Review

An Overview of Hazardous Impacts of Soil Salinity in Crops, Tolerance Mechanisms, and Amelioration through Selenium Supplementation

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Abstract: Soil salinization is one of the major environmental stressors hampering the growth and yield of crops all over the world. A wide spectrum of physiological and biochemical alterations of plants are induced by salinity, which causes lowered water potential in the soil solution, ionic disequilibrium, specific ion effects, and a higher accumulation of reactive oxygen species (ROS). For many years, numerous investigations have been made into salinity stresses and attempts to minimize the losses of plant productivity, including the effects of phytohormones, osmoprotectants, antioxidants, polyamines, and trace elements. One of the protectants, selenium (Se), has been found to be effective in improving growth and inducing tolerance against excessive soil salinity. However, the in-depth mechanisms of Se-induced salinity tolerance are still unclear. This review refines the knowledge involved in Se-mediated improvements of plant growth when subjected to salinity and suggests future perspectives as well as several research limitations in this field.

Keywords: salinity; selenium (Se); crops; reactive oxygen species (ROS); enzymatic anti-oxidative system

1. Introduction

Various abiotic stresses, such as drought, heat, heavy metals, soil salinity, flooding, and cold, are responsible for the reduction of the growth, development, and productivity of crops worldwide [1]. Soil salinity is an overwhelming environmental threat to world food production and agricultural sustainability [2]. A soil with an electrical conductivity (EC) of saturated soil paste extract (ECe) in the plant root zone more significant than 4 dSm−1 (about 40 mM NaCl), 0.2 MPa osmotic stress [3] and
an exchangeable sodium percentage (ESP) of 15% at 25 °C is termed as salt-affected soil [4]. Some of the most discussed reasons for soil salinity are poor soil-sustainable practices, excessive saline water irrigation and a severe usage of mineral fertilizers in arid and semi-arid regions (characterized by high evapotranspiration, high temperature, and low rainfall) across the globe [5]. The area under soil salinity is further enhanced by the conversion of fertile agricultural land into urban area, placing the efforts of scientists to produce 70% more food to feed the population of the world in 2050 of 9.3 billion at risk [6]. In 2001, almost 7% of the soils of the entire world were salt-affected in nature [7]. Globally, salinity is a significant abiotic stress, affecting one-quarter to one-third of the crop productivity of agricultural soils [8]. It was estimated in 2003 that up to the middle of the 21st century, the salinity-induced loss of cultivated soil will reach up to 50% [9]. In 2008, it was reported that, due to high salinization, 77 million hectares of the world’s total cultivated area (1.5 billion hectares) was adversely affected [10]. At present, about 10% of the global land area and 50% of irrigated areas are exposed to salinity, causing a loss of about 12 billion US$ in the agricultural sector [11].

Soil salinity is a complex mechanism that is responsible for adverse effects on the physiological and biochemical pathways of crop plants [12]. Excess accumulation of Na⁺ induces efflux of cytosolic K⁺ and Ca²⁺, consequently, leading to imbalance in their cellular homeostasis, nutrient deficiency, oxidative stress, retarded growth, and cell death [13]. It has been reported in many previous studies that a high level of salinization drastically affects plant photosynthesis due to some stomatal restrictions; for example, stomatal closure [4] and/or non-stomatal restrictions comprising chlorophyll malfunctioning [14], deprivation of enzymatic proteins and membranes of photosynthetic apparatus [15], and chloroplast ultrastructure destruction [16]. Salt-affected soils have higher Na⁺/K⁺ and Na⁺/Ca²⁺ ratios because of the higher amount of Na⁺ in the soil solution. Hence, a reduction in K⁺ and Ca²⁺ uptakes cause the inhibition of the proper functioning of the cell, instability of cell membranes, and hindrance of enzymatic activities [17]. Moreover, some other secondary stresses, such as oxidative stress followed by osmotic pressure and ionic toxicity, are involved in the production of excessive reactive oxygen species (ROS) in cytosol, chloroplast, and mitochondria [2,4] such as O₂⁻ (superoxide radicals), H₂O₂ (hydrogen peroxide), O₂ (singlet oxygen) and OH⁻ (hydroxyl ions). These reactive oxygen species with strong oxidation ability can cause injuries to plant tissue, DNA mutation, cell membrane disruption [18], and the degradation of lipids, proteins, and photosynthetic pigments [19] (Figure 1).

**Figure 1.** Schematic diagram interpreting the hazardous impacts of soil salinity stress in crop plants. The figure is briefly modified from the literature [20].
The application of macro- and micro-nutrients is one of the management approaches for coping with environmental stresses such as soil salinity [21]. Selenium (Se) has been considered as a beneficial element for crop production which plays an important role in physio-biochemical processes [22,23]. Although higher plants do not require Se for their growth and development [24,25], supplementation of Se at lower dosages not only protects plants from ROS induced oxidative damage by activating the antioxidative mechanisms [22], but also improves the Se content in the edible parts of the crop plants [26]. Some studies have shown that Se is an essential element for human and animal, which plays some beneficial roles in higher plants. Selenium application caused an increasing growth in rice (Oryza sativa L.) [27] and wheat (Triticum aestivum L.) [28], under both stressed and non-stressed conditions. Se has been demonstrated to regulate plant growth by strengthening the stress tolerance mechanisms such as antioxidant and secondary metabolite metabolism [29]. It has also been reported previously that Se reversed the negative impacts of soil salinity on the photochemical efficiency of photosystem II [30]. Moreover, Se could also protect the metabolism and cellular functioning by up-regulating the ROS neutralizing pathways and the osmoregulatory mechanisms [28].

Although several excellent investigations have been done on Se induced salinity tolerance mechanisms in various crops, there is no comprehensive review on Se-mediated improvements in crops. In this review article, the role of Se in the improvement of common morpho-physiological and molecular responses of various crop plants subjected to salt stress are briefly discussed and some practical options have been proposed on how Se could play its role to induce salinity tolerance in crops.

2. Hazardous Impacts of Soil Salinity in Crops

Salinity stress is exceptional among all the abiotic stresses limiting crop yield efficiency in arid and semi-arid zones where natural conditions favor salinization due to insufficient precipitation for the leaching of salts [31]. According to the biphasic model of growth reduction via salinization [32], the detrimental impacts of salt-affected soils are coupled with a reduction of osmosis (primary phase) and ion cytotoxicity (secondary phase), in addition to the production of reactive oxygen species (ROS) and nutrient imbalance [4]. A high osmotic stress is linked with the accumulation of soluble salts in soil solution, leading to water stress due to a reduction in the stomatal aperture, which eventually hampers plant growth [33]. Ion cytotoxicity is the effect of the substitution of K\(+\) and Ca\(^{2+}\) by Na\(^{+}\) and Cl\(^{-}\) in different biochemical reactions due to a higher salt concentration in the root zone of crop plants [34,35] (Figure 1).

2.1. Impacts of Salinity on Plant Agronomic Traits

Soil salinity is known for its adverse effects on plant growth and development [36]. However, the inhibitory effect of salt stress depends on various factors such as salt concentration, time interval, plant species and varieties, photochemical quenching capacity, plant growth stages, stress type, gas exchange characteristics, photosynthetic pigments, and environmental conditions [21]. It was concluded in various studies on Zea mays L. [37], Oryza sativa L. seedlings [38], Vigna unguiculata L. [39], Brassica campestris L. [40], and Vicia faba L. [41] that a low level of salinization increased plant length. However, higher concentrations of sodium chloride salt reduced the plant height of Vigna mungo L., [42], Helianthus annuus L. [43], and Taraxacum parthenium L. [44]. The increment in plant height was might be an effect of an adjustment of osmotic activity due to fewer soluble salts in the growth medium, while plant height reduction was an indication of adverse effects of excessive salts on the photosynthetic rate, a decreased level of carbohydrates and growth hormones (causing growth inhibition) and a reduction in protein synthesis by changing antioxidant enzyme activities [45].

Various studies revealed that the plant biomass (fresh and dry biomass), number of leaves and leaf area were drastically affected by salinity levels up to 8 dSm\(^{-1}\) [44,46,47]. In the context of plant growth, it has been reported by many researchers that dry matter production and plant growth retardation under salt-affected soils could be subjected to the inhibition of cell elongation [21] through the direct impairment of the activities of transport proteins such as H\(^{+}\)-ATPase and H\(^{+}\)-PPase [48]. Another
reason for plant growth reduction could be the detrimental effects of salinity stress on photosynthesis, ultimately limiting plant and leaf growth and chlorophyll contents [49]. Furthermore, the fresh and dry biomass of *Brassica napus* L. cv. Talaye was significantly decreased, while root growth was less affected compared to shoot growth under salinity stress [47]. It was hypothesized that, under salinization, a low water uptake efficiency leads to lesser leaf area development than root growth, due to which soil moisture is conserved to prevent the accumulation of the vast amount of soluble salts in the soil [4,47]. Several studies have revealed that a high accumulation of Na$^+$ and Cl$^-$ ions in cell sap excites a low osmotic gradient in the nutrient medium, resulting in reduced water uptake, which in turn affects plant morphological characteristics [50]. It has been documented that high salt density is responsible for lower N accretion in plants due to the interaction between Cl$^-$ and NO$_3^-$ and between Na$^+$ and NH$_4^+$, which subsequently reduces plant growth and crop yield [51]. Another mechanism behind the reduction of plant growth under saline conditions might be the reduction in photosynthesis due to the plant stomatal closure and the resulting reduction of carbon uptake [21]. A significant reduction in the absorption of nutrient elements due to reduced osmotic pressure has also been reported as a secondary impact of salinity stress on reduced plant nourishment [52].

2.2. Impacts of Salinity on Physiological Traits

Soil salinization has been recognized as a severe threat to crop growth and yield, even in irrigated areas, worldwide [2]. It is estimated that salinity can reduce crop production in up to 20% of irrigated lands across the globe, and this loss will increase to about 50% of arable land up to mid-21st century [9]. Recently, various studies have reported that soil salinity stress causes reduction in the physiological attributes of cereal crops such as wheat (*Triticum aestivum* L.) [13,28] and mung bean (*Vigna radiata* L.) [53]. Plant growth and yield reduction induced by soil salinity might occur due to the changes in numerous physiological and biochemical attributes, i.e., the reduction of leaf chlorophyll content (Chl a, b, carotenoids) and photosynthesis capacity, as well as the alteration of energy in the mechanisms of ion exclusion, osmotic adjustment, and nutrient imbalance [54]. Mostly, salt-affected soils affect crops in three ways: osmotic stress, ion imbalance, and oxidative damage [55]. The main response of salt-affected soils is the toxic effects of sodium (Na$^+$) and chloride (Cl$^-$) ion accumulation in plant tissues [55,56]. It has been proven that plants under salinity stress accumulate more Na$^+$ ions, resulting in the agitation of ionic balance and plant metabolism and stimulation of oxidative damage, while the K$^+$ ion status in plant tissues helps plants develop tolerance towards soil salinity [9]. Rice (*Oryza sativa* L.) grown in salt-affected soil slightly impacted the K$^+$ ion contents; however, it enhanced the Na$^+$ contents in leaves and significantly lowered the K$^+$/Na$^+$ ratio [56,57]. Furthermore, a significant reduction was reported in the growth of strawberry plants [58]. These growth retardations could partially be attributed to reduced photosynthetic activity due to decreased Chl a and Chl b under various salinity levels [59]. The entrance of Na$^+$ and Cl$^-$ ions into the plant cell causes ion imbalance in plant and soil, and this ion imbalance in the plant might cause crucial physiological problems [60]. A high concentration of salts in the soil profile may cause physiological drought due to the reduction in water uptake and salt accumulation in the plant’s root zone [54], a decrease of plant osmotic potential, and thereby, the disturbance of cell metabolic functions due to ion toxicity [33,60]. Excess Na$^+$ in plants harms the cell membrane and organelles of the plant, resulting in a reduction in plant physiological mechanisms such as the net photosynthesis rate (P$n$), stomatal conductance (Gs), transpiration rate (Tr), intracellular carbon dioxide (Ci), and soil plant analysis development (SPAD) value, which lead to plant cell death [56,61,62]. In addition, these physiological changes in the plant might include the disruption of the cell membrane, leading to an inability to detoxify the reactive oxygen species (ROS) in the cytoplasm, a reduced photosynthetic rate and transformations of the antioxidant enzymes [62]. These oxidative systems can interrupt the routine functions of various plant cellular components such as proteins, DNA, and lipids, interfering with dynamic cellular functions in plants under abiotic stress, especially soil salinity [63]. Furthermore, plants grown in a saline environment might inhibit chlorophyll formation and trigger various modifications in the functions and structure of the pigment...
protein complex [64]. The inhibition of chlorophyll pigment synthesis under salt stress might be attributed to the declined activity of various enzymes, i.e., porphyrinogen IX oxidase, porphobilinogen deaminase, coproporphyrinogen III oxidase, 5-aminolevulinic acid dehydratase, protochlorophyllide oxidoreductase, and Mg chelatase [65]. These enzymes in turn are responsible for the upgradation of chlorophyllase activity [66] or a reduction in leaf water potential, N uptake, and thereby, the reduced photosynthetic capacity of plants [53]. Chlorophyll degradation might also be carried out by salinity-induced superoxide radicals and H$_2$O$_2$, which degrade the membranes of thylakoids and chloroplast [27].

2.3. Impacts of Salinity on Enzymatic and Non-Enzymatic Antioxidants

Soil salinity stress is accompanied with a robust accumulation of ROS and hampers plant growth and development. Under stressful circumstances (biotic and abiotic), reactive oxygen species (ROS): (O$_2^-$, O$_2^-$, H$_2$O$_2$, and OH$^-$) production is a stress indicator at a cellular level and is known as a secondary messenger which plays its role in the biological activities of plants, ranging from gene expression and translocation to enzymatic chemistry [67,68]. Ultimately, these ROS might cause alterations in the structures of lipids, proteins and nucleic acids, and thereby, cause an interruption of the normal plant metabolism [69]. It has been reported that soil salinity-stimulated oxidative stress due to the accretion of higher levels of H$_2$O$_2$ might induce apoptosis, cell shrinkage, chromatin condensation, and DNA fragmentation [70]. Under salinity stress, higher levels of ROS production might result in the production of malondialdehyde contents (MDA) in the thylakoid membranes. MDA concentration, which is known to be an effective indicator of lipid peroxidation, helps to calculate the lipid peroxidation of plant cells [71]. The balance between ROS production and their elimination by the antioxidative defense mechanism defines the degree of collateral damage to these molecules involved in plant metabolism [72]. Moreover, soil salinization causes acute oxidative damage in the plant tissues, and as a result, plants develop their own complex natural antioxidant defense system to combat with the salinity-induced oxidative stress [73]. The antioxidant enzymes inhibit the cell structural damages caused by salinity-induced ROS [74]. In the presence of an efficient antioxidant system in crop plants, it is believed that salt tolerance is better than for other types of plants. Previously, various researchers have reported the differential impacts of salinity stress on antioxidative enzymatic and non-enzymatic activities in Tanacetum parthenium L. [44], Brassica napus L. [47], Oryza sativa L. [75], and Glycine max L. [76]. The non-enzymatic antioxidative system mainly includes carotenoids, ascorbic acid (vitamin C), α-tocopherol, and flavonoids, while the enzymatic antioxidative system includes peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), polyphenol oxidase (PPO), etc. The major role of the enzymatic antioxidative system is to scavenge the injurious radicals produced during oxidative stress and thus help the crop plants to survive under abiotic stress such as soil salinity [67,77]. There are some natural antioxidants in almost all parts of the plant. These natural antioxidants are vitamins, carotenoids, phenols, dietary glutathione, flavonoids, and endogenous metabolites [78]. In salt-affected soils, the production and scavenging of these antioxidants makes up the first line of defense in plants to handle the oxidative stress.

3. Salinity Tolerance Mechanisms Adopted by Crop Plants

Plants have developed various adaptations at cellular, subcellular and organ levels for their nourishment under salt-affected soils. Some important salt resistance mechanisms are ion homeostasis, stomatal regulation, ion compartmentalization, osmoregulation/osmotic adjustment, hormonal balance changes, stimulation of the antioxidative defense mechanism, and the accumulation/exclusion of toxic ions from cells and tissues. However, all these salt-tolerant mechanisms are complex and vary from specie to specie [4]. According to biomass production under soil salinization, four plant groups are differentiated: (1) true halophytes (Sued sp. and Atriplex sp.), which can invigorate biomass production under salt stress; (2) optional halophytes (Plantago maritima and Aster tripolium), which show a minor increase in biomass at lower salt concentration; (3) nonresistant halophytes (Hordeum sp.), which can
Selenium (Se) has already been proven to be beneficial for humans and animals. However, Se is considered to be a double-edged sword due to its dual response to plants (beneficial or toxic) depending on its concentration and the nature of plant species [100]. Se is available in many forms to plants, such as selenate (Se, VI), selenite (IV), thioselenate, selenide, and elemental Se [101]. The optimum level of Se plays a crucial role in human and animal metabolism, e.g., a low concentration of Se in the

4. Role of Selenium under Abiotic Stresses

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diet is essential for antioxidant production and a healthy life and is recommended in many countries of the world. Thus, the effects of Se on humans and animals are linked with Se in the soil–plant system, because Se contents in edible parts of the plant come from the soil and are consumed by other organisms.

Under low Se levels, it acts as an important protectant in plants grown under different abiotic and abiotic stresses. Selenium causes the disputation of ROS and protects plants from toxic elements-induced oxidative stress. At high levels, Se acts as a pro-oxidant as with other heavy metals/metalloids and enhances the production of ROS, causes protein oxidation, lipid peroxidation, and genotoxicity [102]. Selenium shows a hermetic effect in plants, but the mechanisms, as well as the optimal, essential, and toxic values of Se in the soil, are not well-established for different plant species and soil types. The essentiality of Se in plants depends on the plant species and Se concentration. For example, a hyper-accumulator species of Brassica species (Helianthus, Camelina, and Aster) could accumulate Se up to 100–1000 mg kg⁻¹ DW without showing toxicity symptoms. On the other hand, non-hyper-accumulator species of food crops, grasses, and vegetables hardly accumulate 100 mg kg⁻¹ DW of Se in plant tissues [103]. However, the Se response to salinity stress is not very clear and needs to be explored (Figure 2).

![Figure 2](image)

**Figure 2.** Schematic presentation showing the possible causes that overproduce reactive oxygen species (ROS), which might disturb the normal function of plant cells. The mechanism of antioxidants shown here scavenges the ROS effects as well as ameliorative effects of Se to induce salinity tolerance in crop plants. Se represents “selenium” (25 μM Na₂SeO₄) and S1 and S2 represent salinity stress (100 and 200 mM NaCl), respectively. The seedlings are representative of *Brassica napus* L. (Source: [24]). POD: peroxidase; SOD: superoxide dismutase; APX: ascorbate peroxidase; GSH: reduced glutathione; GSSG: oxidized glutathione; H₂O₂: hydrogen peroxide; NADP⁺: nicotinamide adenine dinucleotide phosphate; MPK: mitogen activated protein kinase gene; CPK: calcium dependent protein kinase gene; NHX: sodium/hydrogen (Na⁺/H⁺) exchanger gene.

### 4.1. Selenium Speciation and Mobility in Soil

Selenium (Se) is present in excess in the Earth’s crust and can be beneficial or toxic to plants depending on the concentration of Se, speciation, and nature of plant species. Se occurs in organic and inorganic forms in soil with different oxidation states (+6, +4, 0, and −2) for selenate, selenite, elemental Se, and selenides, respectively. The most mobile and water-soluble inorganic Se is selenate (SeO₄²⁻), which is present abundantly under oxic soil conditions with low adsorption affinity to oxide surfaces [104]. Selenate could be reduced into selenite due to poor adsorption ability onto the oxide surfaces.
surface under poor redox potential [102]. It has been demonstrated that selenite (SeO$_3^{2-}$, HSeO$_3^-$, H$_2$SeO$_3$) might be the most abundant inorganic Se speciation under an anaerobic soil environment (pH: 7.5–15) [105]. At low pH, selenite has a greater ability to be adsorbed on an oxide surface than selenate and thus has reduced bioavailability to crop plants [104]. Selenite could be reduced into elemental Se, Se$^0$, or selenides, Se$^{2-}$ (unavailable to plants), under strong reducing conditions [102]. Various factors which are responsible for Se mobility and solubility in soil are soil pH, sorption, and desorption reactions, redox potential, organic/inorganic compounds, and dissolution processes in sediments and soils [106].

Soil Se is mainly inorganic but it can also be present in organic forms, such as complexes with organic matter, and incorporated into organic or organo-mineral colloids [107]. Se in organo-Se compounds (e.g., seleno-aminoacids) presents a valence state of −2 and is highly bioavailable. In addition, volatile organic forms of Se such as dimethyl selenide (DMSe) and dimethyl diselenide (DMDSe) may be present in soils. Se accumulation in plants is higher when seleno-amino acids are added to the hydroponic growth medium compared with inorganic forms of Se at the same concentration [108]. Organo-selenium compounds can either be released into the soil from biological decompositions of plant and soil microbial tissues or by Se-based fertilizer addition. Soil organic matter (OM) is shown to influence the retention of Se in [109]; however, the mechanisms of Se–OM interactions are poorly understood. Basically, three hypotheses explaining the OM-mediated retention of Se are generally discussed: (i) OM has increased sorption sites, which facilitates direct complexation with Se [109,110]; (ii) indirect complexation via OM–metal complexes [109]; (iii) microbial reduction and incorporation into amino acids, proteins, and natural organic matter [110]. Depending on the type of binding, Se may be easily mobilized (e.g., through pH adjustment) or immobilized (e.g., covalent incorporation to OM).

4.2. Selenium Uptake and Mobility within the Plants

The Se toxicity or deficiency margin is very small. This small gap between toxicity and essentiality is based on the nature of the organism and Se speciation [100]. It has been reported that a low-Se diet is important for antioxidant protection and a healthy life [111]. Therefore, threshold levels of Se have been added to the nutritional recommendation in various parts of the world such as China (essentiality: $>0.125$ mg kg$^{-1}$; toxicity: $>3$ mg kg$^{-1}$) [112]. Se deficiency or Se excess due to the intake of low or high-Se containing food may cause many health problems in living organisms [102]. Therefore, it is essential to understand and monitor the behavior of Se in the soil–plant system.

The majority of crop plants are able to uptake various inorganic forms such as selenite (+4), selenate (+6) [104], and/or various selenium based organic compounds such as SeCys (methylselenocysteine) and SeMet (selenomethionine) [105]. In contrast, plants are incapable to uptake elemental Se (0), selenide (−2) from the root zone. Even though Se is not an essential element for plants, it plays many significant roles in the plant, which depends on its applied concentration in the growth medium. Lower Se concentrations play a beneficial role and improve plant growth, whereas higher Se concentrations disturb the metabolic processes of the plant and reduce plant growth. The pathway of Se accumulation in plant roots is through specific and non-specific channels of essential nutrients (sulfur and phosphate), whereas the xylem channels and sinks transport Se (VI) into the shoot tissues within plants. Previously, it has been reported that phosphate transporter families (Pht1 and NIP2;1 transporter) are used to take up Se by root cells such as HSeO$_3^-$ and H$_2$SeO$_3$ (selenite) using aquaporins [113]. Afterwards, these Se speciations are translocated from root cells to the plant shoot as selenate via the root symplast and stele. During this whole process, selenite is persuaded into Se-based organic compounds, which stay behind in the plant roots [114,115]. Therefore, selenate and small amounts of SeMet and selenomethionine Se-oxide (SeOMet) have been considered important Se species in the plant xylem [116]. The family of aluminum-activated malate transporter (ALMT) genes are thought to be responsible for carrying selenate in the shoot xylem sap [117], whereas, following the delivery of selenate from root to shoot via
the xylem, the members of the Sulfate transporters (SULTRs) family take it to leaf cells [118], where it is stored in the cell vacuoles [114].

In addition to inorganic Se, plant uptake of organic Se is known to occur and has been reported at much higher rates (20–100 fold greater) than the uptake of inorganic species [108]. Evidence suggests that amino acid transporters are important. To date, no Se-specific uptake mechanisms have been reported [119]. However, SeMet (selenomethionine), SeMeSeCys (Se-methyl selenocysteine) and SeCys (methylselenocysteine) forms of Se are taken up by the plant roots through transporters with the ability to catalyze the uptake of Met and Cys, respectively [120]. A synchrotron-based X-ray fluorescence microtomographic analysis was performed to demonstrate the transport mechanisms of organic species of Se. The authors observed that organic Se (SeMet and SeMeSeCys) was translocated in *Oryza sativa* L. exclusively via the phloem. The results indicated that, for SeMeSeCys- and SeMet-fed grain, Se was distributed throughout the external grain layers and into the endosperm, while SeMeSeCys Se was partitioned into the embryo. They demonstrated that organic Se species (SeMeSeCys and SeMet) are rapidly loaded into the phloem and transported to grain more efficiently than inorganic species [121].

5. Selenium-Mediated Alleviation of Salinity Stress in Plants

The findings to date have shown that Se is not ranked as an essential element for crop plants; however, a low Se concentration exerts beneficial effects on plant growth and development under biotic and abiotic stresses, especially soil salinization (Figure 2). Many studies have reported the effects of the application of Se to evoke tolerance against salt stress depending on the application method, dose of Se, salinity levels, and plant species [58]. For example, a foliar application of selenate (20 mg L⁻¹) mitigated the adverse effects of salinity stress (12 dS m⁻¹) on the growth and development parameters of maize (*Zea mays* L.) [122]. Likewise, another study reported that Se application (20 µM) in the form of sodium selenite causes improvements in the growth and yield of eggplants under varying levels of soil salinity [123]. However, higher doses of selenium were found to have deleterious effects on the growth and development stages of maize under a salt stress of 100 mM NaCl [29]. Even though Se is an essential trace nutrient to humans and other animals as an antioxidant, Se toxicity might appear at higher concentrations due to the substitution of S with Se in the structure of amino acids, followed by the inaccurate folding of proteins and thus the creation of nonfunctional proteins and enzymes [102]. Conclusively, higher doses of Se hamper the growth and development of crop plants, while low doses cause improvements in growth and development mechanisms.

5.1. Improvement in Agronomic Traits

The maintenance of plant growth is directly associated with the survival of crop plants under salt-affected soils. The application of minute levels of Se under salinity stress significantly improved plant growth characteristics such as the shoot length, shoot diameter, and fresh and dry biomass of cucumber (*Cucumis sativus* L.), lemon balm (*Melissa officinalis* L.), cowpea (*Vigna unguiculata* L.), wheat (*Triticum aestivum* L.), and maize (*Zea mays* L.) as compared to salt stress alone [122,124–126] (Table 1). Likewise, Se showed a great potential to improve stem growth (diameter and biomass) in melon (*Cucumis melo* L.) and tomato (*Solanum lycopersicum* L.) when cultivated in salt-affected soils [30,106]. Recently, Astaneh suggested that growth parameters such as the bulb height, fresh and dry biomass of bulbs, bulb diameter, and the number of cloves in one bulb of Garlic (*Allium Sativum* L.) were significantly improved with the addition of Se under salinity stress [127]. Growth characteristics related to plant roots such as length, fresh, and dry weight were significantly improved with the supplementation of smaller amounts of Se alone and/or in combination with NaCl, compared to salinity stress alone [30,122]. Se applications significantly promoted root and shoot fresh weight and shoot dry weight as well as improving relative water contents in tomato (*Solanum lycopersicum* L.) and antioxidants activity and photosynthetic pigments in lettuce plants [100,128]. In addition, added Se also improved the growth parameters of ryegrass (*Lolium perenne* L.) and spinach (*Spinacia oleracea* L.) by improving nutritive values [106].
| Salinity Stress | Plant Species          | Se Dosages            | Se Speciation | Experimental Details       | Various Protective Effects and Mechanisms of Se in Salinity Stressed Plants                                                                 |
|-----------------|------------------------|-----------------------|---------------|----------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| 150 mM          | Oryza sativa L.        | 2, 4, 6, 8, 10, 12 mg L\(^{-1}\) | Se (VI)       | Sand culture               | Enhances plant biomass, K\(^+\)/Na\(^+\) ratio, and Se accumulation; reduces malondialdehyde contents (MDA) and H\(_2\)O\(_2\) contents; increases chlorophyll and water contents; causes upregulation of OsNHX1 gene transcript levels |
| 0, 30, 60, 90 mM | Allium sativum L.      | 0, 4, 8, 16 mg L\(^{-1}\) | Se (VI)       | Hydroponic culture         | Increases root biomass, bulb diameter, bulb height, and photosynthetic pigments; reduces ion leakage and lipid peroxidation; improves K\(^+\) and Na\(^+\) contents, chlorophyll index, carotenoids, and water balance |
| 100 mM          | Triticum aestivum L.   | 5, 10 µM              | Se (VI)       | Reconstituted soil culture (Peat, compost, sand) | Improves wheat growth; promotes the synthesis of photosynthetic pigments, proline, and sugars; reduces H\(_2\)O\(_2\) contents, Na\(^+\) uptake, and Na\(^+\)/K\(^+\) ratio |
| 10, 30, 60, 90 mM| Stevia rebaudiana Bertoni | 20 g/ha (2 ppt)       | Se (IV)       | Field experiment           | Increases leaf and plant biological yields; enhances rebaudioside-A and stevioside of stevia leaves; improved the accumulation of sweet steviol glycosides contents |
| 0.12, 0.30, 0.60 S m\(^{-1}\) | Triticum aestivum L. | 0, 0.5, 1, 4 mg kg\(^{-1}\) | Se (IV)       | Pot soil culture           | Dramatic decrease in shoot dry biomass; chlorophyll a, chlorophyll b, and carotenoid contents increase at lower Se, while they decrease at higher Se; enhances free proline and Se contents in shoots; |
| 8 dS m\(^{-1}\)  | Allium cepa L.         | 0, 0.5, 1 kg ha\(^{-1}\) | Se (IV)       | Field experiment           | Increases bulb yield and dry matter; improves water and chlorophyll contents; causes bulb Se and K enrichment; causes a decrease in Na |
| 0, 100 mM       | Phaseolus vulgaris L.  | 0, 5, 10 µM           | Se (IV)       | Pot soil culture           | Enhances plant growth and seed yield; promotes membrane stability index, photosynthetic capacity, and Rubisco activity; reduces (MDA) and electrolyte leakage |
| 0, 100 mM       | Zea mays L.            | 0, 1, 5, 25 µM        | Se (IV)       | Pot vermiculite culture    | Enhances growth and biomass; improves gas exchange attributes and the shape of thylakoids by alleviation of damage in the ultrastructure of chloroplasts; upregulates ZmMPK5, ZmMPK7, ZmCPK11, and ZmNHX1 genes transcript levels in roots |
| 0, 80 mM        | Petroselinum crispum L.| 1 mg L\(^{-1}\)      | Se (VI)       | Hydroponic culture         | Decreases root to shoot transport of Na\(^+\); improves photochemical efficiency of photosystem II (PSII) and chlorophyll contents; protects photosynthetic apparatus by upregulation of non-photochemical quenching (NPQ); decreases cell sap Na\(^+\) |

References:
[27, 127, 129, 28, 21, 130, 131, 132, 29, 133]
Table 1. Cont.

| Salinity Stress | Plant Species                  | Se Dosages | Se Speciation | Experimental Details | Various Protective Effects and Mechanisms of Se in Salinity Stressed Plants | References |
|-----------------|--------------------------------|------------|---------------|----------------------|--------------------------------------------------------------------------------|-------------|
| 3.22 dS m\(^{-1}\) | *Lactuca sativa* L.          | 16, 32 µM  | *Se* (VI)     | Field experiment     | Improves growth characteristics, yield, and relative water contents; decreases cell membrane permeability and malondialdehyde; enhances chlorophyll, carotenoids, K\(^{+}\)/Na\(^{+}\), and total soluble sugars | [134]       |
| 0, 25, 50 mM    | *Lycopersicon esculentum-Mill.* | 0, 5, 10 µM | *Se* (IV)     | Hydroponic culture  | Enhances growth by improving water balance and cell membrane integrity; increases photosynthetic pigments; decreases proline and phenolics | [128]       |
| 0, 30, 60, 120 mM | *Solanum melongena* L. cv. Baladi | 0, 5, 10, 20, 30 µM | *Se* (IV)     | Bedding sand culture| Increases vegetative growth, yield, nitrogen, phosphorous and potassium NPK contents in leaves and fruits; improves chlorophyll contents (SPAD value) and proline contents; Enhances K\(^{+}\)/Na\(^{+}\) ratio | [135]       |
| 0, 40 mM        | *Lactuca sativa* L. var. capitata | 0, 2, 6 µM  | *Se* (IV, VI) | Hydroponic culture  | Enhances fresh biomass, leaf area, chlorophyll, proline, and carotenoid contents; reduces H\(_2\)O\(_2\) and TBARS; improves shoot ionic concentrations | [100]       |
| 0, 40 mM        | *Melissa officinalis* L.      | 10 mM      | -             | Hydroponic culture  | Improves growth rate; increases photosynthetic pigments, protein, and total amino acid contents; reduces lipid peroxidation to alleviate membrane damage | [125]       |
| 0, 2000, 4000, 6000 mg L\(^{-1}\) | *Brassica napus* L. | 0, 2.5, 5, 10 mg·L\(^{-1}\) | *Se* (VI)     | Pot clay soil culture | Enhances growth, photosynthetic pigments, canola oil quality; increases soluble sugar, polysaccharides, and total carbohydrates; significantly improves saturated and unsaturated fatty acids composition | [136]       |
| 0, 2000 ppm     | *Cucumis sativus* L. cv Zena | 0, 1 ppm   | *Se* (IV)     | Pot soil culture    | Improves plant biomass; increases reduction of oxygen radicals and osmotic regulation by synthesis of osmoregulatory compound such as proline; reduces malondialdehyde concentration and electrolyte leakage | [137]       |
| 0, 50 mM        | *Cucumis sativus* L.         | 0, 5, 10, 20 µM | *Se* (VI)     | Hydroponic culture  | Induces salt tolerance by protection of cell membranes against lipid peroxidation; improves growth rate, photosynthesis, and proline contents; reduces Cl\(^{-}\) contents, while showing no effect on Na\(^{+}\) ions and K\(^{+}\)/Na\(^{+}\) ratio | [124]       |
| 100 mM          | *Rumex patientia × R. tianshanicus* | 0, 1, 3, 5, 10, 30 µM | *Se* (IV)     | Sand culture        | Increases seedling growth; lower Se supply improves total water-soluble sugars, K\(^{+}\), and Na\(^{+}\) concentrations; alleviates integrity of cytoplasmic organelles, plasma and nuclear membranes, root tip cells; makes more legible and increases mitochondrial cristae in leaf mesophyll | [138]       |

The abbreviations are explained in the list of abbreviations.
The application of Se significantly improved the plant growth, photosynthetic activities such as the net
light interception, and accumulation of carbohydrates, proteins, and carotenoids, of which adequate amounts are
required for growth regulation through their impact on the vital metabolic pathways such as antioxidant metabolism, nitrogen assimilation, and
cellular stress signaling [72,91,144]. The Se supply has been reported to be beneficial to increasing the
nitrogen, potassium, and calcium uptake from soils, thereby, leading to a larger production of amino acids, metabolites, and stress signaling for better induction of salinity tolerance in wheat (Triticum aestivum L.) [28]. Another important mechanism is Se-accelerated reduction in the Na+/K+ ratio in plants grown in salt-affected soils, which ultimately induces the protection of some essential processes and balanced osmotic potential [127]. Na+ ions are responsible for inhibiting K+ ion uptake at the membrane transport level, whereas Se might have the ability to influence the expression of Na+ transporters and H+ pumps [145].

5.2. Se-Mediated Improvement in Physiological Attributes

To situate the scientific context compiled in this review article, it should be taken into account that Se at low concentrations helped plants to alleviate exposed stress from its exterior environment, especially regarding soil salinity. Therefore, an exogenous application of Se has gained considerable interest in the scientific community around the world [22,24,94]. For instance, exogenously applied Se played a significant role in appraising the physiological and biochemical mechanisms (Table 1) involved in salinity tolerance in cucumber [124], canola [24], and parsley [133], which as a result helped plants to survive better in salt-stressed environments. Salinity stress in particular not only damages a plant’s osmotic potential, but also accompanies various secondary stresses, such as cellular oxidative damage by the over-generation of reactive oxygen species (ROS) [122]. The maintenance of ROS homeostasis and other physiological functions such as photosynthesis are the chief priorities of plants exposed to salinity stress [29]. Therefore, finding suitable approaches to understand and investigate the mechanisms underpinning plant responses to salinity stress is essential to sustain agricultural production in saline soils. In this regard, the application of Se has been found to reduce the harmful effects of salinity and support the growth of maize (Zea mays L.), tomato (Solanum lycopersicum L.), and garlic (Allium sativum L.) through enhanced photosynthetic performance [29,30,122,129]. Moreover, enhanced growth and nutritional qualities of spinach (Spinacia oleracea L.), ryegrass (Lolium perenne L.), wheat (Triticum aestivum L.), and mung bean (Vigna radiate L.) have also been reported by exogenously applied Se under stressed and non-stressed conditions [22,106,142,146]. Further, a lower Na+ concentration and higher K+/Na+ ratio was observed in selenite-treated plants as compared to untreated plants [27]. Se might have decreased the accretion of Na+ ions which led to an increased K+/Na+ ratio in comparison to the untreated control plants of dill (Anethum graveolens) and garlic (Allium sativum L.) [129,147]. The addition of Se under salinity stress significantly improved the physico-biochemical properties such as the chlorophyll contents, carbohydrates, proteins, and carotenoids, of which adequate amounts are essential to regulate major metabolic processes such as photosynthesis in maize (Zea mays L.) [148]. The application of Se significantly improved the plant growth, photosynthetic activities such as the net
photosynthetic rate, the actual photochemical efficiency of photosystem II (PSII), maximum quantum yield of PSII (FV/Fm), photochemical quenching coefficient (qP), and non-photochemical quenching coefficient (qN) of tomato (*Solanum lycopersicum* L.) cultivars [30]. Similarly, Se application showed a positive effect on growth and improved the photosynthetic pigments and total amino acid contents in lemon balm (*Melissa officinalis* L.) and decreased Na\(^+\), while increasing K\(^+\) concentrations in the roots and shoots of dill (*Anethum graveolens*) plants [133,147]. Furthermore, many other researchers have shown that Se application to salt-stressed cucumber and tomato protected the cell membranes against lipid peroxidation, reduced oxidative stress by regulating the chloroplast, which is strongly linked with increasing the photosynthetic rates by improving the PSII, and thereby, enhanced plant stability [30,124]. Taken together, these findings suggest that Se played a significant role in improving the physiological and biochemical adaptation of plants, which eventually helped plants to survive better in stressed saline conditions.

It has been recognized previously that the amelioration of photosynthetic inhibition through Se supply might be a result of the cumulative impact on the antioxidative defense mechanisms, leading to the simultaneous alleviation of ROS effects, uptake and accumulation of important crop nutrients [149]. Recently, it was shown that a higher Se supply (10 \(\mu\)M) causes retardation in the growth and photosynthetic capacity of wheat (*Triticum aestivum* L.) seedlings [28], which might be attributed to decreased chlorophyll formation due to the inhibition of chlorophyll biosynthesizing enzymes and production of 5-aminolevulinic acid and protochlorophyllide [150]. An increment in Mn, Zn, and Fe contents in plant leaves under Se treatment [151] could also be the reason for the improved photosynthetic apparatus and avoidance of the degradation of chlorophyll [152]. Optimal supplementation of Se modulates photosynthetic functioning by enhancing CO\(_2\) assimilation, photosynthetic rate, and chlorophyll fluorescence characteristics under normal and stressful conditions [149]. Moreover, a Se supply regulated proline accumulation by enhancing the activity of \(\gamma\)-glutamyl kinase (\(\gamma\)-GK) enzyme, leading to the enhanced synthesis of proline with subsequent declines in its degradation via the slowing down of the activity of proline oxidase [28,153]. In halophytic grasses, it has been demonstrated that increased accumulation of proline leads to enhanced photosynthetic efficiency and ATP production, resulting in greater water use efficiency [154]. The above discussion reveals that the application of a low concentration of Se could play an important role in the improvement of the physiological and defensive mechanisms of crop plants under salinity stress.

### 5.3. Se-Mediated Improvement in the Alleviation of ROS Effects

Plants produce an array of antioxidant enzymes once exposed to biotic and abiotic stresses and, interestingly, Se supplementation has been found to upscale these antioxidant enzyme activities to cope with experienced stresses [155]. Se has a significant role in numerous enzymatic processes—i.e., catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione peroxidase (GPX)—and non-enzymatic processes—i.e., phytochelatins and glutathione antioxidants—which help to combat the salt-induced overproduction of reactive oxygen species (ROS), which are responsible for agitating plant cell integrity (Figure 2). Molecular oxygen (O\(_2\)) works as an electron acceptor with a subsequent accretion of reactive oxygen species (ROS) such as singlet oxygen (\(^1\)O\(_2\)), hydroxyl radical (OH\(^-\)), superoxide radical (O\(^-\)\(_2\)), and hydrogen peroxide (H\(_2\)O\(_2\)) under salt-stressed conditions. It has been well proven that lower concentrations of selenate (Na\(_2\)SeO\(_4\)) help to protect plants from ROS-stimulated oxidative damage, but a higher concentration of Se works as a pro-oxidant and stimulates the formation of ROS and induces oxidative stress [92]. Many researchers have described that Se is required to increase the scavenging activity of ROS, decreasing the concentration of MDA and membrane damage [156]. Moreover, decreased generation of H\(_2\)O\(_2\) under Se supplementation has also been confirmed [157,158]. Under salinity stress, lowered H\(_2\)O\(_2\) contents were observed in Se-treated canola (*Brassica napus* L.) plants [136]. Meanwhile, plants exposed to Se showed lower concentrations of MDA under NaCl stress, showing that Se was vital in bringing down the lipid peroxidation by amending the antioxidant enzymes and protecting the
membranous structures of *Oryza sativa* L. [27], *Cucumis sativus* L. [124], *Brassica napus* L. [24], and *Anethum graveolens* [147]. In addition, it was noticed that lipid peroxidation (MDA) production was reduced by elevating Se concentration under salt stress [127]. A comprehensive impact of MDA on plant cells is lowering the fluidity of the membranes to elevate membrane leakiness and avoiding damage to membrane proteins, enzymes, and ion channels [159]. A suitable concentration of Se might be useful to limit the over-expression of lipidoxygenease for sustaining fatty acid formation in addition to the lessered ROS generation, which was led by the upregulation of antioxidant systems [28].

5.4. Se-Mediated Improvement in the Upregulation of Enzymatic and Non-Enzymatic Antioxidants

Under soil salinity stress, ROS can be detoxicated by antioxidant compounds (Figure 2; Table 2). It is believed that enzymatic and non-enzymatic antioxidants, such as SOD, POD, APX, CAT, GSH-Px, and GR, are positively interconnected in response to Se supplementation to induce salinity tolerance in crop plants [22,131]. Researchers postulate that an elevation in the Se-mediated antioxidant defense is one of the vital mechanisms that can save plants from salt-stimulated oxidative stress [58,134]. Antioxidant enzyme activities (SOD, APX, and CAT) significantly improved with exogenous Se treatment in rapeseed (*Brassica napus* L.) and dill (*Anethum graveolens*) seedlings under salinity stress [24,147]. In another study, the accumulation of lowered H$_2$O$_2$ contents in rice plants might have been due to Se-mediated higher levels of APX and CAT activities [27]. An increment in the activities of SOD, CAT, GST, APX, and GR has been noticed in different crops such as *Triticum aestivum* L., *Brassica juncea* L., *Avena sativa* L., and *Solanum lycopersicum* L. [13,144,160,161]. Recently, it was noticed that the translocation of minerals such as iron, zinc, and manganese was significantly increased in the shoots of rice (*Oryza sativa* L.) with Se application [151]. These minerals are essential components of antioxidant enzymes and responsible for increasing the activities of SOD, POD and CAT [162]. Under salinity stress, the exogenous supplementation of Se to maize (*Zea maize* L.) plants resulted in the upregulation of expression of mitogen activated protein kinase (MAPK5 and MAPK7) and calcium-dependent protein kinase (CPK11) genes and stimulated the antioxidant defense system under salt stress [29,163]. It has been reported that MAPK flow is at the center of cell signal transduction and implicated in stress-related signal pathways [164]. Abscisic acid (ABA) accumulation could be stimulated under salinity stress [165], which in turn produces H$_2$O$_2$, causing the activation of MAPK, resulting in stimulated expression and activities of antioxidant enzymes [166]. Furthermore, NAD kinase-2 (NADK2) mutation impaired ABA-induced stomatal closure and ABA inhibition of light-promoted stomatal opening. NADK2 disruption also impaired the ABA-stimulated accumulation of H$_2$O$_2$ [167,168]. Elevation of SOD activity due to Se supplementation evolved in the quick transformation of the superoxide radicals into H$_2$O$_2$, which was produced at the chloroplast and mitochondrial electron transport chain. The evolving H$_2$O$_2$ was counteracted either by CAT in the cytoplasm or by APX in the ascorbate glutathione (AsA–GSH) pathway. Furthermore, increased SOD activity in Se-supplemented seedlings altered the chances of hydroxyl (OH$^-$) radical composition, following a better defense of chloroplast function [162].
Table 2. Selenium (Se) supplementation mitigates salinity-induced oxidative damage by changing different antioxidant enzymatic and non-enzymatic activities in the leaves of different salt-stressed plants (↑ indicates an increase, while ↓ indicates a decrease).

| Salinity Stress | Plant Species | Se Dosages | Se Speciation | Experimental Details | Antioxidant Activity | % Increase or Decrease | Reference |
|-----------------|--------------|------------|---------------|----------------------|----------------------|------------------------|-----------|
| 150 mM          | Oryza sativa L. | 2, 4, 6, 8, 10, 12 mg·L⁻¹ | Se (VI) | Sand culture | ↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑↑∪
The scavenging of H$_2$O$_2$ and lipid peroxide (MDA) into water and lipid alcohol is done by two important enzymes: glutathione peroxidase (GSH-Px) and glutathione reductase (GR) [20]. GSH-Px is considered to be a vital enzyme, which is strongly activated by Se in different plants under various environmental stresses [173]. In the presence of Se, GSH-Px quenches H$_2$O$_2$ and then APX, CAT, and GR remove the leftover of H$_2$O$_2$. Under salinity stress, regardless of the mode of Se application, Se enhanced the GSH-Px and GR activity compared to controls [27,28]. Under the availability of Se, GSH-Px activity might be modulated due to higher selenocysteine formation at the catalytic site of GSH-Px [27,173]. The enhanced activity of GSH-Px and GR lowered the levels of H$_2$O$_2$ and MDA and improved the growth of rapeseed (Brassica napus L.) and rice (Oryza sativa L.) plants by overcoming ROS-stimulated oxidative damage under soil salinity stress [24]. APX lowers the level of H$_2$O$_2$, while GR impacts the preservation of GSH and AsA content resulting in reasonable cellular redox [72]. The supplementation of Se in wheat (Triticum aestivum L.) seedlings upregulated the AsA–GSH pathway by increasing the activities of APX and GR. Furthermore, elevating the AsA and GSH contents consistently evolved in the defense of the photosynthetic electron transport chain by sustaining better nicotinamide adenine dinucleotide phosphate (NADP$^+$) levels and limiting the composition of toxic radicals [28]. These results revealed that the wise use of Se could be beneficial to improving the plant antioxidative defense mechanism under soil salinity stress.

5.5. Se-Mediated Gene Expression Modifications under Salinity Stress

Very few studies have elucidated the role of Se in the alleviation of Na$^+$ accumulation and its hazardous impacts on plant growth and development at the gene level. In an experiment on maize (Zea mays L.), Jiang investigated the expression levels of associated genes such as ZmMPK5, ZmMPK7, and ZmCPK11, which are responsible for the antioxidant defense system in roots, while the expression of ZmNHX1 gene clarified Se’s involvement in Na$^+$ and K$^+$ homeostasis under salt-affected soils [29] (Figure 2). In previous studies, the contribution of genes to the removal of ROS has been well documented. It has been reported that H$_2$O$_2$ is the activator of ZmMPK5, and hence, the antioxidant defense system of maize leaves was enhanced [174]. Similarly, the expression of ZmCPK11 increased the activities of APX and SOD in maize (Zea mays L.) leaves [175]. Moreover, under a stress salt environment, the ZmMPK7 gene was found to be a good alleviator of ROS-induced damages in tobacco (Nicotonia tobaccum L.), resulting in low H$_2$O$_2$ accumulation [155]. Likewise, it was described that a small amount (1 $\mu$M) of Se (Na$_2$SeO$_3$) addition under osmotic stress enhanced the upregulation of ZmMPK5, ZmMPK7, and ZmCPK11 genes in roots of maize (Zea mays L.) [29]. In many previous findings, NHX gene overexpression in transgenic plant species—i.e., rapeseed [176], tomato [81], and poplar [14]—is responsible for Na$^+$ compartmentalization and an enhancement of salt resistance. Recently, it was proven that ZmNHX1 expression was significantly up-regulated in maize after 24 h of salinity stress exposure, which may contribute to Na$^+$ compartmentalization under osmotic stress [29].

Furthermore, it was reported that OsNHX1 (vacuolar Na$^+$/H$^+$ antiporter gene) is responsible for maintaining plant osmotic balance by reducing the hindrance of Na$^+$ ions during water movement towards plant shoots [14], which might be due to the sequestration of sodium ions in vacuoles of roots and/or shoots [177]. Previously, this phenomenal mechanism was strengthened by research work on tomato (Solanum lycopersicum L.) and rapeseed (Brassica napus L.), respectively [81,176]. Recently, Se (Na$_2$SeO$_4$) was supplied to salinity-stressed rice (Oryza sativa L.) plants grown under a saline environment in a mixture of sand and polymer, and it was observed that plants receiving Se exhibited a higher transcription level of OsNHX1 gene [27]. The researchers concluded that it could be imagined that a higher OsNHX1 transcript level promoted Na$^+$ sequestration within the root vacuoles and therefore reduced the Na$^+$ accumulation in rice shoots, which ultimately improved plant growth and antioxidative defense mechanism. However, further research work is needed to explore how Se is involved in antioxidant defense genes and how these genes are up and downregulated to induce antioxidant defense systems in salt-stressed plants under Se supplementation.
6. Conclusions and Future Perspectives

Soil salinization has become an overwhelming environmental threat to world food production and agricultural sustainability. Selenium (Se) is recognized as an essential trace element for human beings and animals, although this is controversial for different plant species. However, based on published relevant literature, it is widely accepted that Se is capable of remediating various biotic and abiotic environmental stresses including soil salinity. The important mechanisms involved in Se-mediated salinity tolerance in crop plants include a reduction in Na⁺ ion accumulation in plant parts through the overexpression of the Na⁺/H⁺ antiport, chelation and boosting of the antioxidative defense system in plants, Na⁺ compartmentalization, improvement in various structural compositions, and the upregulation of Na⁺ and Cl⁻ ions transporter genes. However, these salinity-tolerance mechanisms are still highly controversial and are influenced by growth conditions, growth medium (soil or water), stress duration, plant genotypes, plant species types, Se doses, speciation, and many more. Therefore, it is difficult to predict a general conclusion for the Se-mediated alleviation of salinity-induced phytotoxicity in crop plants. More precisely, at lower concentrations, Se can mediate plant growth and physiological characteristics (acts as a beneficial element), while at higher concentrations; it disturbs various plant metabolic processes, and thereby suppresses plant growth under salinity stress. Moreover, Se triggers the dismutation of ROS generated under salt stress and protects plants from oxidative damage. In conclusion, this review article has shed light on the hazardous impacts of soil-affected soils, various salinity tolerance mechanisms adopted by crops and the prospective mechanisms involved in Se-mediated salinity tolerance as well as improvements in the growth and productivity of various crop plants cultivated in salt-affected soils.

In this review paper, after critically reviewing the best available data to date, the authors anticipated that there would be an emergent interest in the scientific community to studying the mechanisms of Se-assisted salinity tolerance in plants in the near future; therefore, the following research gaps need to be explored in future.

On an instructive note, the suitable concentration of Se supplementation is still a matter of research. Complete interpretation of the role of Se as well as detailed protective mechanisms would be helpful for developing salinity tolerance in plants.

The Se transformations in the plants are still unclear. Therefore, future studies are required to explore the exact mechanisms involved in Se transformations inside plant species that enhance Se transfer to the plant shoots and its volatilization from aerial plant parts.

Previous researchers have focused on evaluating the role of Se in individual plant species grown in salt-affected soils; however, there is still a need to better understand its ameliorative roles in more plant species under various environmental factors for the confirmation of the Se-mediated amelioration of salinity-induced phytotoxicity on a larger scale.

According to the reviewed data, Se in most experiments was used under saline nutrient mediums (hydroponics). Such experimental results can overestimate the Na⁺ uptake and translocation within the plant body. It is advised to conduct future experiments on natural saline soils (pots or field), as soil is a complex system, which will provide a better understanding of Se-mediated salinity-tolerance mechanisms. Moreover, such experiments will help the local farming community to learn about the use of Se in farming practices.

More importantly, to date, most soil-based experiments have been executed over the short term, which raises questions on Se’s potential to remediate salt-affected soils in the long term. Therefore, well-planned, comprehensive, and long-term field experiments are needed to check the productivity and economic feasibility of Se-based ameliorations of saline soils.

Despite the widespread occurrence of Se deficiency globally, Se toxicity (selenosis) is a problem in some areas. Some soils and mineral deposits are naturally Se rich, and exploitation of these seleniferous soils can lead to toxic accumulation of Se in the environment. Therefore, effective enrichment of agricultural crops with Se via soil using Se-enriched fertilizers can be challenging due to varying soil
Se concentrations, soil types, soil redox potentials, soil pH, and microbiological activity. Furthermore, the high cost of Se fertilizer, in combination with the modest incorporation rate, should be considered.

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**Abbreviations**

| Abbreviation | Definition |
|--------------|------------|
| Se-NPs | Selenium-nanoparticles |
| GSH | Reduced glutathione |
| GSSG | Oxidized glutathione |
| DHAR | Dehydroascorbate reductase |
| MDHAR | Monodehydroascorbate reductase |
| GST | Glutathione S-transferase |
| GR | Glutathione reductase |
| POX | Peroxidase |
| PAL | Activity of phenylalanine ammonia-lyase |
| GSH-Px | Glutathione peroxidase |
| CAT | Catalase activity |
| APX | Ascorbate peroxidase activity |
| SOD | Superoxide dismutase activity |
| POD | Peroxidase activity |
| GPX | Glutathione peroxidase activity |
| MDAR | Monodehydroascorbate reductase activity |
| RWC | Relative water contents |
| TBARS | Thiobarbituric acid reactive substances |
| NPQ | Non-photochemical quenching |
| MDA | Malondialdehyde |
| RuBPCase | Ribulose-1,5-bisphosphate-carboxylase/oxygenase content |
| SPAD | Chlorophyll content in leaves |
| H₂O₂ | Hydrogen peroxide |
| ATP | Adenosine triphosphate |
| NADP⁺ | Nicotinamide adenine dinucleotide phosphate |
| MAPK | Mitogen activated protein kinase gene |
| CPK | Calcium dependent protein kinase gen |
| NADK2 | NAD kinase2 gene |
| ALMT | Aluminum-activated malate transporters |
| SULTRs | Sulfate transporters |
| γ-GK | γ-Glutamyl kinase |
| NHX | Sodium/hydrogen (Na⁺/H⁺) exchanger gene |
| PSII | Photosystem II |
| NPK | Nitrogen, phosphorous, and potassium |

**References**

1. Gontia-Mishra, I.; Sasidharan, S.; Tiwari, S. Recent developments in use of 1-aminocyclopropane-1-carboxylate (ACC) deaminase for conferring tolerance to biotic and abiotic stress. *Biotechnol. Lett.* **2014**, *36*, 889–898. [CrossRef] [PubMed]

2. Abbasi, G.H.; Akhtar, J.; Ahmad, R.; Jamil, M.; Anwar-Ul-Haq, M.; Ali, S.; Ijaz, M. Potassium application mitigates salt stress differentially at different growth stages in tolerant and sensitive maize hybrids. *Plant Growth Regul.* **2015**, *76*, 111–125. [CrossRef]
3. Wallender, W.W.; Tanji, K.K. Agricultural Salinity Assessment and Management; American Society of Civil Engineers: Reston, VA, USA, 2011.

4. Munns, R.; Tester, M. Mechanisms of Salinity Tolerance. *Ann. Rev. Plant Biol.* 2008, 59, 651–681. [CrossRef] [PubMed]

5. Abdel Latef, A.A. Changes of antioxidative enzymes in salinity tolerance among different wheat cultivars. *Cereal Res. Commun.* 2010, 38, 43–55. [CrossRef]

6. Shabala, S.; Cuin, T.A. Potassium transport and plant salt tolerance. *Physiol. Plant.* 2008, 133, 651–669. [CrossRef]

7. Ruiz-Lozano, J.M.; Collados, C.; Barea, J.M.; Azcón, R. Arbuscular mycorrhizal symbiosis can alleviate drought-induced nodule senescence in soybean plants. *New Phytol.* 2001, 151, 493–502. [CrossRef]

8. Munns, R. Comparative physiology of salt and water stress. *Plant Cell Environ.* 2002, 25, 239–250. [CrossRef]

9. Wang, W.; Vinocur, B.; Altman, A. Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. *Planta* 2003, 218, 1–14. [CrossRef]

10. Sheng, M.; Tang, M.; Chen, H.; Yang, B.; Zhang, F.; Huang, Y. Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress. *Mycorrhiza* 2008, 18, 287–296. [CrossRef]

11. Flowers, T.J.; Galal, H.K.; Bromham, L. Evolution of halophytes: Multiple origins of salt tolerance in land plants. *Funct. Plant Biol.* 2010, 37, 604–612. [CrossRef]

12. Nabati, J.; Kafi, M.; Nezami, A.; Moghaddam, P.R.; Ali, M.; Mehrjerdi, M.Z. Effect of salinity on biomass production and activities of some key enzymatic antioxidants in Kochia (*Kochia scoparia*). *Pak. J. Bot.* 2011, 43, 539–548.

13. Ahanger, M.A.; Agarwal, R.M. Salinity stress induced alterations in antioxidant metabolism and nitrogen assimilation in wheat (*Triticum aestivum* L.) as influenced by potassium supplementation. *Plant Physiol. Biochem.* 2017, 115, 449–460. [CrossRef] [PubMed]

14. Jiang, C.; Zheng, Q.; Liu, Z.; Xu, W.; Liu, L.; Zhao, G.; Long, X. Overexpression of Arabidopsis thaliana Na⁺/H⁺ antiporter gene enhanced salt resistance in transgenic poplar (*Populus × euramericana “Neva”).* *Trees* 2012, 26, 685–694. [CrossRef]

15. Mittal, S.; Kumari, N.; Sharma, V. Differential response of salt stress on *Brassica juncea*: Photosynthetic performance, pigment, proline, D1 and antioxidant enzymes. *Plant Physiol. Biochem.* 2012, 54, 17–26. [CrossRef] [PubMed]

16. Gengmao, Z.; Shuhui, L.; Xing, S.; Yizhou, W.; Zipan, C. The role of silicon in physiology of the medicinal plant (*Lonicera japonica* L.) under salt stress. *Sci. Rep.* 2015, 5, 12696. [CrossRef] [PubMed]

17. Quintero, J.M.; Fournier, J.M.; Benlloch, M. Na⁺ accumulation in shoot is related to water transport in K⁺-starved sunflower plants but not in plants with a normal K⁺ status. *J. Plant Physiol.* 2007, 164, 60–67. [CrossRef] [PubMed]

18. Noctor, G.; Foyer, C.H. Ascorbate and Glutathione: Keeping Active Oxygen Under Control. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 1998, 49, 249–279. [CrossRef]

19. Pitzschke, A.; Forzani, C.; Hirt, H. Reactive oxygen species signaling in plants. *Antioxid. Redox Signal.* 2006, 8, 1757–1764. [CrossRef]

20. Farooq, M.; Hussain, M.; Wakeel, A.; Siddique, K.H. Salt stress in maize: Effects, resistance mechanisms, and management. *A Rev. Agron. Sustain. Dev.* 2015, 35, 461–481. [CrossRef]

21. Aghighi Shahverdi, M.; Omidi, H.; Tabatabaei, S.J. Plant growth and steviol glycosides as affected by foliar application of selenium, boron, and iron under NaCl stress in Stevia rebaudiana Bertoni. *Ind. Crops Prod.* 2018, 125, 408–415. [CrossRef]

22. Iqbal, M.; Hussain, I.; Liaoqat, H.; Ashraf, M.A.; Rasheed, R.; Rehman, A.U. Exogenously applied selenium reduces oxidative stress and induces heat tolerance in spring wheat. *Plant Physiol. Biochem.* 2015, 94, 95–103. [CrossRef] [PubMed]

23. Sieprawska, A.; Kornaś, A.; Filek, M. Involvement of selenium in protective mechanisms of plants under environmental stress conditions—Review. *Acta Biol. Crac. Ser. Bot.* 2015, 57, 9–20. [CrossRef]

24. Hasanuzzaman, M.; Hossain, M.A.; Fujita, M. Selenium-induced up-regulation of the antioxidant defense and methylglyoxal detoxification system reduces salinity-induced damage in rapeseed seedlings. *Biol. Trace Elem. Res.* 2011, 143, 1704–1721. [CrossRef] [PubMed]
25. Versini, A.; Di Tullo, P.; Aubry, E.; Bueno, M.; Thiry, Y.; Pannier, F.; Castrec-Rouelle, M. Influence of Se concentrations and species in hydroponic cultures on Se uptake, translocation and assimilation in non-accumulator ryegrass. *Plant Physiol. Biochem.* **2016**, *108*, 372–380. [CrossRef]

26. Babalar, M.; Mehebbi, S.; Zamani, Z.; Askari, M.A. Effect of foliar application with sodium selenate on selenium biofortification and fruit quality maintenance of Starking Delicious apple during storage. *J. Sci. Food Agric.* **2019**, *99*, 5149–5156. [CrossRef]

27. Subramanyam, K.; Du Laing, G.; Van Damme, E.J.M. Sodium selenate treatment using a combination of seed priming and foliar spray alleviates salinity stress in rice. *Front. Plant Sci.* **2019**, *10*, 116. [CrossRef]

28. Elkelish, A.A.; Soliman, M.H.; Alhaithloul, H.A.; El-Esawi, M.A. Selenium protects wheat seedlings against salt stress-mediated oxidative damage by up-regulating antioxidants and osmolytes metabolism. *Plant Physiol. Biochem.* **2019**, *137*, 144–153. [CrossRef]

29. Jiang, C.; Zu, C.; Lu, D.; Zheng, Q.; Shen, J.; Wang, H.; Li, D. Effect of exogenous selenium supply on photosynthesis, Na\(^+\) accumulation and antioxidative capacity of maize (*Zea mays* L.) under salinity stress. *Sci. Rep.* **2017**, *7*, 42039. [CrossRef]

30. Diao, M.; Ma, L.; Wang, J.; Cui, J.; Fu, A.; Liu, H.Y. Selenium Promotes the Growth and Photosynthesis of Tomato Seedlings Under Salt Stress by Enhancing Chloroplast Antioxidant Defense System. *J. Plant Growth Regul.* **2014**, *33*, 671–682. [CrossRef]

31. Kusvuran, S.; Kiran, S.; Ellialtioglu, S.S. Antioxidant Enzyme Activities and Abiotic Stress Tolerance Relationship in Vegetable Crops. In *Abiotic and Biotic Stress in Plants—Recent Advances and Future Perspectives*; IntechOpen: London, UK, 2016.

32. Munns, R. Physiological processes limiting plant growth in saline soils: Some dogmas and hypotheses. *Plant Cell Environ.* **1993**, *16*, 15–24. [CrossRef]

33. Evelin, H.; Kapoor, R.; Giri, B. Arbuscular mycorrhizal fungi in alleviation of salt stress: A review. *Ann. Bot.* **2009**, *104*, 1263–1280. [CrossRef] [PubMed]

34. Hajiboland, R.; Aliasgharzad, N.; Laiegh, S.F.; Poschenrieder, C. Colonization with arbuscular mycorrhizal fungi improves salinity tolerance of tomato (*Solanum lycopersicum* L.) plants. *Plant Soil* **2010**, *331*, 313–327. [CrossRef]

35. Hussain, M.; Park, H.W.; Farooq, M.; Jabran, K.; Lee, D.J. Morphological and physiological basis of salt resistance in different rice genotypes. *Int. J. Agric. Biol.* **2013**, *15*, 113–118.

36. Hachicha, M.; Kahlaoui, B.; Khamassi, N.; Misle, E.; Jouzdan, O. Effect of electromagnetic treatment of saline water on soil and crops. *J. Saudi Soc. Agric. Sci.* **2018**, *17*, 154–162. [CrossRef]

37. Hamada, A.M. Alleviation of the adverse effects of NaCl on germination, seedling, growth and metabolic activities of maize plants by calcium salts. *Bull. Fac. Sci. Assiut Univ.* **1995**, *24*, 211–220.

38. Lee, D.G.; Park, K.W.; An, J.Y.; Sohn, Y.G.; Ha, J.K.; Kim, H.Y.; Bae, D.W.; Lee, K.H.; Kang, N.J.; Lee, B.H.; et al. Proteomics analysis of salt-induced leaf proteins in two rice germplasms with different salt sensitivity. *Can. J. Plant Sci.* **2011**, *91*, 337–349. [CrossRef]

39. Ibrahim, E.A. Seed priming to alleviate salinity stress in germinating seeds. *J. Plant Physiol.* **2016**, *192*, 38–46. [CrossRef]

40. Memon, S.A.; Hou, X.; Wang, L.J. Morphological analysis of salt stress response of pak choi. *Electron. J. Environ. Agric. Food Chem.* **2010**, *9*, 1.

41. Hanafy, M.S.; El-Banna, A.; Schumacher, H.M.; Jacobsen, H.J.; Hassan, F.S. Enhanced tolerance to drought and salt stresses in transgenic faba bean (*Vicia faba* L.) plants by heterologous expression of the PR10a gene from potato. *Plant Cell Rep.* **2013**, *32*, 663–674. [CrossRef]

42. Kapoor, K.; Srivastava, A. Assessment of Salinity Tolerance of Vigna mungo Var. Pu-19 Using ex vitro and in vitro Methods. *Asian J. Biotechnol.* **2010**, *2*, 73–85. [CrossRef]

43. Anwar-ul-Haq, M.; Akram, S.; Akhtar, J.; Saqib, M.; Saqib, Z.A.; Abbasi, G.H.; Jan, M. Morpho-physiological characterization of sunflower genotypes (*Helianthus annuus* L.) under saline condition. *Pak. J. Agric. Sci.* **2013**, *50*, 49–54.

44. Mallahi, T.; Saharkhiz, M.J.; Javanmardi, J. Salicylic acid changes morpho-physiological attributes of feverfew (*Tanacetum parthenium* L.) under salinity stress. *Acta Ecol. Sin.* **2018**, *38*, 351–355. [CrossRef]

45. Qados, A.M.S.A. Effect of salt stress on plant growth and metabolism of bean plant *Vicia faba* (L.). *J. Saudi Soc. Agric. Sci.* **2011**, *10*, 7–15.
46. Hajiboland, R.; Norouzi, F.; Poschenrieder, C. Growth, physiological, biochemical and ionic responses of pistachio seedlings to mild and high salinity. *Trees Struct. Funct.* 2014, 28, 1065–1078. [CrossRef]

47. Ahmadi, F.I.; Karimi, K.; Struik, P.C. Effect of exogenous application of methyl jasmonate on physiological and biochemical characteristics of *Brassica napus* L. cv. Talaye under salinity stress. *S. Afr. J. Bot.* 2018, 115, 5–11. [CrossRef]

48. Shi, Q.; Ding, F.; Wang, X.; Wei, M. Exogenous nitric oxide protects cucumber roots against oxidative stress induced by salt stress. *Plant Physiol. Biochem.* 2007, 45, 542–550. [CrossRef] [PubMed]

49. Netondo, G.W.; Oryango, J.C.; Beck, E. Sorghum and salinity: II. Gas exchange and chlorophyll fluorescence of sorghum under salt stress. *Crop Sci.* 2004, 44, 806. [CrossRef]

50. Sapre, S.; Gontia-Mishra, I.; Tiwari, S. Klebsiella sp. confers enhanced tolerance to salinity and plant growth promotion in oat seedlings (*Avena sativa*). *Microbiol. Res.* 2018, 206, 25–32. [CrossRef]

51. Rozef, N. Sugarcane and salinity—A review paper. *Sugarcane Cane* 1995.

52. Cantabella, D.; Piquerás, A.; Acosta-Motos, J.R.; Bernal-Vicente, A.; Hernández, J.A.; Díaz-Vivancos, P. Salt-tolerance mechanisms induced in *Stevia rebaudiana* Bertoni: Effects on mineral nutrition, antioxidative metabolism and steviol glycoside contents. *Plant Physiol. Biochem.* 2017, 115, 484–496. [CrossRef]

53. Khan, M.I.R.; Asgher, M.; Khan, N.A. Alleviation of salt-induced photosynthesis and growth inhibition by salicylic acid involves glycinebetaine and ethylene in mungbean (*Vigna radiata* L.). *Plant Physiol. Biochem.* 2014, 80, 67–74. [CrossRef] [PubMed]

54. Munns, R. Genes and salt tolerance: Bringing them together. *New Phytol.* 2005, 167, 645–663. [CrossRef] [PubMed]

55. Hussain, S.; Zhang, J.H.; Zhong, C.; Zhu, L.F.; Cao, X.C.; Yu, S.M.; Allen Bohr, J.; Hu, J.J.; Jin, Q.Y. Effects of salt stress on rice growth, development characteristics, and the regulating ways: A review. *J. Integr. Agric.* 2017, 16, 2357–2374. [CrossRef]

56. Hussain, S.; Zhong, C.; Bai, Z.; Cao, X.; Zhu, L.; Hussain, A.; Zhu, C.; Fahad, S.; James, A.B.; Zhang, J.; et al. Effects of 1-Methylcyclopropene on Rice Growth Characteristics and Superior and Inferior Spikelet Development Under Salt Stress. *J. Plant Growth Regul.* 2018, 37, 1368–1384. [CrossRef]

57. Lee, M.H.; Cho, E.J.; Wi, S.G.; Bae, H.; Kim, J.E.; Cho, J.Y.; Lee, S.; Kim, J.H.; Chung, B.Y. Divergences in morphological changes and antioxidant responses in salt-tolerant and salt-sensitive rice seedlings after salt stress. *Plant Physiol. Biochem.* 2013, 70, 325–335. [CrossRef] [PubMed]

58. Zahedi, S.M.; Abdelrahman, M.; Hosseini, M.S.; Hoveizeh, N.F.; Tran, L.P. Alleviation of the effect of salinity on growth and yield of strawberry by foliar spray of selenium-nanoparticles. In *Environmental Pollution*; Elsevier: Amsterdam, The Netherlands, 2019.

59. Gururani, M.A.; Venkatesh, J.; Tran, L.S.P. Regulation of photosynthesis during abiotic stress-induced photoinhibition. *Mol. Plant* 2015, 8, 1304–1320. [CrossRef]

60. James, R.A.; Blake, C.; Byrt, C.S.; Munns, R. Major genes for Na+ exclusion, Nax1 and Nax2 (wheat HKT1;4 and HKT1;5), decrease Na+ accumulation in bread wheat leaves under saline and waterlogged conditions. *J. Exp. Bot.* 2011, 62, 2939–2947. [CrossRef]

61. Singam, K.; Juntaowong, N.; Cha-Um, S.; Kirdmanee, C. Salt stress induced ion accumulation, ion homeostasis, membrane injury and sugar contents in salt-sensitive rice (*Oryza sativa* L. *indica*) roots under isosmotic conditions. *Afr. J. Biotechnol.* 2011, 10, 1340–1346.

62. Hussain, S.; Bai, Z.; Huang, J.; Cao, X.; Zhu, L.; Zhu, C.; Khashkeli, M.A.; Zhong, C.; Jin, Q.; Zhang, J. 1-methylcyclopentene modulates physiological, biochemical, and antioxidant responses of rice to different salt stress levels. *Front. Plant Sci.* 2019, 10. [CrossRef]

63. Demiral, T.; Türkan, I. Comparative lipid peroxidation, antioxidative defense systems and proline content in roots of two rice cultivars differing in salt tolerance. *Environ. Exp. Bot.* 2005, 53, 247–257. [CrossRef]

64. Levitt, J. Responses of Plants to Environmental Stresses. *J. Range Manag.* 1985, 38, 480. [CrossRef]

65. Pattanayak, G.K.; Tripathy, B.C. Overexpression of protochlorophyllide oxidoreductase c regulates oxidative stress in arabidopsis. *PloS ONE* 2011, 6, e26352. [CrossRef] [PubMed]

66. Santos, M.G.; Ribeiro, R.V.; Machado, E.C.; Pimentel, C. Photosynthetic parameters and leaf water potential of five common bean genotypes under mild water deficit. *Biol. Plant.* 2009, 53, 229–236. [CrossRef]

67. Foyer, C.H.; Noctor, G. Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. *Physiol. Plant.* 2003, 119, 355–364. [CrossRef]
68. Kamran, M.; Malik, Z.; Parveen, A.; Huang, L.; Riaz, M.; Bashir, S.; Mustafa, A.; Abbasi, G.H.; Xue, B.; Ali, U. Ameliorative Effects of Biochar on Rapeseed (Brassica napus L.) Growth and Heavy Metal Immobilization in Soil Irrigated with Untreated Wastewater. In *Journal of Plant Growth Regulation*; Springer: Berlin, Germany, 2019; pp. 1–16.

69. Adly, A.A.M. Oxidative stress and disease: An updated review. *Res. J. Immunol.* 2010, 3, 129–145.

70. Houot, V.; Etienne, P.; Petitot, A.S.; Barbier, S.; Blein, J.P.; Suty, L. Hydrogen peroxide induces programmed cell death features in cultured tobacco BY-2 cells, in a dose-dependent manner. *J. Exp. Bot.* 2001, 52, 1721–1730.

71. Farmer, E.E.; Mueller, M.J. ROS-Mediated Lipid Peroxidation and RES-Activated Signaling. *Ann. Rev. Plant Biol.* 2013, 64, 429–450. [CrossRef]

72. Asada, K. Production and Action of Active Oxygen Species in Photosynthetic Tissues. In *Causes of Photooxidative Stress and Amelioration of Defense Systems in Plants*; CRC press: Boca Raton, FL, USA, 1994; pp. 77–104. ISBN 0-8493-5443-9.

73. Drobot, L.B.; Samoylenko, A.A.; Vorotnikov, A.V.; Turyan -Kuzmin, P.A.; Bazalii, A.V.; Kietzmann, T.; Tkachuk, V.A.; Komisarenko, S.V. Reactive oxygen species in signal transduction. *Ukrain’skyi Biokhimichnyi Zhurnal* 2013, 85, 209–217. [CrossRef]

74. Ramachandra Reddy, A.; Chaitanya, K.V.; Jutur, PP.; Sumithra, K. Differential antioxidative responses to water stress among five mulberry (Morus alba L.) cultivars. *Environ. Exp. Bot.* 2004, 52, 33–42. [CrossRef]

75. Li, M.; Guo, S.; Xu, Y.; Meng, Q.; Li, G.; Yang, X. Glycine betaine-mediated potentiation of HSP gene expression involves calcium signaling pathways in tobacco exposed to NaCl stress. *Physiol. Plant.* 2014, 150, 63–75. [CrossRef]

76. Farhangi-Abiriz, S.; Ghassemi-Golezani, K. How can salicylic acid and jasmone acid mitigate salt toxicity in soybean plants? *Ecotoxicol. Environ. Saf.* 2018, 154, 1010–1016. [CrossRef] [PubMed]

77. Kamran, M.; Malik, Z.; Parveen, A.; Zong, Y.; Shaaban, M.; Mustafa, A.; Bashir, S.; Rafay, M.; et al. Biochar alleviates Cd phytotoxicity by minimizing bioavailability and oxidative stress in pak choi (Brassica chinensis L.) cultivated in Cd-polluted soil. *J. Environ. Manag.* 2019, 250, 109500. [CrossRef] [PubMed]

78. Krishnaiah, D.; Sarbatly, R.; Nithyanandam, R. A review of the antioxidant potential of medicinal plant species. *Food Bioprod. Process.* 2011, 89, 217–233. [CrossRef]

79. Cheeseman, J.M. The evolution of halophytes, glycophytes and crops, and its implications for food security under saline conditions. *New Phytol.* 2015, 206, 557–570. [CrossRef] [PubMed]

80. Mbarki, S.; Sytar, O.; Cerda, A.; Zivcak, M.; Rastogi, A.; He, X.; Zoghliami, A.; Abdellcy, C.; Brestic, M. Strategies to mitigate the salt stress effects on photosynthetic apparatus and productivity of crop plants. In *Salinity Responses and Tolerance in Plants, Volume 1: Targeting Sensory, Transport and Signaling Mechanisms*; Springer: Berlin, Germany, 2018; ISBN 9-7833-1975-6714.

81. Zhang, H.X.; Blumwald, E. Transgenic salt-tolerant tomato plants accumulate salt in foliage but not in fruit. *Nat. Biotechnol.* 2001, 19, 765. [CrossRef]

82. Takahashi, R.; Liu, S.; Takano, T. Isolation and characterization of plasma membrane Na+/H+ antiporter genes from salt-sensitive and salt-tolerant reed plants. *J. Plant Physiol.* 2009, 166, 301–309. [CrossRef]

83. Zhang, J.; Wang, F.; Zhang, C.; Zhang, J.; Chen, Y.; Liu, G.; Zhao, Y.; Hao, F.; Zhang, J. A novel VIGS method by agroinoculation of cotton seeds and application for elucidating functions of GhBI-1 in salt-stress response. *Plant Cell Rep.* 2018, 37, 1091–1100. [CrossRef]

84. Demidchik, V.; Cuin, T.A.; Svistunenko, D.; Smith, S.J.; Miller, A.J.; Shabala, S.; Sokolik, A.; Yurin, V. Arabidopsis root K+–efflux conductance activated by hydroxyl radicals: Single-channel properties, genetic basis and involvement in stress-induced cell death. *J. Cell Sci.* 2010, 123, 1468–1479. [CrossRef]

85. Islas, R.; Aragüés, R. Yield and plant ion concentrations in maize (Zea mays L.) subject to diurnal and nocturnal saline sprinkler irrigations. *Field Crops Res.* 2010, 123, 1468–1479. [CrossRef]

86. Wakeel, A.; Farooq, M.; Qadir, M.; Schubert, S. Potassium substitution by sodium in plants. *Crit. Rev. Plant Sci.* 2011, 30, 401–413. [CrossRef]

87. Bhosale, R.; Boudolf, V.; Cuevas, F.; Lu, R.; Eekhout, T.; Hu, Z.; Van Isterdael, G.; Lambert, G.M.; Xu, F.; Nowacky, M.K.; et al. A spatiotemporal dna endoploidy map of the arabidopsis root reveals roles for the endocycle in root development and stress adaptation. *Plant Cell* 2018, 30, 2303–2351. [CrossRef] [PubMed]

88. Lv, S.; Yu, D.; Sun, Q.; Jiang, J. Activation of gibberellin 20-oxidase 2 undermines auxin-dependent root and root hair growth in NaCl-stressed Arabidopsis seedlings. *Plant Growth Regul.* 2018, 84, 225–236. [CrossRef]
98. Menezes-Benavente, L.; Kernodle, S.P.; Margis-Pinheiro, M.; Scandalios, J.G. Salt-induced antioxidant metabolism defenses in maize (Zea mays L.) seedlings. *Redox Rep.* **2004**, *9*, 29–36. [CrossRef] [PubMed]
99. Uddin, M.N.; Hanstein, S.; Leubner, R.; Schubert, S. Leaf Cell-Wall Components as Influenced in the First Phase of Salt Stress in Three Maize (Zea mays L.) Hybrids Differing in Salt Resistance. *J. Agron. Crop Sci.* **2013**, *199*, 405–415. [CrossRef]
100. Hawrylak-Nowak, B. Selenite is more efficient than selenate in alleviation of salt stress in lettuce plants. *Acta Biol. Crac. Ser. Bot.* **2015**, *57*, 49–54. [CrossRef]
101. Mehdi, Y.; Hornick, J.L.; Istasse, L.; Dufrasne, I. Selenium in the environment, metabolism and involvement in body functions. *Molecules* **2013**, *18*, 3292–3311. [CrossRef]
102. Shahid, M.; Niazi, N.K.; Khalid, S.; Murtaza, B.; Bibi, I.; Rashid, M.I. A critical review of selenium biogeochemical behavior in soil-plant system with an inference to human health. *Environ. Pollut.* **2018**, *234*, 915–934.
103. Galeas, M.L.; Zhang, L.H.; Freeman, J.L.; Wegner, M.; Pilon-Smits, E.A.H. Seasonal fluctuations of selenium and sulfur accumulation in selenium hyperaccumulators and related nonaccumulators. *New Phytol.* **2007**, *173*, 517–525. [CrossRef]
104. Hartikainen, H. Biogeochemistry of selenium and its impact on food chain quality and human health. *J. Trace Elem. Med. Biol.* **2005**, *18*, 309–318. [CrossRef]
105. White, P.J. Selenium accumulation by plants. *Ann. Bot.* **2015**, *117*, 217–235. [CrossRef]
106. Cartes, P.; Gianfreda, L.; Paredes, C.; Mora, M.L. Selenium uptake and its antioxidant role in ryegrass cultivars as affected by selenite seed pelletization. *J. Soil Sci. Plant Nutr.* **2011**, *11*, 1–14. [CrossRef]
107. Nakamura, Y.M.; Altansuvd, A.; Moradi, F.; Sanavy, S.A.M.M.; Allahdadi, I. The role of phytohormones in alleviating salt stress in crop plants. *Aust. J. Crop Sci.* **2011**, *5*, 726.
108. Kikkert, J.; Berkelaar, E. Plant uptake and translocation of inorganic and organic forms of selenium. *Arch. Environ. Contam. Toxicol.* **2013**, *65*, 458–465. [CrossRef] [PubMed]
109. Bruggeman, C.; Maes, A.; Vanclooyen, J. The interaction of dissolved Boom Clay and Gorleben humic substances with selenium oxyanions (selenite and selenate). *Appl. Geochem.* **2007**, *22*, 1371–1379. [CrossRef]
10. Shand, C.A.; Eriksson, J.; Dahlin, A.S.; Lumsdon, D.G. Selenium concentrations in national inventory soils from Scotland and Sweden and their relationship with geochemical factors. *J. Geochem. Exp.* 2012, 121, 4–14. [CrossRef]

11. Beckett, G.J.; Arthur, J.R. Selenium and endocrine systems. *J. Endocrinol.* 2005, 184, 455–465. [CrossRef] [PubMed]

12. Tan, J.; Zhu, W.; Wang, W.; Li, R.; Hou, S.; Wang, D.; Yang, L. Selenium in soil and endemic diseases in China. *Sci. Total Environ.* 2002, 284, 227–235. [CrossRef]

13. Song, Z.; Shao, H.; Huang, H.; Shen, Y.; Wang, L.; Wu, F.; Han, D.; Song, J.; Jia, H. Overexpression of the phosphate transporter gene OsPT8 improves the Pi and selenium contents in *Nicotiana tabacum*. *Environ. Exp. Bot.* 2017, 137, 158–165. [CrossRef]

14. Wang, P.; Menzies, N.W.; Lombi, E.; McKenna, B.A.; James, S.; Tang, C.; Kopittke, P.M. Synchrotron-based X-ray absorption near-edge spectroscopy imaging for laterally resolved speciation of selenium in fresh roots and leaves of wheat and rice. *J. Exp. Bot.* 2015, 66, 4795–4806. [CrossRef]

15. Yang, X.; Lu, C. Photosynthesis is improved by exogenous glycinebetaine in salt-stressed maize plants. *Physiol. Plant.* 2005, 124, 343–352. [CrossRef]

16. Huang, Q.Q.; Wang, Q.; Wan, Y.N.; Yu, Y.; Jiang, R.F.; Li, H.F. Application of X-ray absorption near edge spectroscopy to the study of the effect of sulphur on selenium uptake and assimilation in wheat seedlings. *Biol. Plant.* 2017, 61, 726–732. [CrossRef]

17. Malcheska, F.; Ahmad, A.; Batool, S.; Müller, H.M.; Ludwig-Müller, J.; Kreuzwieser, J.; Randewig, D.; Hänsch, R.; Mendel, R.R.; Hell, R.; et al. Drought-enhanced xylem sap sulfate closes stomata by affecting ALMT12 and guard cell ABA synthesis. *Plant Physiol.* 2017, 174, 789–814. [CrossRef]

18. Gigolashvili, T.; Kopriva, S. Transporters in plant sulfur metabolism. *Front. Plant Sci.* 2014, 5, 442. [CrossRef] [PubMed]

19. Winkel, L.H.E.; Vriens, B.; Jones, G.D.; Schneider, L.S.; Pilon-Smits, E.; Bañuelos, G.S. Selenium cycling across soil-plant-atmosphere interfaces: A critical review. *Nutrients* 2015, 7, 4199–4239. [CrossRef] [PubMed]

20. Wang, J.; Cappa, J.J.; Harris, J.P.; Edger, P.P.; Zhou, W.; Pires, J.C.; Adair, M.; Unruh, S.A.; Simmons, M.P.; Schiavon, M.; et al. Transcriptome-wide comparison of selenium hyperaccumulator and nonaccumulator Stanleya species provides new insight into key processes mediating the hyperaccumulation syndrome. *Plant Physiol.* 2018, 174, 797–814. [CrossRef]

21. Carey, A.M.; Scheckel, K.G.; Lombi, E.; Newville, M.; Choi, Y.; Norton, G.J.; Price, A.H.; Meharg, A.A. Grain accumulation of selenium species in rice (*Oryza sativa* L.). *Environ. Sci. Technol.* 2012, 46, 5557–5564. [CrossRef] [PubMed]

22. Ashraf, M.A.; Akbar, A.; Parveen, A.; Rasheed, R.; Hussain, I.; Iqbal, M. Phenological application of selenium differentially improves growth, oxidative defense and ion homeostasis in maize under salinity stress. *Plant Physiol. Biochem.* 2018, 123, 268–280. [CrossRef]

23. Butt, M.; Ayyub, C.M.; Amjad, M.; Ahmad, R. Proline application enhances growth of chilli by improving physiological and biochemical attributes under salt stress. *Pak. J. Agric. Sci.* 2016, 53, 43–49.

24. Hawrylak-Nowak, B. Beneficial effects of exogenous selenium in cucumber seedlings subjected to salt stress. *Biol. Trace Elem. Res.* 2009, 132, 259–269. [CrossRef]

25. Habibi, G.; Sarvary, S. The Roles of Selenium in Protecting Lemon Balm against Salt Stress. *Iran. J. Plant Physiol.* 2015, 5, 1425–1433.

26. Sattar, A.; Cheema, M.A.; Abbas, T.; Sher, A.; Ijaz, M.; Hussain, M. Separate and combined effects of silicon and selenium on salt tolerance of wheat plants. *Russ. J. Plant Physiol.* 2017, 64, 341–348. [CrossRef]

27. Astaneh, R.K.; Bolandnazar, S.; Nahandi, F.Z.; Oustan, S. Effects of selenium on enzymatic changes and productivity of garlic under salinity stress. *S. Afr. J. Bot.* 2019, 121, 447–455. [CrossRef]

28. Mozafariyan, M.; Kamelimanesh, M.M.; Hawrylak-Nowak, B. Ameliorative effect of selenium on tomato plants grown under salinity stress. *Arch. Agron. Soil Sci.* 2016, 62, 1368–1380. [CrossRef]

29. Astaneh, R.K.; Bolandnazar, S.; Nahandi, F.Z.; Oustan, S. The effects of selenium on some physiological traits and K, Na concentration of garlic (*Allium sativum* L.) under NaCl stress. *Inf. Process. Agric.* 2018, 5, 156–161. [CrossRef]

30. Atarodi, B.; Fotovat, A.; Khorassani, R.; Keshavarz, P.; Hawrylak-Nowak, B. Selenium improves physiological responses and nutrient absorption in wheat (*Triticum aestivum* L.) grown under salinity. *Toxicol. Environ. Chem.* 2018, 100, 440–451. [CrossRef]
131. Bybordi, A.; Saadat, S.; Zargaripour, P. The effect of zeolite, selenium and silicon on qualitative and quantitative traits of onion grown under salinity conditions. *Arch. Agron. Soil Sci.* 2018, 64, 520–530. [CrossRef]

132. Moussa, H.R.; Hassen, A.M. Selenium Affects Physiological Responses of Phaseolus vulgaris in Response to Salt Level. *Int. J. Veg. Sci.* 2018, 24, 236–253. [CrossRef]

133. Habibi, G. Selenium ameliorates salinity stress in Petroselinum crispum by modulation of photosynthesis and by reducing shoot Na accumulation. *Russ. J. Plant Physiol.* 2017, 64, 368–374. [CrossRef]

134. Khalifa, G.S.; Abdelrassoul, M.; Hegazi, A.; Elsherif, M.H. Mitigation of Saline Stress Adverse Effects in Lettuce Plant Using Selenium and Silicon. *Middle East J. Agric. Res.* 2016, 347–361.

135. Abul-Soud, M.A.; Abd-Elrahman, S.H. Foliar application of selenium increases fertility and grain yield under foliar application of manganese. *Acta Physiol. Plant.* 2003, 23, 545–555. [CrossRef]

136. Hashem, H.A.; Hassanein, R.A.; Bekheta, M.A.; El-Kady, F.A. Protective role of selenium in canola (*Brassica napus* L.) plant subjected to salt stress. *Egypt. J. Exp. Biol.* 2013, 9, 199–211.

137. Selenium Induces Antioxidant Defensive Enzymes and Promotes Tolerance Against Salinity Stress in Cucumber Seedlings (*Cucumis sativus*). *Arab. Univ. J. Agric. Sci.* 2010, 18, 65–76.

138. Kong, L.; Wang, M.; Bi, D. Selenium modulates the activities of antioxidant enzymes, osmotic homeostasis and promotes the growth of sorrel seedlings under salt stress. *Plant Growth Regul.* 2005, 45, 155–163. [CrossRef]

139. Rietz, D.N.; Haynes, R.J. Effects of irrigation-induced salinity and sodicity on soil microbial activity. *Soil Biol. Biochem.* 2003, 35, 845–854. [CrossRef]

140. Carillo, P.; Mastrolonardo, G.; Nacca, F.; Fuggi, A. Nitrate reductase in durum wheat seedlings as affected by nitrate nutrition and salinity. *Funct. Plant Biol.* 2005, 32, 209–219. [CrossRef]

141. Shahzadi, I.; Iqbal, M.; Rasheed, R.; Arslan Ashraf, M.; Perveen, S.; Hussain, M. Foliar application of selenium increases fertility and grain yield in bread wheat under contrasting water availability regimes. *Acta Physiol. Plant.* 2017, 39, 173. [CrossRef]

142. Zhang, Y.; Wang, L.; Liu, Y.; Zhang, Q.; Wei, Q.; Zhang, W. Nitric oxide enhances salt tolerance in maize (*Zea mays* L.) plants by modulating chlorophyll fluorescence, osmolyte accumulation, and antioxidant system. *Protoplasma* 2018, 255, 459–469. [CrossRef]

143. Alyemeni, M.N.; Ahanger, M.A.; Wijaya, L.; Alam, P.; Bhardwaj, R.; Ahmad, P. Selenium mitigates cadmium-induced oxidative stress in tomato (*Solanum lycopersicum* L.) plants by modulating chlorophyll fluorescence, osmyolute accumulation, and antioxidant system. *Protoplasma* 2018, 255, 459–469. [CrossRef] [PubMed]

144. Padmaja, K.; Prasad, D.D.K.; Prasad, A.R.K. Effect of selenium on chlorophyll biosynthesis in mung bean seedlings. *Phytochemistry* 1989, 28, 3321–3324. [CrossRef]

145. Moulick, D.; Santra, S.C.; Ghosh, D. Seed priming with Se mitigates As-induced phytotoxicity in rice seedlings by enhancing essential micronutrient uptake and translocation and reducing As translocation. *Environ. Sci. Pollut. Res.* 2018, 25, 26978–26991. [CrossRef]

146. Carvalho, E.R.; Oliveira, J.A.; Von Pinho, E.V.D.R.; Costa Neto, J. Enzyme activity in soybean seeds produced under foliar application of manganese. *Ciência e Agrotecnologia* 2014, 38, 317–327. [CrossRef]
153. Asgher, M.; Per, T.S.; Verma, S.; Pandith, S.A.; Masood, A.; Khan, N.A. Ethylene Supplementation Increases PSI Efficiency and Alleviates Chromium-Inhibited Photosynthesis Through Increased Nitrogen and Sulfur Assimilation in Mustard. *J. Plant Growth Regul.* **2018**, *37*, 1300–1317. [CrossRef]

154. Guo, C.Y.; Wang, X.Z.; Chen, L.; Ma, L.N.; Wang, R.Z. Physiological and biochemical responses to saline-alkaline stress in two halophytic grass species with different photosynthetic pathways. *Photosynthetica* **2015**, *53*, 128–135. [CrossRef]

155. Zong, X.J.; Li, D.P.; Gu, L.K.; Li, D.Q.; Liu, L.X.; Hu, X.L. Abscisic acid and hydrogen peroxide induce a novel maize group C MAP kinase gene, ZmMPK7, which is responsible for the removal of reactive oxygen species. *Planta* **2009**, *229*, 485–495. [CrossRef]

156. Filek, M.; Keskinen, R.; Hartikainen, H.; Szarejko, I.; Janiak, A.; Miszalski, Z.; Golda, A. The protective role of selenium in rape seedlings subjected to cadmium stress. *J. Plant Physiol.* **2008**, *165*, 833–844. [CrossRef]

157. Saleem, M.H.; Kamran, M.; Zhou, Y.; Parveen, A.; Rehman, M.; Ahmar, S.; Malik, Z.; Mustafa, A.; Anjum, R.M.A.; Wang, B.; et al. Appraising growth, oxidative stress and copper phytoextraction potential of flax (*Linum usitatissimum L.*) grown in soil differentially spiked with copper. *J. Environ. Manag.* **2020**, *257*, 109994. [CrossRef] [PubMed]

158. Ahanger, M.A.; Agarwal, R.M.; Tomar, N.S.; Shrivastava, M. Potassium induces positive changes in nitrogen metabolism and antioxidant system of oat (*Avena sativa L.* cultivar Kent). *J. Plant Interact.* **2015**, *10*, 211–223. [CrossRef]

159. Zhang, A.; Jiang, M.; Zhang, J.; Tan, M.; Hu, X. Mitogen-activated protein kinase is involved in abscisic acid signaling regulation and salt stress resistance. *Plant Physiol.* **2018**, *173*, 412–426. [CrossRef]

160. Liu, J.; Wang, J.; Yang, J.; Gao, W.; Gu, L.; Hu, X. Mitogen-activated protein kinase is involved in abscisic acid signaling regulation and salt stress resistance. *Plant Physiol.* **2018**, *173*, 412–426. [CrossRef]

161. Gao, W.; Xu, F.C.; Guo, D.D.; Zhao, J.R.; Liu, J.; Guo, Y.W.; Singh, P.K.; Ma, X.N.; Long, L.; Botella, J.R.; et al. Calcium-dependent protein kinases in cotton: Insights into early plant responses to salt stress. *BMC Biol.* **2018**, *16*, 15. [CrossRef]

162. Sripinyowanich, S.; Klomsakul, P.; Boonburapong, B.; Bangyeekhun, T.; Asami, T.; Gu, H.; Buaboocha, T.; Chachawan, S. Exogenous ABA induces salt tolerance in indica rice (*Oryza sativa L.)*: The role of OsP5CS1 and OsSP5CR gene expression during salt stress. *Environ. Exp. Bot.* **2013**, *81*, 475–487. [CrossRef] [PubMed]

163. Zhang, A.; Jiang, M.; Zhang, J.; Tan, M.; Hu, X. Mitogen-activated protein kinase is involved in abscisic acid-induced antioxidant defense and acts downstream of reactive oxygen species production in leaves of maize plants. *Plant Physiol.* **2014**, *165*, 475–487. [CrossRef]

164. Liu, J.; Wang, J.; Lee, S.; Wen, R. Copper-caused oxidative stress triggers the activation of antioxidant enzymes via ZmMPK3 in maize leaves. *PLoS ONE* **2018**, *13*, e0203612. [CrossRef]

165. Shalaby, T.; Bayoumi, Y.; Elshaal, T.; Elhawat, N.; Sztrik, A.; El-Ramady, H. Selenium fortification induces growth, antioxidant activity, yield and nutritional quality of lettuce in salt-affected soil using foliar and soil applications. *Plant Soil* **2017**, *421*, 245–258. [CrossRef]

166. Ardebili, N.O.; Saadatmand, S.; Niknam, V.; Khavari-Nejad, R.A. The alleviating effects of selenium and salicylic acid in salinity exposed soybean. *Acta Physiol. Plant.* **2014**, *36*, 3199–3205. [CrossRef]

167. Hasanuzzaman, M.; Fujita, M. Selenium pretreatment upregulates the antioxidant defense and methylglyoxal detoxification system and confers enhanced tolerance to drought stress in rapeseed seedlings. *Biol. Trace Elem. Res.* **2011**, *143*, 1758–1776. [CrossRef] [PubMed]
173. Feng, R.; Wei, C.; Tu, S. The roles of selenium in protecting plants against abiotic stresses. *Environ. Exp. Bot.* 2013, 87, 58–68. [CrossRef]

174. Zhang, A.; Zhang, J.; Ye, N.; Cao, J.; Tan, M.; Zhang, J.; Jiang, M. *ZmMPK5* is required for the NADPH oxidase-mediated self-propagation of apoplastic H$_2$O$_2$ in brassinosteroid-induced antioxidant defence in leaves of maize. *J. Exp. Bot.* 2010, 61, 4399–4411. [CrossRef] [PubMed]

175. Ding, Y.; Cao, J.; Ni, L.; Zhu, Y.; Zhang, A.; Tan, M.; Jiang, M. *ZmCPK11* is involved in abscisic acid-induced antioxidant defence and functions upstream of *ZmMPK5* in abscisic acid signalling in maize. *J. Exp. Bot.* 2013, 64, 871–884. [CrossRef] [PubMed]

176. Zhang, H.X.; Hodson, J.N.; Williams, J.P.; Blumwald, E. Engineering salt-tolerant Brassica plants: Characterization of yield and seed oil quality in transgenic plants with increased vacuolar sodium accumulation. *Proc. Natl. Acad. Sci. USA* 2001, 98, 12832–12836. [CrossRef]

177. Almeida, D.M.; Gregorio, G.B.; Oliveira, M.M.; Saibo, N.J.M. Five novel transcription factors as potential regulators of *OsNHX1* gene expression in a salt tolerant rice genotype. *Plant Mol. Biol.* 2017, 93, 61–77. [CrossRef]