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*Review*

# Unravelling the Efficient Applications of Zinc and Selenium for Mitigation of Abiotic Stresses in Plants

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**Abstract:** Abiotic stress factors are considered a serious threat to various growth parameters of crop plants. Stressors such as drought, salinity, and heavy metals (HMs) hamper the chlorophyll content in plants, resulting in low photosynthesis, hinder the integrity of cell membranes, reduce biomass, and overall growth and development of crops which ultimately results in the sharp decline of crop yield. Under such stressful conditions, various strategies are employed to overcome hazardous effects. Application of Zinc (Zn) or Selenium (Se) in different forms is an effective way to alleviate the abiotic stresses in plants. Zn and Se play a pivotal role in enhancing the chlorophyll level to improve photosynthesis, reducing oxidative stress by limiting reactive oxygen species (ROS) production, controlling HMs absorption by plant roots and their accumulation in the plant body, maintaining homeostasis, and alleviating all the detrimental effects caused by abiotic stress factors. The current review is focused on the usefulness of Zn and Se application, their uptake, sensitization, and different defence mechanisms to relieve adverse effects of abiotic stresses (such as drought, salinity, and HMs) on crops. In this connection, research gaps have also been highlighted.

**Keywords:** abiotic stress; drought; heavy metals; salinity; selenium; zinc

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## 1. Introduction

Stress refers to a change in a physiological condition caused by the modification in equilibrium. It can negatively impact plant growth, development, and productivity, along with a drastic alteration in their morphological, physiological, and biochemical structures. There are several types of stresses, including both biotic and abiotic, that plants face during their whole life span [1]. Abiotic stress can be any environmental factor that causes damage to plant growth and its yield [2]. During the early 1980s, environmental factors were considered responsible factors for decreasing crop productivity by almost 70% [3]. Later, the hypothesis that the reduction in plant productivity was due to abiotic stress was supported by many studies [4,5]. There are multiple abiotic stress factors, viz., heat, cold, drought, salinity, heavy metals (HMs), etc., that cause severe unalterable damage in the agricultural field and finally affect crop productivity [2]. It is always a challenging task for growers to overcome those significant hazardous abiotic stressors under farm conditions.

For the last few decades, to withstand these stresses (such as drought, HMs, salinity, etc.), several methods have been applied either to soil or plants. Among them, the application of zinc (Zn) and selenium (Se) in the form of solution for either plants or soil is one of the most reliable methods to reduce the negative impacts of different environmental stresses on plant growth, development, and its nutritive value [6,7]. Interestingly, Zn or Se deficiency can be harmful to plants, and additionally, it has significant roles in combatting drought [8], salinity [9,10] and heavy metal stresses [11] as well as many biotic stresses [12]. Deficiency of Zn restricts protein synthesis, which in turn results in a reduction in plant root development [7,13]. Shortage of Zn in the soil decreases plant growth by reducing nutrient uptake and water absorption capacity from the soil [14]. Factors responsible for Zn deficiency in the soil include high soil pH, the quantity of phosphorus and bicarbonates in the soil, etc. [15]. Zn and Se are important microelements for plants, showing their regulatory action as cofactors for several enzymes [7,16], and they also control the growth and development of plants.

The nonmetal Se was first discovered by Berzelius in 1817, similar to sulphur, based on its chemical properties. It is regarded as a trace element in both humans and animals. In recent times, the functional roles of Se in plants have been of major interest to many research groups. In plants, both organic and inorganic Se forms are found [17]. Reports have shown that Se can function as an essential micronutrient in plants. The beneficial element Se is shown to enhance photosynthesis, antioxidant metabolism, carbohydrates, and secondary metabolites in leaves of higher plants [18]. Application of Se at a low concentration reduces the reactive oxygen species (ROS) by enhancing the antioxidant mechanism [19]. Other physiological parameters in plants may also be altered to benefit plants by the application of Se at proper concentrations. In this context, the present review emphasizes the strategic application, importance, and beneficial functions of Zn and Se in the mitigation of abiotic stresses in plants.

## 2. Zinc (Zn) and Selenium (Se) Absorption and Transport in Plants

In normal soil conditions, Zn can react with hydroxides, carbonates, and phosphates to form insoluble precipitates. However, a gradual increase in the soil pH decreases the solubility of Zn. Plants can be able to increase their capacity for Zn uptake by gradual acidification of the rhizosphere. The uptake of Zn depends mainly on two key factors, the type of plant species and the composition of the Zn in media. Translocation of Zn takes place via both the symplast and apoplast pathways from the roots to other plant tissues [20]. In most cases, Zn is absorbed by the plant roots in bivalent forms ($Zn^{2+}$). However, in some cases, roots take up Zn in the form of ligand–Zn complexes. Among several approaches to Zn absorption, the first significant one is the outflow of organic acids and hydrogen ions ($H^+$), inducing the liberation of $Zn^{2+}$ ions for the roots of the epidermis to absorb. Another approach is the release of phytosiderophore compounds, which helps in the easy absorption of $Zn^{2+}$ ions by the roots of cereal crops by making stable complexes [21].

There are some dictatorial proteins that help in Zn transportation, such as the ZIP family protein, the heavy metal ATPase (HMA) and metal tolerant proteins (MTP). Among these three kinds of transport protein groups, the ZIP family proteins are known to regulate the absorption of Zn into the cytosol of the cell. On the other hand, members of the MTP protein family promote the segregation of Zn into the vacuoles and endoplasmic reticulum (ER), whereas transportation of $Zn^{2+}$ ions through the apoplast pathway is mediated by the HMA group of transport proteins [19]. Hyperpolarization of root hair cell plasma membrane (RCPM) is the main energy source for the absorption of $Zn^{2+}$ ions, mediated by the action of RCPM $H^+$/ATPase. Such action enhances the external pumping of $H^+$ ions in the rhizosphere, which, in turn, hyperpolarizes RCPM and lowers the pH of the soil, resulting in an increased rate of cation intake [22]. As the transporter proteins are not closely linked to the disintegration of ATP, the mechanism of passive Zn intake (through nonselective channels of cations) is more efficient than the active Zn uptake mechanism [23].

Zn transport through roots starts from the epidermal layer and, after that, reaches the endodermis. From the endodermis, $Zn^{2+}$ ions pass the barriers of the Casparian strip zone and enter the zone of living tissue (pericycle and xylem parenchyma) following the symplast pathway. This living zone of the xylem parenchyma allows continuous functioning of the $H^+$/ATPase system, which eventually induces hyperpolarization of RCPM, resulting in the restriction in $Zn^{2+}$ ion efflux of the cytosol [24].

Se exists in nature in both organic and inorganic forms. Inorganic forms are elemental Se, selenite ($SeO_3^{2-}$), selenate ($SeO_4^{2-}$), and selenide ($Se^{2-}$). On the other hand, major organic forms are SeMet and SeCys [25]. It shares chemical properties with elemental sulfur and thereby can be taken up via sulfate transporters present in the root cells' plasma membrane and assimilated by sulfur-assimilating pathways inside the plants [25]. Finally, it can be volatilized as either Dimethyldiselenide (DMDSe) or Dimethylselenide (DMSe) into the atmosphere [26]. As per the capacity to hold Se inside the cell, plants can be broadly classified into non-accumulator (can accumulate less than 100 mg Se per kg dry weight), secondary accumulator (can accumulate 100–1000 mg Se per kg dry weight), and hyperaccumulator (can accumulate more than 1000 mg Se per kg dry weight) [26]. Younger leaves show higher Se content than older leaves [27], and the vacuole is the main storehouse of Se inside the plant cell [28]. The uptake and distribution of Se in the plant tissue need further investigation to find their transporter proteins and other related factors. The simplest possible routes of Zn and Se uptake and their downstream movement in plants are depicted in Figure 1.

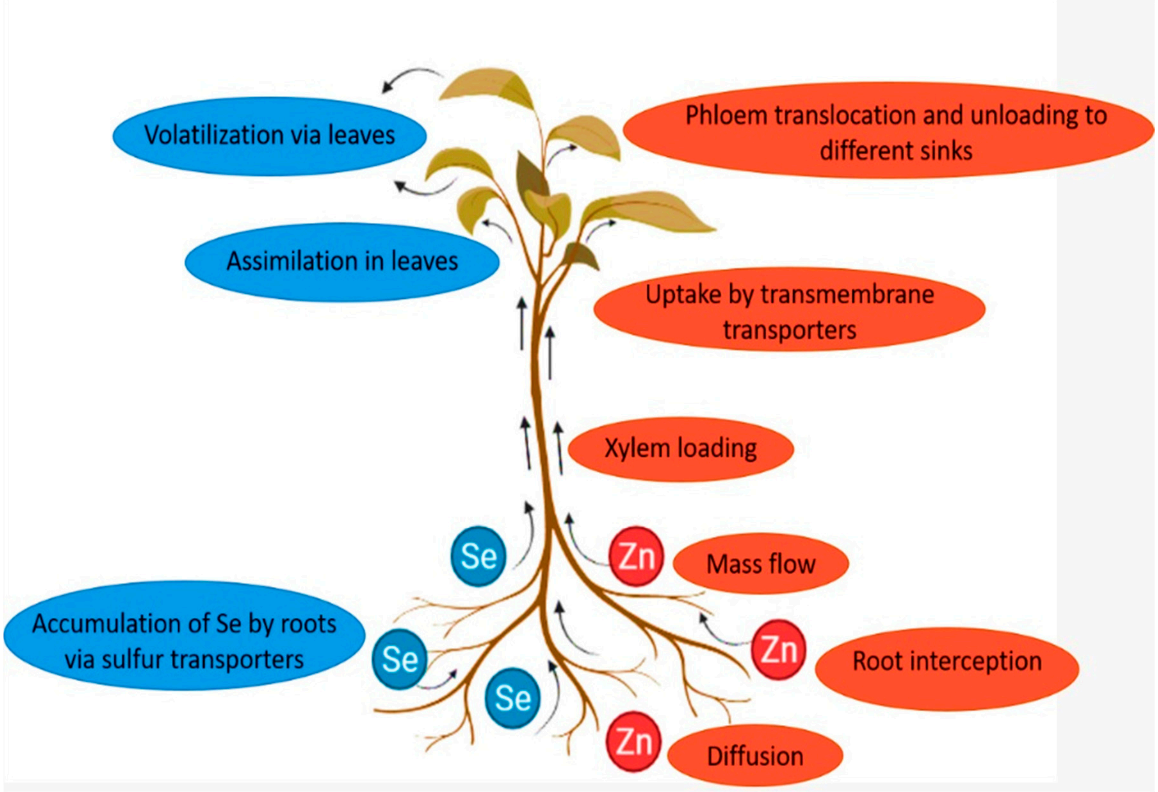

**Figure 1.** Zinc and selenium uptake and transport in plants.

## 3. Importance of Zinc and Selenium and the Effects of Their Deficiency on Plants

Zinc and Selenium are the most important micronutrients for plant growth and crop productivity (Figure 2). The average requirement of Zn by the plants lies between 15 and 55 ppm [20]. However, in Se-rich soil, the plant is able to intake 55–200 µg per day [26]. Improvement in the quality and quantity of the crops has been noticed after the application of Zn or Se to the soil [29–31]. The deficiency of Zn or Se in the soil affects the quality of the crop and also its yield [32]. The application of Zn directly on the leaves of wheat seedlings promotes plant growth and development under critical conditions [33]. It is also helpful in enhancing the chlorophyll content and the rate of photosynthesis in cauliflower plants, consequently advancing plant growth [34]. Similar to Zn, Se promotes the content of chlorophyll and overall growth by reducing oxidative damage in plants. At low concentrations, Se plays an important role in regulating the structure of chloroplast and the fluidity of plasma membrane [35] and delaying senescence. Se induces the absorption of essential macro- and micronutrients in plants. Zn and Se are both considered excellent stress-managing nutrients for a wide variety of crops. They are able to mitigate several abiotic stresses such as salinity [9,10], drought [8], and heavy metal [11], and biotic stresses such as herbivores and pathogens [12]. The positive effects of Zn and Se have been summarized in Figure 2.

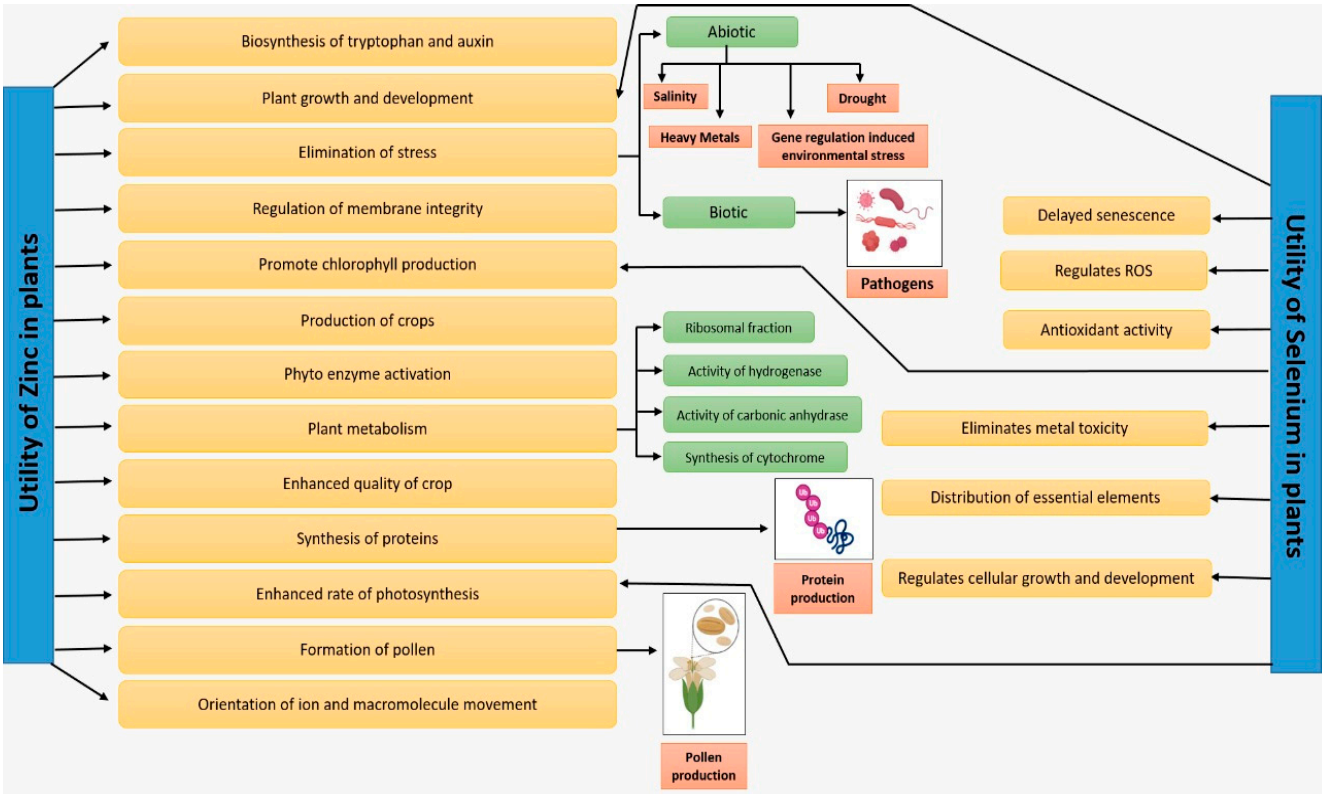

**Figure 2.** Positive effects of zinc and selenium in plants.

Zn is also useful in contributing to the pigmentation of leaves. However, there are several effects of Zn deficiency observed in different plant parts (Figure 3). Discolouration of leaves (i.e., chlorosis) is an indicator of Zn deficiency in the soil. Such discolouration may start at the bottom parts of plants and then gradually spread to the upper parts of plants [20]. At first, after two to four weeks of the sowing of rice seedlings, the initial symptom of chlorosis appears along the midrib region of the leaves, and then gradually, brown spots are observed on the older leaves. Later, these spots elongate, integrate, and provide brown colouration of the leaves. Loss of turgidity is one of the most notable symptoms of Zn deficiency [6]. Zn can regulate the hydrogenase and carbonic anhydrase activity and maintain ribosomal fractions and cytochrome synthesis, which, in turn, play a key role in controlling plant metabolism [36]. Zn activates plant enzymes, helping the conservation of cellular membrane integrity, synthesis of protein, formation of pollen, and balancing the synthesis of auxin [37]. It plays an important role in plants by helping them tolerate several environmental stresses by regulating genes and perpetuating gene expression [36]. Synthesis of a vital plant growth hormone IAA (indole acetic acid) or auxin and its precursor tryptophan is dependent on Zn [38]. Zn is also required for the coherence properties of cellular membranes to conserve the fundamental orientation of macromolecules and ion movement status. It links to the sulfhydryl groups and phospholipids of the transmembrane proteins and ultimately helps regulate the entire membrane [35–38].

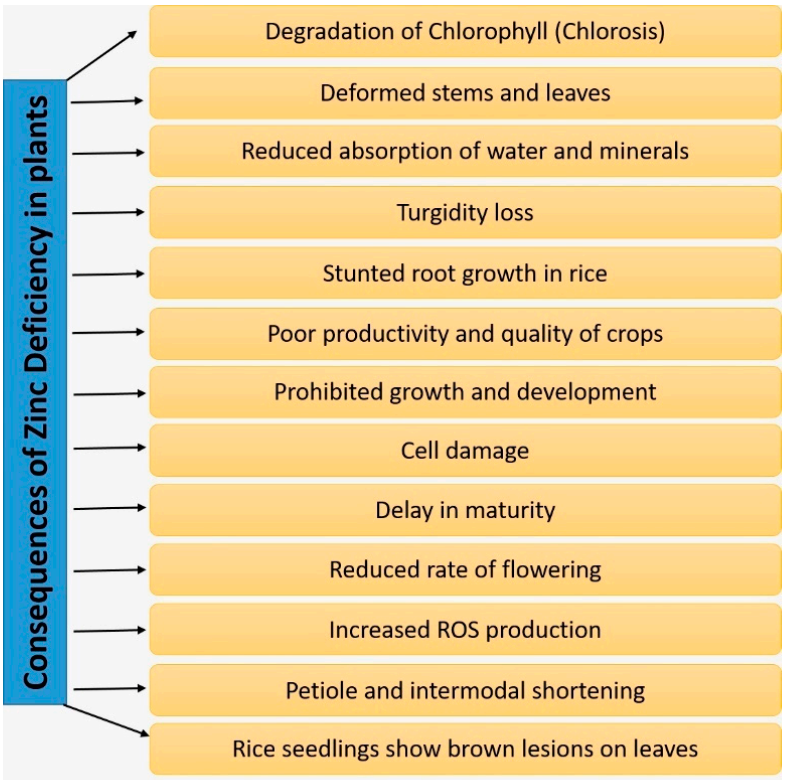

**Figure 3.** Deficiency effects of zinc in plants.

The quality and productivity of most of the crops are directly proportional to the application of Zn as a mineral nutrient in the soil [39]. There are certain factors responsible for decreased amount of Zn in the soil, such as high $CaCo_3$ content, high pH, phosphate, clay [40], the content of organic matter, type of crop, and the cultivars [6]. Zn deficiency is generally found in some specific types of soils, for example, sandy soils, calcareous soils, soils with a high amount of silicon and phosphorus, and peat soils [14,38]. Numerous visible symptoms of Zn deficiency usually appear up to two to three weeks from the time of the transplantation of the seedlings [41,42]. Such instances have been revealed in some studies with rice seedlings, in which symptoms such as the development of brown-coloured blotches on leaves, stunted growth of the seedlings, a significant delay in maturity, reduced productivity, diminished length of internodes and petioles, and deformed leaves (small in size) and stems have been common. Such distorted-shaped leaves sometimes may appear as 'rosette', and stems exhibit fan-shaped structures in the early stages of monocots and dicots, respectively [43]. Moreover, severity may even lead to the death of the rice seedlings [44–46]. The correlation between Zn and nitrogen metabolism in plants has been closely observed by many researchers. It is stated that a deficiency of Zn in the soil directly affects root development in lowland rice seedlings [13]. Apart from the root system, a considerable decrease in the absorption of both water and minerals from the soil, reduction in plant growth and crop productivity [14], depletion in the blossoming process [6], high production of ROS, and cell damage [47] have also been noticed in plants as a result of Zn deficiency.

The complex relationships among soil Se concentrations, geology, uptake, and effects in plants, and biofortification in animals were primarily examined in the early stages of research. It has been observed that the varying degree of Se concentration in the soil can produce Se-rich crop plants, which may have toxic effects on livestock. On the other hand, it is also evident that the presence of Se in high doses may also alter the natural growth and development of plants. Plants may suffer because of Se toxicity to various extents. Their growth is generally stunted, and plants may die prior to the normal ones. Mostly the leaves show symptoms in the affected plants and may exhibit chlorosis. Sometimes drying and withering of leaves were observed, caused by the high toxic concentration of Se in the soil. On the other hand, few plants are able to safely accumulate huge amounts of Se into different storage organs, while others cannot. Furthermore, the effects are completely reversed in the absence of Se in soil. As the requirement of Se for regular plant metabolism is minimal, there are no such prominent Se-deficiency effects observed in plants. However, the quality and productivity may be hampered [31].

## 4. Process of Zn and Se Application, Its Downstream Effects on Plants

There are several methods tested for the safe application of Zn to the soil or the plant. However, the process of absorption of Zn by plants mainly depends on the type and form of the soil [20]. The soil containing a relatively larger amount of sand possesses a lower Zn absorption capacity compared with the soil containing more clay. The Higher Zn absorption capacity of the clayey soil is regulated by its higher CEC value (i.e., an estimation of the soil's absorption and retention of water). So, eventually, the sandy soil (lighter in weight) has a lower CEC value. As the clayey soil has a high CEC value and has the ability to fix more Zn, it results in the unavailability of this mineral nutrient for the plants [6].

Zn and Se can be implemented in various ways (Figure 4), for instance, by spraying the leaves in the agricultural field and using Zn powder or solution on the seeds [6]. Sometimes plant leaves are treated with Zn sprinkled upon them, by which Zn can be easily absorbed by plant leaves (most commonly used method). Foliar Zn application (1.5 kg ha$^{-1}$) is reported as the easiest and most economical way to improve the yield of maize and wheat [48]. According to Leach and Hameleers [49], a remarkable increase has been observed in the starch quantity and crop yield in corn after the foliar application of Zn (140 g Zn L$^{-1}$). Similar to Zn, foliar and soil applications of Se are very useful for crop plants. According to Boldrin et al. [50], the quantity of Se in the soil increases because of its application directly to the soil. They also showed that foliar application of Se in the form of selenate and that, consequently, selenite enhances the productivity of rice. However, soil application of Se was found to be more effective than its foliar application for the production of shoot dry matter. Impact of Zn and Se application on plants has been summarized in Table 1.

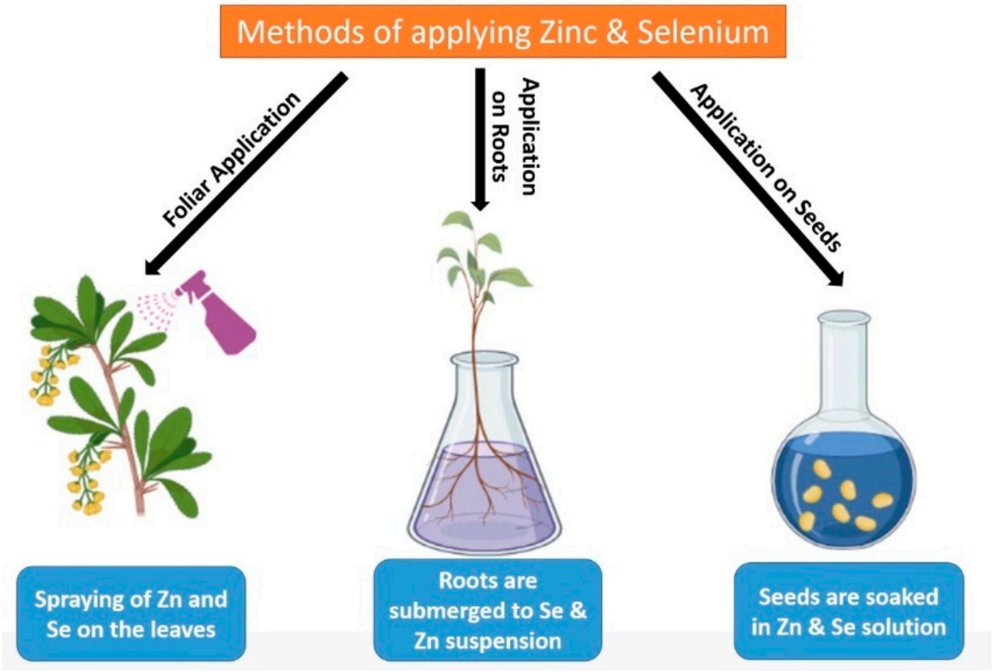

**Figure 4.** Methods of application of both Zn and Se in plants.

**Table 1.** Impact of Zinc and Selenium application on plant leaves and soil.

| Name of Plant. | The Part on Which Zn Is Applied | Utilities as a Result of Zn Application | References |
|---|---|---|---|
| Maize | Foliar application | Increases starch content<br>Improves crop yield | [46] |
| Mungbean | Foliar application | Increases the growth and productivity of the crop | [48] |
| Maize and Wheat | Foliar application | Enhances the yield of both the grains | [45] |
| French Bean | Foliar application | Improves in the physiological traits<br>Enhances crop quality<br>Improves productivity of grains | [49] |
| Maize | Soil | Advances crop yield | [51] |
| Wheat | Soil | Increases in grain productivity | [52] |
| Wheat | Foliar + soil | remarkable boost in the yield | [27] |
| Bread wheat | Foliar + soil | Improves the growth rate<br>Enhances crop productivity<br>Increases Zn content in wheat | [28] |
| Garden pansy | Foliar application of Se in the form of sodium selenate | Increases fresh weight by 25.10%<br>Increases dry weight by 25.41% | [51] |
| Rice | Foliar application of Se in the form of selenate and selenite | Enhances the productivity of rice grains | [47] |
| Rice | Soil application of Se | Produces more shoot dry matter | [47] |
| Oat | Foliar + soil application of Se in the form of Se fertilizer | Improves Se transport<br>Enhances crop yield | [52] |
| *Atractylodes macrocephala* | Foliar application of Se | Increases the growth and survival rate<br>Enhances crop yield | [53] |

Another study stated that foliar application of Zn in the form of Zn-EDTA (300 ppm) is able to increase the growth rate and productivity of mungbean [54]. Improvements in the physiological trait, quality, and productivity have been noted in beans (*Phaseolus vulgaris* L.) as a result of foliar application of Zn with 3 mg $L^{-1}$ [55]. Soil can be fortified with a larger quantity of Zn as a mineral nutrient by direct spray [56]. Soil supplied with Zn (12 kg $ha^{-1}$) exhibited improvement in the maize yield [57]. This is supported by another study in which it is clearly documented that the application of Zn (15 kg $ha^{-1}$) to the soil shows a crucial increase in the productivity of wheat grains [58]. Sometimes a combined Zn application to both leaves and the soil enhances the results. For instance, soil treated with 50 kg $ZnSO_4$ $ha^{-1}$ and leaves with 0.5% $ZnSO_4$ together resulted in a remarkable boost in the yield of wheat seedlings [29]. Improvement in the growth rate, productivity, and the content of Zn have been found in bread wheat after the application of Zn treatment to both the soil and leaves (50 kg $ZnSO_4$ $ha^{-1}$ in soil + 0.5% $ZnSO_4$ prepared from 0.3 M $ZnSO_4$) [30]. In other cases, seeds are treated with either Zn powder or Zn solutions, allowing the seeds to soak in those [6]. This way of Zn application to the seeds increases the rate of germination, growth rate, as well as yield [59]. However, when seeds are treated with a high concentration of Zn (2 g Zn $kg^{-1}$ seed), seed germination and growth are severely affected [60]. There is another way for plant roots to absorb Zn, in which plant roots are immersed in the suspension of Zn salts [6].

## 5. Role of Zn and Se in Plants under Drought Stress

Drought stress is one of the most noteworthy abiotic stresses on plants causing many devastating effects on a variety of crops (Table 2). All the growth stages, and specifically one reproductive stage, i.e., the grain-filling stage of wheat, are adversely affected by drought stress [61]. The active functions of some enzymes responsible for sucrose and starch synthesis end as a result of terminal drought stress [62,63]. It damages the capacity of nutrient uptake, transportation, and absorption, thus affecting the entire nutrient relation in plants [64]. Drought is responsible for promoting oxidative stress as a result of ROS, such as hydrogen peroxide, superoxide, etc., which are produced excessively, disrupting the biological membrane [65–67]. It damages plant growth and development, plant–water relations, and stability of cell membrane, and lowers the photosynthetic rate [8].

**Table 2.** Impact of drought stress on a variety of plants.

| Name of Plant Affected by Drought Stress | Effect of Drought Stress on the Crop | References |
|---|---|---|
| Wheat | Affects all growth stages<br>Affects the grain-filling stage of reproduction | [55] |
| Spring wheat | Terminates the enzyme activities responsible for sucrose and starch synthesis | [57] |
| Wheat | Damages nutrient uptake capacity<br>Disrupts nutrient transport and absorption<br>Affects plant-nutrient relation | [58] |
| Maize | Damages growth and crop yield significantly | [62–64] |
| Tomato | Prevents stomatal closure | [65] |
| Maize | Provokes several morphological changes in the crop | [66] |
| Legumes | Decreases water absorption capacity<br>Reduces the rate of gaseous exchange<br>Hampers crop productivity | [68] |
| Lentils | Affects stomatal movement<br>Ultimately results in the drooping of leaves | [68,69] |
| Chickpea | Damages penetrability of the membrane, nutrient intake, rate of chlorophyll synthesis, and photosynthesis | [70,71] |
| Barley | Reduces crop yield | [72] |

The growth and yield of maize are critically damaged by drought stress [68–70]. It provokes several morphological, physiological, and biochemical changes in crop plants [71–73]. In the case of leguminous plants, drought stress causes a decrease in the water intake capacity and rate of gaseous exchange, which ultimately leads to hampered crop yield [74]. It also affects stomatal movement and gradually results in the drooping of leaves [74,75]. Besides these, certain critical factors, such as penetrability of the membrane, nutrient intake, rate of chlorophyll synthesis, and photosynthesis, are disrupted remarkably during drought-stressed conditions [16,76–78].

Zn application triggers many parameters which are useful for the plants to overcome a number of drought-induced damaging effects (Figure 5). Exogenous foliar application of Se has been very successful in boosting the growth of wheat under drought-stressed condition. Herein Se was used in the fabricated form. It is reported that a 30 mg/L dose is efficient in improving morphological attributes such as root and shoots length, fresh and dry weight, etc. When the dose is increased to 40 mg/L, it shows diminished growth of wheat plants [79].

The osmotic adjustment strategy includes an accumulation of a few low molecular weight substances, such as L-proline, soluble protein, and soluble sugar [8]. Accumulation of proline provides protection to the cells and enzymes that are required for osmoregulation and also saves plants from osmotic stress [80]. Soluble proteins and soluble sugars can enhance the water retention power of the plant roots by reducing the drought-mediated damages, such as movement of stomata for efficient $CO_2$ absorption, turgidity of leaf, etc. [81,82]. The expression of Zn finger proteins is induced by the addition of Zn, which ultimately promotes the accumulation of soluble sugars and proline under drought stress in rice and cotton [5,83,84]. Zn application is also useful to enhance the leaf–water relation under drought-stressed conditions in red cabbage and tomato [85].

Under water deficit conditions (drought stress), Zn application results in an increase in WUE by regulating leaf temperature and stomatal conductance [8], enhancing the rate of photosynthesis and transpiration [86]. Under drought stress, photosynthesis is induced by the stabilization of membrane permeability and integrity by the application of Zn on wheat plants [87]. It is reported that exogenous Zn application shows a remarkable increase in the Zn content in wheat leaves under drought stress [88]. Foliar and soil application of Se also showed some excellent results in combating drought stress in potato plants [89]. They reduced the irrigation level to create water-stressed conditions. Both proline and soluble sugars showed a remarkable increase under drought stress. Potato tubers also showed a notable increase in the WUE under a water-stressed situation (Figure 5). By enhancing nutrient status, antioxidant activity, activities of photosynthetic pigments, and total phenolic content, Se nanoparticles help the plant overcome drought stress in pomegranates [90]. Se application successfully controls the water status in plants under drought-stressed conditions [91].

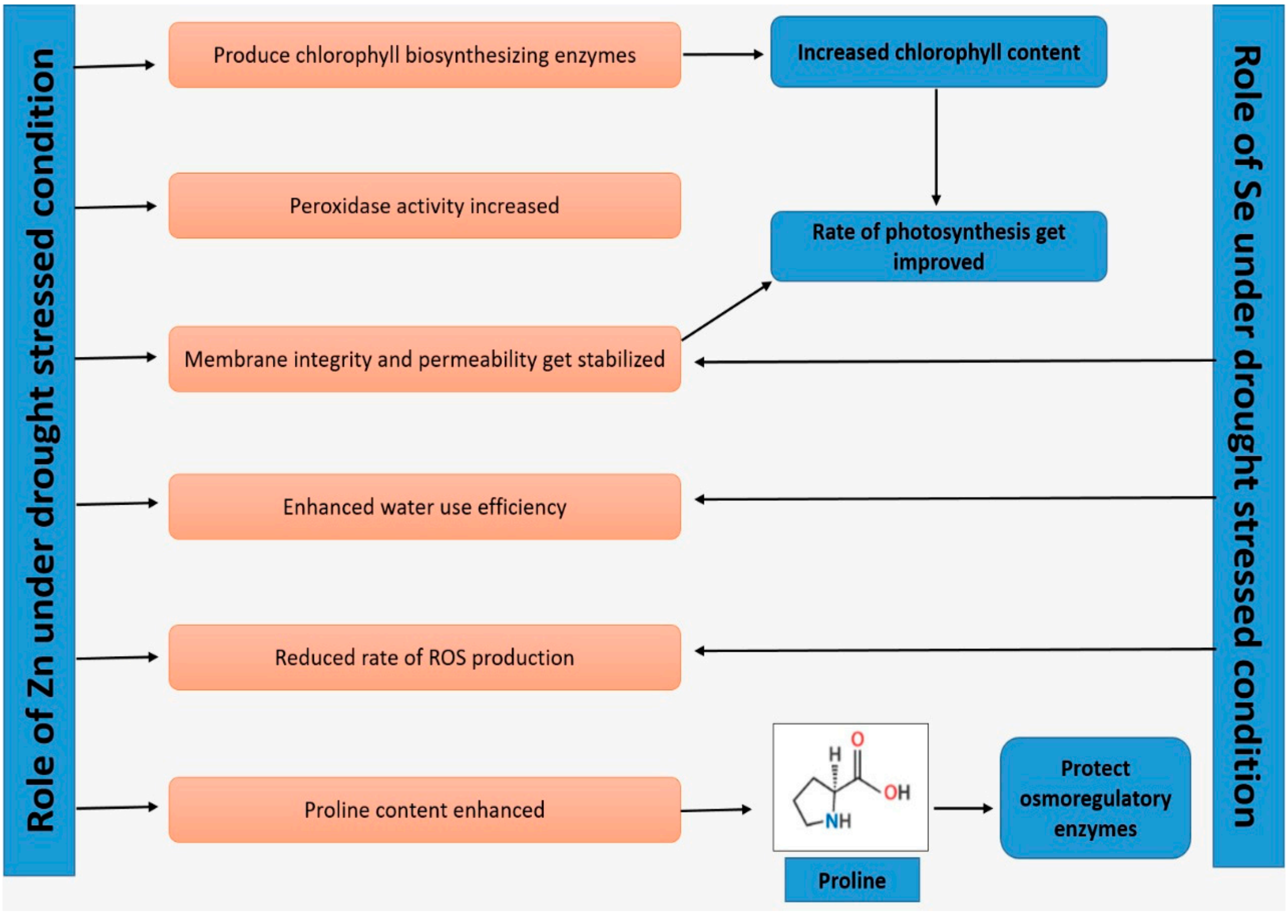

**Figure 5.** Diagram showing how Zn and Se help the plants alleviate and overcome the adverse effects of drought.

In similar stress conditions, Zn application has successfully shown enhancement in nutrient uptake, especially of manganese and iron [92]. Zn can enhance drought tolerance in maize by improving melatonin content [93]. Application of Zn under water-stressed conditions shows improvement in the expression of root aquaporins (known as PIP or plasma membrane intrinsic proteins), such as PIP1 and PIP4 [94].

## 6. Role of Zn and Se in Plants under Salinity Stress

Salinity stress or salt stress in the soil is one of the most common factors well known for its several deleterious effects on a variety of plants. Salinity in the soil makes it really difficult to produce a significant amount of crops [95]. It leads to an increase in sodium and chloride ions in the soil in considerable amounts [96]. Salt stress is one the major reasons for nutrient imbalance both in the soil and crops, which eventually results in the inhibition of enzymatic actions, membrane damage, and may even lead to plant death [97]. Salinity stress enhances the toxicity level of ions in the soil and decreases the accumulation of essential nutrients, as a result of which water availability is reduced in crop seedlings [98].

Among all the essential micronutrients, Zn is known for its ability to alleviate salinity stress in the soil for better growth of crops [99]. Al-Zahrani et al. [9] used *Vigna radiata* (L.) Wilczek seedlings as their experimental plant material. They compared the effects of salt stress in the control set of mung beans (without Zn treatment) to salt-stressed mung bean seedlings with Zn treatment. From this comparative study, they reported less oxidative damage in the Zn-treated mung bean seedlings than in the control set. They also concluded that salt-stressed plants with Zn treatment show more enzymatic activity in comparison with mung beans with Zn application. In this way, Zn improves tolerance against salt stress. Hussein and Abou-Baker [10] studied the contribution of nano Zn in cotton plants under salinity stress. They used nano Zn as soil fertilizer in their study and found some positive responses. At the end of their experiments, they concluded that nano Zn-treated cotton leaves could alleviate the detrimental effects of salt stress by enhancing growth rate and productivity.

Under high salinity stress, the application of nano Zn to the soil enhanced crop productivity in Triticale by 39% compared with the control set without nano Zn addition [100]. Significant improvement in fresh weight and dry weight in rice [101], production of biomass in sunflower [102], and crop yield in wheat [92] have been reported under salt stress as a result of the application of nano Zn at the rates of 25 or 50 $\text{mgl}^{-1}$.

On the other hand, Alharby et al. [103] used soybean to show the effects of salinity stress and also the role of Se in mitigating the damage caused by salt application to soybean plants. As per their study, foliar application of Se exogenously enhanced some antioxidant enzyme activities such as catalase (CAT), peroxidase (POD), and glutathione reductase (GR) (Figure 5), together with a few nonenzymatic antioxidants such as glutathione (GSH) and GSH/glutathione disulfide (GSSG). As a result, soybean plants dispose of the adverse effects of oxidative damage by activating an antioxidant defence mechanism. Instead of individual application of Se and Zn, El-badri et al. [104] used Se and Zn together in the form of oxide nanoparticles (SeNPs and ZnONPs) to show their combined role in combating salt stress in *Brassica napus* during the early stage of germination. In this study, SeNPs and ZnONPs exhibited significant elevations in the rate of germination, antioxidant enzyme activity, the microstructure of the seeds, and an overall improvement in plant growth and development under salt stress. Reports have also shown significant promotion in the growth and rate of photosynthesis in tomato seedlings with the application of Se under salt stress by boosting chloroplast antioxidant defence mechanisms [35].

## 7. Role of Zn and Se in Plants under Heavy Metal Stress

Similar to other abiotic stresses, heavy metal stress has been a burning issue in recent times because of uncontrolled industrial activities, rapid urbanization, excessive use of sprays, pesticides, and fertilizers in the agricultural fields, the release of heavy metal wastes to the nearby water bodies, and so on. As a result of all these factors, the quality and productivity of the crops become severely impaired [105–107]. Agricultural soil contains a number of heavy metals such as cadmium (Cd), copper (Cu), chromium (Cr), nickel (Ni), lead (Pb), etc. [108]. These heavy metals cause damage in crop plants, including a decrease in root growth, loss of plant biomass, chlorosis, reduction in dry weight, etc. Several strategies have been used to keep heavy metal stress under control, of which the first effective way is to reduce or cease the metal uptake from the soil or alleviate the bioavailability of the heavy metals present in the soil. It results in the hindrance of the heavy metal entrance through the plant roots [109]. The second strategy is to tolerate the heavy metal stress and also to limit heavy metal accumulation and movement from the roots upwards to other plant parts [110].

Zn is a transition heavy metal [111], and it is able to decrease HM toxicity in crop plants by restricting the bioavailability of those HMs; homeostasis is well maintained in the plant tissues [112]. Unlike other HMs, Zn plays an important role in plant growth and development [113]. It can trigger many enzymes responsible for the synthesis of proteins and metabolic activities of lipids and nucleic acids [114]. Zn limits the toxic radical production by being tightly attached to the cellular membrane [15,40,115]. In this way, Zn plays a pivotal role in the amelioration of the HMs stress. The application of Zn in various host and HM stress conditions is summarized in Table 3. For example, in accordance with Hafeez et al. [6], Zn contributes to the reduction in Cu-caused toxicity and the improvement in the Zn absorption and translocation in several plants.

**Table 3.** Effects of Zn and Se against HMs in different plant species.

| Name of Plant Species | Name of Microelement Showing Ameliorating Effects | Name of Heavy Metal | Ameliorating the Role of Zn against That Heavy Metal | References |
|---|---|---|---|---|
| Rice | Zn | Cu | Reduces Cu-induced toxicity<br>Decreases oxidative stress | [110] |
| Rice | Zn | Cu | Reduces oxidative damage<br>Impedes phytotoxic symptoms in rice | [113,114] |
| Rice | Zn | Cd | Enhances chlorophyll content and rate of photosynthesis<br>Increases plant biomass<br>Improves overall growth | [111] |
| Wheat | Zn | Cd | Reduces Cd-induced toxicity to the growth parameters | [112] |
| Tomato | Zn | Cd | Limits Cd accumulation<br>Reduces Cd-induced toxic effects | [115] |
| *Ceratophyllum demersum* | Zn | Cd | Attenuates membrane damage<br>Reduces oxidative stress | [116] |
| Bread wheat and durum wheat | Zn | Cd | Alleviates Cd toxicity | [117] |
| Angiosperms | Zn | Cd | Alleviates Cd toxicity | [118] |
| *Chara australis* | Zn | Cd | Diminishes Cd uptake and accumulation | [119] |
| Marigold | Zn | Cd | Diminishes Cd uptake and accumulation | [120] |
| Bread wheat and durum wheat | Zn | Cd | Treats chlorosis and necrosis induced by Cd | [121] |
| *Brassica napus* and *B. juncea* | Se | Cd | Improves Cd accumulation capacity | [122] |
| Pepper | Se | Cd | Enhances the antioxidant activities | [123] |
| Rape seedlings | Se | Cd | Reduces Cd stress | [116] |
| Ramie (*Boehmeria nivea* (L.) Gaud | Se | Cd | Enhances antioxidative capacity in) | [117] |

There is also evidence that Zn can reduce Cu stress in rice seedlings (*Oryza sativa* L.). Zn reduces the toxicity caused by Cu in rice by regulating oxidative stress with the help of its oxidative mechanism [118]. Cd stress is also controlled by Zn in rice [119] and wheat [120] seedlings by inducing oxidative stress. Cd affected the biomass, rate of photosynthesis, and the overall growth of rice plants, whereas Zn has been able to improve all the parameters by showing enhanced chlorophyll content, photosynthetic rate, and also biomass and overall growth [119]. Application of high concentrations of Zn to the soil resulted in a reduction in Cd-induced toxicity in the growth parameters of winter wheat cultivars [120].

Cu causes oxidative damage and promotes phytotoxic symptoms in rice, which is impeded by the application of Zn in higher concentrations [121,122]. The relationship between Zn and Cd has been observed by Cherif et al. [123] in tomato plants, in which Zn has significantly limited Cd accumulation and decreased the toxic effects caused by Cd. According to the study by Arvind and Prasad [124], Zn attenuates membrane damage and oxidative stress in *Ceratophyllum demersum* caused by Cd toxicity. Ameliorating actions of Zn against Cd toxicity have also been reported in bread and durum wheat [125] as well as in angiosperms [126]. Uptake and accumulation of Cd are diminished in *Chara australis* [127] and marigold (*Calendula officinalis* L.) plants [128] by Zn treatment. Cd-mediated chlorosis and necrosis are defended by the action of Zn in the bread wheat and durum wheat seedlings [129].

Besides Zn, Se has also shown some magnificent results in alleviating the HMs stress in plants, especially against Cd. For instance, improvement in Cd accumulation capacity (Figure 5) has been observed in two species of the mustard family, *Brassica napus* and *Brassica juncea* [130]. For the purpose of the experiment, they used three different valence states of Se, and these are Se(II), Se(IV) and Se(VI), among which Se(II) showed the best results in decreasing Cd toxicity in *Brassica*. Reports revealed the effects of Se supplementation to reduce oxidative damage caused by Cd and Pb in oilseed rape plants. Se has an efficient role in decreasing Cd toxicity by enhancing the antioxidant activities in pepper leaves. Under Cd-stressed conditions, Se has a noteworthy contribution to plant growth [131].

## 8. Role of Se in Plants to Overcome Heat Stress

Among all the abiotic stresses, heat stress is a prime concern for soil fertility and agricultural growth across the globe. It has many adverse effects on the plants, which include damaging cell division and cell cycle, reduction in the height of the plant, and decreasing crop yield in wheat [132]. Heat stress directly affects some major target sites for photosynthesis, such as Rubisco, Photosystem II (PS II), Cytochrome b 559, and Plastoquinone, which eventually leads to a reduction in crop productivity [133]. In this state, it is of utmost importance to keep the heat stress-derived adverse effects under control. When techniques such as genetic engineering, QTL mapping, hybridization, and molecular-assisted selection were not fully successful in mitigating heat-caused effects either because of their operational problems or high cost, the introduction of biogenic Se nanoparticles showed some excellent results. The addition of biogenic Se nanoparticles at a concentration of 150 mg/L enhanced heat resistance greatly in chrysanthemum [134]. Apart from that, there are many reports which confirmed the beneficial contribution of Se applied at a lower concentration. It has been documented that Se application at a low dose has improved the physiology and biochemistry of the crops such as soybean, wheat, and mung bean under heat-stressed conditions. Studies also reported that Se nanoparticles diminish the deleterious effects of heat stress in sorghum [127].

## 9. Conclusions and Future Prospect

Abiotic stress factors have several deleterious effects on different parameters of crop plants. Zn and Se act as major contributing factors in defence against different abiotic stresses by inducing the enzymes involved in chlorophyll synthesis, bringing stability to membrane permeability and integrity, reducing ROS production to keep oxidative stress under control, etc. These two most important micronutrients also play a vital role in plants against biotic stresses. Sometimes, both express their protection to some crops by the presence at low concentrations, whereas in some other cases (especially in hyperaccumulating plant species), higher or even toxic concentrations of Zn or Se result in efficient defence mechanisms against both abiotic and biotic stress factors.

Although plenty of findings related to the contributions of Zn or Se to the plants under several abiotic stresses are available, the reports about the resistance ability of Zn or Se against biotic stresses are quite limited so far. Different toxic effects of Zn and Se on plants and the environment should be given more attention. Remediation of toxic effects in different ways may open a new area for future research. Studying different Zn and Se transporters, along with the mechanism of translocation in plants, may put some light on their phytotoxicity. Different omics approaches nowadays, along with gene identification, may initiate more precise areas of research in plant physiology. Moreover, the ameliorating role of Zn or Se has been discussed against very few HMs. Therefore, more detailed and extensive investigations are required to clarify the alleviating role of Zn or Se against other groups of HMs. Further studies are also needed to elucidate the interplay between Zn and Se in plants against different abiotic stresses. Nevertheless, finding out the common cascades of Zn and Se in plants may be able to solve numerous problems related to plant stress.

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