11(5): 543–556.*
24. *Herrroway, P. (2022). Heavy metal pollution in agriculture. Journal of Environmental Science and Sustainability, 18(2): 33–48.*
25. *Huang, J., Wang, J., Yang, X., Fan, L. and Chen, C. (2021). Antioxidant responses and oxidative stress in cadmium-stressed plants. Plant Physiology and Biochemistry, 160: 74–84.*
26. *Hussain, S., Rizwan, M., Ali, Q. and Ali, S. (2019). Mechanisms of cadmium toxicity in plants and its alleviation by calcium application. Plant Physiology and Biochemistry, 144: 215–223.*
27. *Ismael, M. A., Elyamine, A. M., Moussa, M. G., Cai, M., Zhao, X., and Hu, C. (2019). Cadmium in plants: uptake, toxicity, and its interactions with selenium fertilizers. Metallomics, 11(2): 255-277.*
28. *Jarup, L. and Akesson, A. (2009). Current status of cadmium as an environmental health problem. Toxicology and Applied Pharmacology, 238(3): 201–208.*
29. *Katoch, K. and Singh, K.J. (2014). Role of calcium in antagonizing cadmium induced heavy metal toxicity in mungbean seedlings. Indian Journal of Plant Sciences, 3(3): 1–6.*
30. *Kaur, G. and Singh, K.J. (2023). Ascorbic acid and calcium silicate improve morpho-physiological characteristics of cadmium stressed mung bean crop. Current Agriculture Research, 11(1): 167-176.*

31. *Kapur, D. and Singh, K.J. (2019). Zinc alleviates cadmium induced heavy metal stress by stimulating antioxidative defense in soybean [Glycine max (L.) Merr.] crop. Journal of Applied and Natural Science, 11(2): 338–345.*
32. *Kapur,D. and Singh, K.J. (2023). The effect of exogenous Zn application on photosynthetic pigments, electrolyte leakage and carbohydrate metabolism in soybean plants subjected to Cd stress. Scope, 13(4): 1070–1083.*
33. *Krämer, U. (2010). Metal hyperaccumulation in plants. Annual Review of Plant Biology, 61: 517–534.*
34. *Kudla, J., Becker, D., Grill, E., Hedrich, R., Hippler, M., Kummer, U., Parniske, M., Romeis, T. and Schumacher, K. (2018). Advances and current challenges in calcium signaling. New Phytologist, 218(2): 414–431.*
35. *Lux, A., Martinka, M., Vaculík, M. and White, P.J. (2011). Root responses to cadmium in the rhizosphere: a review. Journal of Experimental Botany, 62(1): 21–37.*
36. *Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. Trends in Plant Science, 7(9): 405–410.*
37. *Nazir, M.M., Li, G., Nawaz, M., Noman, M., Zulfiqar, F., Ahmed, T., Jalil, S., Ijaz, M., Kuzyakov, Y. and Du, D. (2024). Ionic and nano calcium to reduce cadmium and arsenic toxicity in plants: review of mechanisms and potentials. Plant Physiology and Biochemistry, 216: 109169.*
38. *Rizwan, M., Ali, S., Abbas, T., Zia ur Rehman, M., Hannan, F., Keller, C., Al-Wabel, M.I., Ok, Y.S. and Rinklebe, J. (2016). Cadmium minimization in wheat: a critical review. Ecotoxicology and Environmental Safety, 130: 43–53.*
39. *Romero-Puertas, M.C., Rodriguez-Serrano, M., Corpas, F.J., Gómez, M., del Río, L.A. and Sandalio, L.M. (2004). Cadmium-induced subcellular accumulation of O2 and H2O2 in pea leaves. Plant, Cell and Environment, 27(9): 1122–1134.*
40. *Sanità di Toppi, L. and Gabbrielli, R. (1999). Response to cadmium in higher plants. Environmental and Experimental Botany, 41(2): 105–130.*
41. *Schulz, P., Herde, M. and Romeis, T. (2013). Calcium-dependent protein kinases: hubs in plant stress signaling and development. Plant Cell, 25(2): 523–538.*
42. *Singh, H.P., Mahajan, P., Kaur, S., Batish, D.R. and Kohli, R.K. (2013). Chromium toxicity and tolerance in plants. Environmental Chemistry Letters, 11: 229–254.*
43. *Song, W.Y., Mendoza-Cózatl, D.G., Lee, Y., Schroeder, J.I., Ahn, S.N. and Lee, H.S. (2010). Arsenic tolerance in Arabidopsis is mediated by two ABCC-type phytochelatin transporters. Proceedings of the National Academy of Sciences, 107(49): 21187–21192.*
44. *Ueno, D., Yamaji, N. and Ma, J.F. (2008). Further characterization of ferric-chelate reductase for iron uptake in rice. Soil Science and Plant Nutrition, 54(3): 334–338.*

45. *Uraguchi, S. and Fujiwara, T. (2012). Cadmium transport and tolerance in rice: perspectives for reducing grain cadmium accumulation. Rice, 5(1): 5.*
46. *Verbruggen, N., Hermans, C. and Schat, H. (2009). Molecular mechanisms of metal hyperaccumulation in plants. New Phytologist, 181(4): 759–776.*
47. *Xiong, Z.T., Liu, C. and Geng, B. (2009). Phytotoxic effects of copper, zinc, and cadmium in rice seedlings and their interactions with calcium. Biologia Plantarum, 53(1): 129–132.*
48. *Yadav, S.K. (2010). Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. South African Journal of Botany, 76(2): 167–179.*
49. *Yang, X., Long, X.X., Ye, H.B., He, Z.L., Calvert, D.V. and Stoffella, P.J. (2004). Cadmium tolerance and hyperaccumulation in a new species of Sedum affine. Environmental Pollution, 132(1): 145–152.*
50. *Zhao, F.J., Ma, Y., Zhu, Y.G., Tang, Z. and McGrath, S.P. (2015). Soil contamination in China: current status and mitigation strategies. Environmental Science and Technology, 49(2): 750–759.*
51. *Zhou, Y., Zhou, Y., Mao, C. and Jin, C. (2020). Calcium application reduces cadmium accumulation in wheat and enhances antioxidant defense. Ecotoxicology and Environmental Safety, 195: 110472.*
52. *Zhou, W. and Goldsbrough, P.B. (1994). Functional homologs of metallothionein genes from Arabidopsis. Plant Cell, 6(6): 875–884.*
53. *Zhang, X., Yang, M., Yang, H., Pian, R., Wang, J. and Wu, A.-M. (2024). The uptake, transfer, and detoxification of cadmium in plants and its exogenous effects. Cells, 13(11): 907.*