



Zinc: A Critical Micronutrient for Growth and Development of Plants

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ABSTRACT

Zinc is indeed a critical micronutrient found in very low amounts in the soil, which may limit the growth and reproduction of crops. The absorption of Zn by plants is directly influenced by several factors such as high pH, amount of organic matter, high humidity associated with low temperatures, and soil microorganisms. Zinc is an integral component of enzyme structures and it is also a regulatory cofactor for many enzymes that are required for the synthesis of chlorophyll, proteins, and carbohydrates. Zinc is important for enzymatic activity, being a constituent part of the enzyme's alcohol dehydrogenase, carbonic anhydrase, Cu/Zn superoxide dismutase enzyme, and polymer RNA, in addition to participating in the synthesis of precursor tryptophan in the metabolism of indoleacetic acid, which is a plant hormone directly related to the development of plants. The functioning of these enzymes is affected significantly due to Zn deficiency and there will be a retarded growth and low productivity of crops because these enzymes are crucial for the growth and overall health of the plant. Zinc deficiency in plants is characterized by shortened internodes, reduced leaf area and size, the formation of rosettes, chlorosis, and necrosis. Almost half of the world's cereal crops are deficient in Zn, leading to poor crop yield. One-third of the world's population is at risk of Zn deficiency. Zn deficiency in agricultural soils is also a major global problem affecting both crop yield and quality. This review aims to outline the key aspects of zinc as a nutrient in the soil and its roles in plants.

KEY WORDS: Alcohol dehydrogenase, Critical micronutrient, Carbonic anhydrase, Regulatory cofactor, Zinc deficiency

INTRODUCTION

Micromineral zinc (Zn) is important for human health and has many functions in the body, including metabolic pathways, gene control, enzymatic reactions, protein synthesis, and keeping cells healthy (Chasapis *et al.*, 2020; Wessels *et al.*, 2022; Barman *et al.*, 2018). The optimal range of zinc (Zn) levels required for the healthy growth of most crops typically falls between 30 and 200 µg Zn g⁻¹ dry weight (DW) (Marschner, 2011). Moreover, zinc is necessary for tryptophan synthesis, an amino acid that acts as a precursor to auxin (Tsonev & Lidon, 2012). Elevated concentrations of zinc in soils are hazardous to plants, leading to various structural and functional abnormalities that ultimately impair plant growth and performance. Zinc plays a crucial function in nitrogen metabolism by acting as both a catalyst and a structural component of enzymes (Broadley *et al.*, 2007). Various factors such as soil characteristics, Zn concentrations,

and interactions with other metals like cadmium (Cd) influence the crucial process of zinc uptake in plants.

Researchers are exploring innovative agricultural practices, like the use of zinc-solubilizing microbes, to increase zinc availability in soils for sustainable crop production and human health. (Zhou *et al.*, 2023) research has shown that Zn plays a vital role in plant biochemistry and metabolism, impacting growth, development, and yield. Soil properties, particularly available phosphorus levels, can affect Zn availability in plants, with poorly crystalline Fe oxides and phosphorus availability positively influencing Zn uptake (Saleem *et al.*, 2022). The application of zinc has reduced heavy metal (HM) toxicity in plants by improving physiological and biochemical functions, anti-oxidant activities, osmolyte accumulation, and gene expression (Hassan *et al.*, 2022). Furthermore, Zn plays a significant role in developing plant defense mechanisms against diseases by enhancing enzyme and protein

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functions, antioxidant systems, and defense pathways, ultimately improving membrane integrity and defense responses (Bastakoti, 2023). However, excessive Zn levels can lead to phytotoxicity, affecting plant growth and photosynthesis and causing an imbalance in mineral nutrition due to the generation of reactive oxygen species (Kaur & Garg, 2021).

Zinc toxicity leads to chlorosis in young leaves, stunted growth, and reduced Rubisco activity, impacting growth yield and quality of crops, while excess zinc results in chlorosis in leaves and causes toxicity (Barman *et al.*, 2018). The plant has severe yield loss as a result of the excessive Zn content, which also induces chlorosis and hinders the synthesis of biomass (Pandey *et al.*, 2013), cell division, nutrient uptake, and enzymes (Ul Hassan *et al.*, 2017). The presence of zinc (Zn) may lead to an elevation in anthocyanins, which could potentially improve the antioxidant capacity and/or metal chelation in plants. Understanding Zn uptake dynamics is essential for biofortification strategies to address Zn deficiency in crops, emphasizing the need for sustainable approaches to enhance Zn utilization efficiency in plants (Saxena *et al.*, 2023). Researchers see biofortification as a potential solution to the significant health issues humans face, given that crop fertilizer typically recovers less than 1% of zinc (Wang *et al.*, 2016). Surface and groundwater contain Zn, and it gets there from a variety of places, including mine drainage, industrial and municipal waste, urban runoff, and, most importantly, the erosion of Zn-containing soil particles (Hasballah & Beheary, 2016). Typically, plants have a zinc content of 30-100 mg Zn/kg dry matter, while concentrations over 300 mg/kg are considered hazardous. Crops that are particularly vulnerable to zinc deficiency include beans, grapes, citrus, rice, sorghum, and maize. Several studies have shown that uncontaminated soils can have total Zn concentrations ranging from 10 to 100 mg/kg (Alloway, 2012). A novel method has been proposed by Anisimov *et al.* (2021) to assess soil buffer capacity for zinc uptake in various plant species. Mishra *et al.* (2020) investigated zinc (Zn) uptake and speciation in radish, spinach, and clover grown in smelter-contaminated soils.

Zinc as a Mineral Nutrient

Zinc deficiency is a nutritional problem that is most common in low- and middle-income nations because of low availability of zinc-rich foods, a less diverse diet, and a heavy dependence on cereal-based meals. The bioavailability of zinc in this type of diet is poor because of phytate binding (Gupta *et al.*, 2020). Furthermore, there is a correlation between low levels of zinc in the soil and a high incidence of zinc insufficiency, particularly in poor countries (De Groote *et al.*, 2021). The United States and

other developed nations also face a shortage of zinc. As a case study, 15% of the US adult population consumes less Zn than the estimated average requirement (EAR) (Reider *et al.*, 2020). Experts estimate that 17.1% of the world's population is at risk of consuming insufficient amounts of zinc. Variables such as the world's expanding population, climate change, pandemics of infectious diseases like COVID-19, and conflicts could exacerbate the problem (Wessels *et al.*, 2022). Nutrient priming enriches seeds with Zn, boosting fresh yield and dry biomass by boosting germplasm growth, seed vigor, and rooting (Montanha *et al.*, 2020). However, Zn enrichment can have a detrimental effect on crop output above a particular threshold that may be crop-specific (Baczek-Kwinta *et al.*, 2020). Zinc deficiency results in inadequate seed growth, impaired pollen function, and diminished fertilization. To mitigate this issue, crops in areas with zinc deficiency can be treated with foliar zinc treatment at the beginning of the reproductive period (Pathak *et al.*, 2012). The use of zinc (Zn) in fertilization strategies greatly improved the physiological and biochemical defenses of tomato plants infected with *Alternaria solani* (Awan *et al.*, 2019). In addition, Paradisone *et al.* (2021) found that the presence of K_2SiO_3 reduced the harmful effects of Zn by decreasing the availability of Zn to plants in the growth medium.

Zinc's Role in Root Architecture

Zinc (Zn) is mostly taken up by the roots in its divalent form (Zn^{2+}), and the absorption rate, transportation to the shoot, and compartmentalization in various organelles might vary across different species (Oliveira *et al.*, 2023). Roots are where Zn is mostly absorbed through facilitated diffusion and organic ligand-Zn complexes. Several studies have shown that root activities like the secretion of root exudates (Khoshgoftarmanesh *et al.*, 2018) and changes in root morphology (Mori *et al.*, 2016) may make soil zinc more bioavailable for roots to take up and improve ZIE. A decrease in root growth causes a delay in the assimilation of water and minerals, which also impacts shoot growth (Zhang *et al.*, 2018). Tokumoto *et al.* (2023) revealed that high concentrations of zinc have been shown to inhibit root elongation and affect various morphological characteristics, such as calluses, root initiation, and shoot development. Furthermore, studies have found that soil Zn fertilization increases root dry weight, length density, and surface area, while higher Zn application rates lead to slight decreases in these parameters (Bouain *et al.*, 2018). Saleem *et al.* (2022) said that adding Zn to winter wheat roots greatly increases their dry weight, length density, and surface area within the soil depth. This has a positive effect on shoot biomass, Zn accumulation, and post-anthesis Zn uptake, highlighting how important Zn fertilization is for plants to grow and develop properly.

Excess zinc in the root area can hinder shoot apex growth and delay organogenesis, leading to abnormal cell metabolism and inhibition of root elongation (Muthukumar & Jaison, 2018; Kaznina *et al.*, 2022). Under stress, pathogen-infected plants treated with zinc alone or other nutrient combinations showed the most improvement, with their roots growing by 48-168% when treated with NPK fertilizer and 5.0 mg/kg zinc (Awan *et al.*, 2019). Zn mediates the molecular mechanism underlying the decline in root water transport characteristics. The reduction in root and shoot hydraulic conductivity, which was facilitated by down-regulating AQPs (HvPIP1;2, HvPIP2;4, and HvPIP2;5) activity and gene expression as well as increased submerization in endodermis, was due to the decrease in barley root-intrinsic water transport property in response to high Zn (Gitto & Fricke, 2018). Moreover, the researchers indicated that the surplus of zinc caused a decrease in the rate of water flow in barley plants by simultaneously reducing the hydraulic characteristics of the roots (AQPs) and the stomata in the shoots. Fatemi *et al.* (2020) have found a decrease in root hydraulic conductance and the participation of all PIP1 isoforms, PIP2;6, and PIP2;7 to determine the long-term response to Zn treatments in *Brassica rapa* plants. These results indicate that an excess of zinc leads to changes in the structure and function of plants, affecting their capacity to uptake and transport water.

Metal Transporters Involved in Zinc Uptake

Multiple metal transporters have been discovered in plants, such as the families of zinc-regulated transporters, the iron-regulated transporters-like protein (ZIP) family, the Heavy metal ATPases (HMA) family, the Natural Resistance-Associated Macrophage protein (NRAMP) family, and the Cation Diffusion Facilitator (CDF) family (Xu *et al.*, 2021). A significant approach for coping with the stress of zinc deficiency is thought to be to regulate the ZIP gene family. Zinc uptake in plants utilizes P1B-ATPase, ZIP, NRAMP, and CDF/MTP transporters, facilitating movement from roots to shoots via the xylem and potential re-translocation through the phloem, demonstrating the complexity of zinc distribution and regulation in plant physiology (Moreira *et al.*, 2018). In rice, zinc deficiency induces the production of OsZIP1, OsZIP2, OsZIP4, OsZIP5, OsZIP6, OsZIP7, and OsZIP8 proteins which involved in the absorption, transport, or allocation of zinc in rice (Kavitha *et al.*, 2015; Sasaki *et al.*, 2015). In rice, the OsZIP5 and OsZIP9 genes cooperatively uptake zinc and cadmium, with OsZIP9 playing a more pivotal role. Mutations in these genes impair zinc and cadmium uptake, and the double mutant exacerbates deficiency, underscoring their critical function in rice (Tan *et al.*, 2020). Zinc deficiency stress caused an up-regulation of HvZIP genes (HvZIP3, HvZIP5, HvZIP7, HvZIP8,

HvZIP10, and HvZIP13) expression to improve zinc absorption and movement from the roots to the shoots in Barley (Tiong *et al.*, 2015). The five ZIP genes (ZmZIP3, ZmZIP4, ZmZIP5, ZmZIP7, and ZmZIP8) exhibit differential expression in maize roots under zinc deficiency, indicating a possible function for these genes in altering zinc deficiency tolerance across maize lines (Xu *et al.*, 2021). The increased expression of PaMTP1 in normal plants when exposed to metals indicates its role in Zn detoxification. Conversely, the decreased levels observed in ScZRC1-expressing plants, both in normal and treated conditions, are likely due to the overlapping functions of ScZRC1 and PaMTP1 in storing metals in vacuoles. (DalCorso *et al.*, 2021). The level of NRAMP1.3 expression in the roots of *canescens* × *Populus* was elevated when exposed to ABA treatment. Nevertheless, when the shoots were exposed to Pb, the amount of NRAMP1.3 decreased even in the absence of exogenous ABA (Shi *et al.*, 2019). Research reveals a diverse range of behaviors in metal transporters, greatly influenced by the organ analyzed, the treatment administered, and the specific species studied.

Zinc in Combination with Other Metals

The study explored how varying concentrations of cadmium (Cd) and zinc (Zn) affect their uptake and translocation in plants. Lower Zn levels increased lighter Cd isotopes in plants, with contrasting effects under different Cd conditions. It suggests competitive interactions between Cd and Zn for transport mechanisms within plants (Zhou *et al.*, 2023). Poudel *et al.* (2023) noted similar effects on Mn and Cu and an increase in B content with ZnSO₄ application. The only impact of Zn nutri-priming on sunflower shoots was the increase in Zn content. Studies (Di Gioia *et al.*, 2019; Sahin, 2021) have linked excess Zn application to reduced Fe and N uptake, which impacts chlorophyll content due to Fe's role in chlorophyll synthesis, potentially leading to impaired photosynthetic activity and decreased plant growth. However, because Zn and Ca compete to acquire absorption sites in root regions, additionally, there has been a discussion of a negative relationship between them (Rugeles-Reyes *et al.*, 2019), which varies depending on the species (D'Imperio *et al.*, 2022). According to Prasad *et al.* (2016), an increase in calcium concentration in the culture medium reduces zinc absorption and movement, potentially mitigating zinc toxicity. The deficiency of iron (Fe) and copper (Cu) caused by zinc (Zn) can impact both oxidative and photophosphorylation processes in many plant tissues (Kaur *et al.*, 2021). An adequate supply of zinc (Zn) and boron (B) can also boost the plant's defenses against fungal infection by promoting plant growth and reducing the severity of potato early blight disease

(Machado *et al.*, 2018). Similarly, magnesium (Mg), which serves as a pivotal element in the structure of chlorophyll during plant photosynthesis and facilitates the transportation of photosynthates via the phloem, plays a significant role in the management of diseases in several crops such as rice, poppy, wheat, citrus, potato, and beans (Senbayram *et al.*, 2015).

Photosynthesis and Respiration

Excess zinc reduced the efficiency of PSII (photosystem) and non-cyclic photophosphorylation through structural disruption of the PSII core complex, interaction with the donor side of PSII, or displacement of non-heme Fe in PSII of *Beta vulgaris*, reducing the quantum yield of electron flow through PSII in *Z. fabago* (Kaur & Garg, 2021) and this reduction is due to Zn disrupts the reaction center complexes (Paunov *et al.*, 2018). A decreased rate of electron transfer from QA to QB at the acceptor side of PS II, which lowers the electron flow from PSII to PSI, may cause the harmful effects of zinc on photosynthesis in *Triticum durum* (Paunov *et al.*, 2018). Szopinski *et al.* (2019) found that when exposed to Cd and Zn stress, both *A. halleri* and *A. arenosa* noticed a decrease in electron transport flux and the percentage of active reaction centers. In *Polypogon monspeliensis*, a perennial grass, specific effects on PSII photochemistry have been linked to the competitive dislocation of Mn by Zn in the photolysis of water, impeding electron transport and O₂ evolution (Kaur & Garg, 2021). CaSiO₃ improved the performance of PS II by increasing the number of active reaction centers, the flow of energy through PSII, the size of the Q-pool, and the efficiency of electron transfer, subsequently raising the availability of energy for photosynthesis (Paradisone *et al.*, 2021). In addition, high levels of Zn can disrupt the structure of chloroplasts, leading to a decrease in thylakoid and grana, an increase in plastoglobuli and starch grains, and the breakdown of chloroplast membranes in plants such as *Sedum alfredii* and *Populus deltoides* (Kaur & Garg, 2021). The ratio of chlorophyll a to chlorophyll b has been observed to decrease when exposed to high levels of zinc, indicating that chlorophyll a is more sensitive to zinc stress than chlorophyll b (Garg & Singh, 2018). Since LHC II has more chlorophyll b than PSII chlorophyll-binding proteins, it could be the result of an increase in LHC II (PS II light-harvesting complexes) relative to reaction centers. The inverse relationship between excess Zn and photosynthetic pigments could be due to the suppression of enzyme activity associated with chlorophyll production (Kaur & Garg, 2021). Chlorophyll biosynthesis genes may also be suppressed by ERF VII proteins (group VII Ethylene Response Factors), which are produced in poplar under Zn stress (Carbonare *et al.*, 2019). Reduced root

hydraulic function and a decline in the photosynthetic rate in *B. rapa* cause the stomatal conductance to decrease whenever the plant has high levels of zinc (Fatemi *et al.*, 2020). Kaur & Garg (2021) suggested in their study that the effects of excess zinc on photosynthesis are not limited to a single target; rather, it can set off a series of actions. The primary cause of Zn toxicity in photosynthesis appears to be disrupted mineral nutrition, namely concerning iron (Fe), manganese (Mn), and magnesium (Mg), which subsequently leads to other negative effects. Furthermore, the impacts of excessive zinc on photosynthesis and respiration vary among different plant species.

Zinc Role in Osmotic Equilibrium

Studies have shown that Zn is more effective than alternative treatments in lowering potassium ion levels in leaves, improving photosynthetic pigments, maintaining relative water content (RWC), enhancing stomatal conductance, increasing seed yield, and reducing sodium ion (Na⁺) levels, malondialdehyde levels, and electrolyte leakage percentage. This leads to an increase in strong antioxidant defense activities, which helps plants better tolerate water stress caused by salinity (Osman *et al.*, 2021). The reduced growth and productivity of numerous plants globally, which has contributed to food insecurity, is a result of hyper-osmotic and ionic effects, as well as the overabundance of reactive oxygen species (ROS) under high salinity (Siddiqui *et al.*, 2019). An elevated zinc accumulation in the transgenic shoot lines causes a modest generation of free radicals, imposing oxidative stress and activating antioxidant defense mechanisms that help restrict cellular damage (Ma³ęcka *et al.*, 2019). Plants expressing ScZRC1 may have developed a more effective antioxidant system due to the enhanced activity of antioxidant enzymes, resulting in enhanced tolerance to high levels of zinc (Dal Corso *et al.*, 2021), a heat-shock transcription factor A4a (PuHSA4a), which acts as a positive regulator of high Zn tolerance in transgenic *Populus ussuriensis* (Zhang *et al.*, 2019). Although excessive zinc (Zn) can have detrimental impacts on the environment and organisms, it is not possible to eliminate zinc due to its dual function.

Zinc stress induces the accumulation of glycine, proline, betaine, soluble sugars, and free amino acids known as stress metabolites, in addition to enzymatic and non-enzymatic defensive mechanisms. These metabolites are essential for plants to adapt osmotically and endure high levels of heavy metal stress, such as zinc (Kaur & Garg, 2017). Proline (Pro) content increases as a result of salt, which hinders the soybean's important physiological and biochemical traits such as carotenoid and chlorophyll contents, relative water content (RWC), and antioxidant enzyme activity (Rahman *et al.*, 2021). Also, seed priming

with zinc sulfate and various concentrations of NaCl on the leaf Relative water content and proline content of soybeans were examined by Nowroz *et al.* (2022). According to Kaur & Garg, (2021), an increase in proline and Glycine Betaine in *Lactuca sativa* could be an indicator of Zn stress rather than a resistance mechanism. Numerous other osmotic stress-related metabolites, such as terpenoids, hydroxycinnamic acids, and sesquiterpene lactones, are enhanced under zinc stress (*e.g.*, lettuce) (Kaur & Garg, 2021). The Brazilian native legume trees *Erythrina speciosa* and *Mimosa caesalpiniaefolia* accumulated higher levels of soluble free amino acids in their leaves, suggesting that these species have a tolerance response to zinc stress (Souza *et al.*, 2020). Elazab *et al.*, (2021) demonstrated in bananas that zinc mitigates heavy metal toxicity by preserving chlorophyll and carotenoids, regulating the levels of non-enzymatic antioxidants like ascorbic acid and proline, which help in combating oxidative stress, maintaining protein content, influencing non-protein thiol proteins, and reducing oxidative stress under cadmium stress. Although osmoprotectant accumulation plays important roles in plant adaptation and survival under zinc stress, the results suggest that there is currently no direct genetic evidence supporting osmoprotectant accumulation as a definitive tolerance mechanism.

Zinc Mitigates Heavy Metal Toxicity

Heavy metals like lead, cadmium, mercury, and arsenic seriously threaten plants and human health. These metals have a detrimental effect on plant growth, leading to decreased agricultural yields and contamination of edible items, which can potentially enter the food chain. Heavy metals (HMs) disrupt the physiological and biochemical processes of plants, impair soil health, and negatively affect plant growth (Abdel Salam *et al.*, 2022), HM pollution is a serious issue that requires an immediate and effective solution to minimize its hazards to soils and crops (Alengebawy *et al.*, 2021). Because of anthropogenic activity, its intensity of it has consistently risen (Zainab *et al.*, 2021). The global concern over their mobility and bioavailability arises from the uptake of these heavy metals by plants, followed by an increase in human exposure through the consumption of contaminated foods (Mapodzeke *et al.*, 2021). Recently, a growing problem with heavy metals has caused issues in agriculture. These metals accumulate in the soil and get absorbed by plants, which can seriously disrupt farming. In addition, heavy metals (HMs) cause the denaturation of proteins and enzymes, create an imbalance of nutrients and water, limit plant development and biomass production, and generate reactive oxygen species (ROS), which have the potential to damage plants (Raza, 2020; Sultan *et al.*, 2021; Batool *et al.*, 2022). The formation of ROS, which damages plant

DNA, lipids, and proteins, is one evident result of HM stress. These consequences result in a substantial decline in growth and ultimately end in the death of the plant (Sanjosé *et al.*, 2021).

Zinc is an essential element for the growth of the plant, but it can also dramatically improve a plant's tolerance to heavy metals (HMs) by promoting the accumulation of potential osmolytes, lowering ROS generation (Faran *et al.*, 2019), reducing the uptake and translocation of HMs (Abdelrahman *et al.*, 2021), preserving the integrity of cell membranes and preventing the development of reactive oxygen species (ROS), which can harm plant cells. Additionally, Zn inhibits HM uptake and increases the accumulation of osmolytes (proline) and antioxidant activity (APX, ascorbate peroxidase; CAT, catalase; POD, peroxidase; and SOD, superoxide dismutase). Zinc increases the tolerance of plants against heavy metals by decreasing the translocation of heavy metals within the plant body (Li *et al.*, 2020). Research shows that zinc supplementation has a protective effect against heavy metal-induced toxicity by inhibiting the uptake and movement of heavy metals in plant organisms (Hassan *et al.*, 2022). The findings of Priyanka *et al.* (2021) suggest that ZnONPs, together with Cd and Pb treatments, may protect cotton seedlings from the negative consequences of heavy metal toxicity, ameliorating the toxic effects of Cd on *Triticum aestivum* by enhancing plant growth parameters, and chlorophyll content (Singh *et al.*, 2020). Zinc can attenuate Cu phytotoxicity in plants growing in Cu-contaminated soils at particular ratios (Stuckey *et al.*, 2021). As suggested by Wu C. *et al.* (2020), Zn is an appropriate option for mitigating the toxicity of heavy metals (HMs) and enhancing plant tolerance to HMs.

CONCLUSION

Zinc is a vital micronutrient to both human and plant growth for carrying out various physiological and biochemical parameters. Soil-bound Zinc and bioavailable forms of Zn are essential for assessing the potential threat of zinc transmission along the soil-plant-human chain. Plants use multiple transporters to facilitate the translocation and homeostasis of zinc. In the current era of genomics and proteomics, the use of advanced techniques has made it easier to comprehend the role of Zinc transporters. Plants absorb zinc based on soil properties, metal interactions and zinc-solubilizing microorganisms. It increases osmolytes, antioxidants, and photosynthetic efficiency, which lowers heavy metal uptake and translocation. Overall, understanding the zinc involvement in plant physiology and metal interactions is essential for sustainable crop production and human health.

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