



REVIEW

Selenium: A Game Changer in Plant Development, Growth, and Stress Tolerance, via the Modulation in Gene Expression and Secondary Metabolite Biosynthesis

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ABSTRACT

The presence of selenium (Se) is not widely established as crucial for crops, although it is commonly recognized as an important nutrient for animals as well as humans. Even so, it is inevitably accepted that Se usually contributes positively to the life cycle of plants. Previous findings suggested that small amounts of Se seem to have a productive role in growth and production. As a result, Se is assumed to function in multiple ways, primarily by influencing a variety of biochemical and physiological functions. Also, Se also acts as a plant antioxidant and pro-oxidant and confers tolerance against different abiotic stresses, including salinity, drought, extreme temperature, and toxic metals/metalloids stresses. It reflects a defensive barrier against stress by increasing chlorophyll content synthesis, photosynthesis, oxygen supply, osmoprotectant concentration, and secondary metabolite acquisition. One other crucial role of Se is its ability to strengthen antioxidant performance in plants, thereby decreasing the concentration of reactive-oxygen-species (ROS). Furthermore, Se generates and modifies genes and proteins that respond situationally to stress, and the presence of high Se concentrations in the growth-medium can cause phytotoxic conditions via excessive ROS production, and through pro-oxidative Se occurrence, suppression of chlorophyll contents in the biosynthetic pathway, and the inhibition of plant developmental and normal physiological functions. Like a phytofortifier, the correct amount of Se can indeed enhance the nutrient quality of both crop and fodder production. Furthermore, crops have naturally developed ways to combat Se-deficiency and Se-toxicity. The current review focuses on recent advances in understanding the dynamics of Se, the positive and negative roles of Se in crop management, and its efficiency in countering abiotic stress.

KEYWORDS

Gene expression; phytohormones; photosynthesis; selenium; secondary metabolites

1 Introduction

Selenium (Se) is a toxic metalloid and a rare element. The Earth's crust, a variety of ecosystems, aquatic systems, and soil profiles all contain significant levels of Se, but in varying proportions, depending on geographical characteristics [1–3]. One of the elements included in the category of micronutrients that are required in low contents for organisms to operate properly is Se. Selenium aids in the detoxification of



heavy metals, the control of the immune and reproductive systems, and the defense of cells against excessive H_2O_2 . Selenium causes selenoprotein production, which is important in the organism's antioxidant defense system. Selenium is a major component of mammalian protein, often called selenoproteins [4]. There are 25 selenoproteins widely recognized and classified. Twelve of them are involved in redox homeostasis and are important for antioxidant capacity. Antioxidant selenoenzymes are the remaining proteins [5]. Glutathione peroxidase (GPX) and thioredoxin reductases (TrxRs) are essential selenoproteins. Selenoproteins form anti-oxidant barriers to defend the organism from harmful impacts such as ROS [6]. TrxRs are proteins that are in charge of cellular redox situation maintenance, prediction, and signaling [7]. Selenoprotein P (SePP) is an antioxidant present in blood plasma, and its activity is dependent on the amount of selenium in the animal tissue or plant cell [8]. Selenium has been shown to have anticarcinogenic properties [9]. In crops, the form of Se is either inorganic or organic [10]. Se is exclusively found in a few minerals and is rarely found in its basic form in nature [3]. It has been shown that Se is important for humans, animals, and some microbes. While its essentiality for plants is still debatable and unproven, it is nevertheless recognized as a positive component. Se can function optimally in countering the adverse impacts of abiotic stress and could enhance plant development and growth once applied at low amounts [11] and its useful role in low doses has indeed been thoroughly researched. It has reportedly benefited crop development by enhancing antioxidant enzyme activity [12] while making plants more resistant to multiple forms of abiotic stress, such as drought [13], UV-induced stress [14], cold [15], salinity [16], and metals/metalloids [17]. In addition, it potentially increases agricultural output, thereby demonstrating its significance in plant development and growth [18]. Similarly, Se has been successfully offered to plants in many situations and assimilated by them as an effective solution to the problem of Se-deficiency [19]. Also, Se enhances photosynthesis, promotes ion homeostasis, and initiates a series of downstream processes that aid in stress reduction. It promotes adaptability in the face of salt stress. Knowing the effect of Se, such as Se take-up, transport, and movement, and how it impacts various plant operations, would provide another opportunity to improve plant salt tolerance [20]. Much plant research on the defensive impacts of Se during drought stress suggested that the impacts of Se are related to its capacity to control the water condition of plants in a water shortage. According to Aissa et al. [21], adding 0.1 or 0.25 mM Se induced a 2%–6% rise in leaf water content, enhancing drought tolerance. At the optimal rate of water supply, the effect of Se on the amount of intracellular water was likewise less noticeable. In *Fagopyrum esculentum*, Tadina et al. [22] discovered that plants under water stress had considerably reduced the stomatal conductance (gs), but Se supplementation greatly enhanced gs. Selenium boosted PSII performance, which was ascribed to betterment in plant water status. In the study conducted by Sieprawska et al. [23], the rise in the content of anthocyanin, sugars, and proline in the application of Se in adequate dosages may suggest the interference of non-enzymatic substances synthesis [23]. The PSII system also showed a rise in chlorophyll concentration and photosynthetic quantum performance activities [24].

Furthermore, various forms of Se can be applied as soil amendments, e.g., selenate [SeO_4^{2-}] or selenite [SeO_3^{2-}]. According to the latest findings on tomatoes, using low Se concentrations improved antioxidative properties, including superoxide dismutase (SOD), GPX, and catalase (CAT) [25], glutathione reductase (GR), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), SOD activity, and monodehydroascorbate reductase (MDHAR) in maize [26], as well as GPX and GR activities in wheat [27]. As a result of the Se supplementation, plant oxidative stress was decreased. Excessive Se, on the other hand, causes toxicity in crops, which ultimately results in chlorosis and necrosis, in addition to limited growth and decreased protein biosynthetic pathways [28]. So, more research is needed to see whether Se is essential for plant development and growth. Plants, on the other hand, may engage, accumulate, and adapt to Se. As a result, this review focuses on the potential beneficial or harmful impacts of Se on plant growth and development, and also Se absorption, transport, and metabolism. Also,

the dynamics of Se absorption, allocation, and metabolic activity are discussed analytically to arrive at a comprehensive standpoint on the importance, function, and interactivity of Se.

2 Multidimensional Functionality of Se, Affecting Plant Development, Growth, and Stress Tolerance

By the beginning of this century, Se was already found to have advantageous functions in plants that can accumulate huge amounts of this element [19]. In many contexts, Se works in a dose-dependent manner [29]. Fig. 1 depicts some of Se's positive and negative impacts, although the available literature lacks complete information on the exact necessity of Se for plant metabolism and cellular maintenance [11]. Fayram [30] identified three levels of biological action by Se: (i) detection of Se concentration needed for growth and development; (ii) adequate density that may be saved to preserve homeostatic operations; and (iii) toxic concentrations. In lettuce plants (*Lactuca sativa*) and ryegrass (*Lolium perenne*), Se exerted beneficial effects at low concentrations (0.1 mg kg^{-1}), whereas higher levels ($>10 \text{ mg kg}^{-1}$ and 1.0 mg kg^{-1}) led to toxicity in lettuce and ryegrass, respectively [31]. Regarding the antioxidative properties of Se which counterbalance oxidative stress, plants have been observed to grow healthily by the effect of Se at low doses [21]. Seed germination is also another process that benefits from supplementary Se. According to Puccinelli et al. [32], excessive Se concentrations ($>29 \text{ mg kg}^{-1}$ soil) had adverse effects on the seed germination of (*Raphanus sativus*) radishes and (*Solanum lycopersicum*) tomatoes. In contrast, using SeO_3^{2-} as a seed priming agent increased the growth of *Momordica charantia* seedlings. Lapaz et al. [33] provided evidence that adding Se to the nutrient solution enhanced carbohydrate concentration in early-age leaves and stolons of potato plants, but that was not linked to a higher photoassimilate yield because the supplementary Se did not change the net photosynthesis [34]. Following Se supplementation, Hasanuzzaman et al. [35] reported substantial increases in the expansion and synthesizing of carotenoids and chlorophyll activity (chl a, b) in ornamental gerberas ($5\text{--}20 \text{ mg L}^{-1}$).

Se could indeed boost agricultural output by having a significant influence on cellular metabolism [18]. Similarly, the problem of Se-deficiency can be addressed in many plants by adequate supplements of Se [19]. Furthermore, several forms of Se have the capacity to serve as efficient fertilizers (e.g., selenite [SeO_3^{2-}] and selenate [SeO_4^{2-}]). In response to Se supplementation, plants reportedly developed lower levels of oxidative stress. Excessive Se, on the other hand, causes toxicity in crops, which ultimately results in chlorosis and necrosis, in addition to constrained development and weakened protein biosynthetic pathways [28]. Several other research findings have demonstrated that Se, at low doses, promotes crop production (Table 1). In a relevant study, it was observed that treating chili pepper plants with $5 \text{ }\mu\text{M}$ Se caused the architectural volume of roots to expand, compared to the control treatment, and, also, the relative-water-content (RWC) increased by 13% [36]. Likewise, the application of Se (3 and $5 \text{ }\mu\text{M}$) increased the leaf area by 25%, resulting in greater plant growth and biomass. According to Chauhan et al. [17], rice crops improved in terms of production and growth, as they benefited from small doses of Se.

There are indications that Se has anti-senescence properties, assisting with the maintenance of cell components and actions, thereby improving plant longevity [37]. The inclusion of Se in nutrient solutions can promote plant development and growth. Research by Wang et al. [38] and Hemmati et al. [18] showed that optimizing the availability of Se in arable lands seems to be a feasible and effective way to enhance production. Lettuce seedlings in trays grew more vigorously in response to different doses of Se (two concentrations of $0, 30 \text{ mg.dm}^{-3}$), compared to the control group [2]. Furthermore, positive impacts of Se were observed in the absorption and utilization of essential nutritional components, even in the case of crops grown on different forms of media [39].

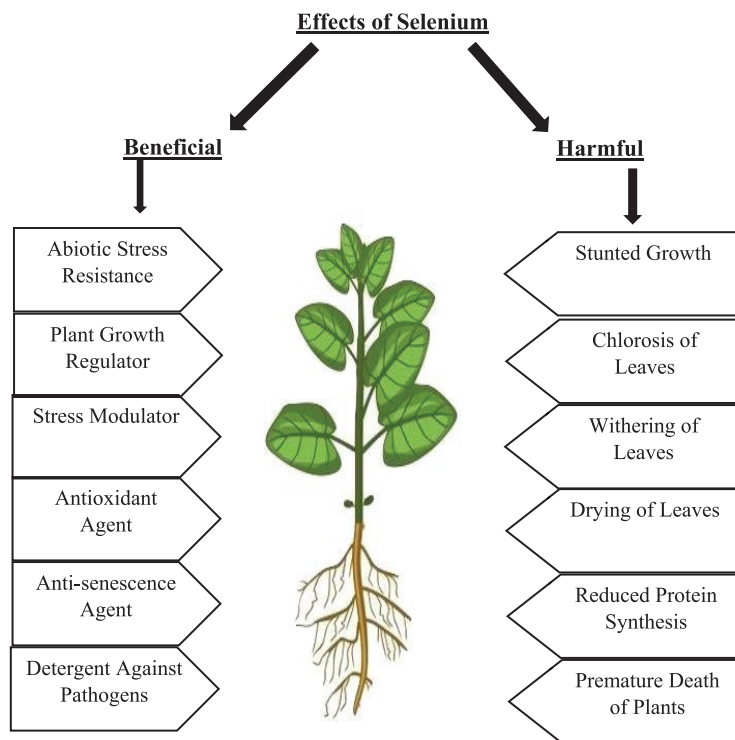


Figure 1: Selenium can bring advantages or disadvantages to plants, depending on the dose of supplementation. Low doses usually benefit plants, whereas high doses tend to have the opposite effect. The negative effects often result from an excessive presence of Se in the nutrient solution or the soil. Nonetheless, exact thresholds of advantageous/disadvantageous concentrations largely remain undiscovered in the case of many plant species

Table 1: Plant development and growth, as affected by the presence of Se

Plant species	Experimental conditions	Se application (dose and form)	Positive outcomes of Se application	References
<i>Glycine max</i>	Pots in a glasshouse	Supplemented as spray; Na ₂ SeO ₄ (500 ppm)	Improved shoot dry-matter weight	[40]
<i>Gerbera jamesonii</i>	Pots	Supplemented as spray; Se (20 ppm), 28 days	Increase in leaf count and height of plants	[41]
<i>Lolium perenne</i>	Growth-chamber	Supplemented to the growing media; Na ₂ SeO ₃ ·5H ₂ O (2 μM), 20 days	Enhancements in shoot growth and root development	[42,43]
<i>Cucumis sativus</i>	Greenhouse	Added to the nutrient-solution; Na ₂ SeO ₃ (2 g.L ⁻¹), 35 days	Increase in shoot biomass and root volume	[44]
<i>Capsicum annum</i>	Greenhouse	Added to the nutrient-solution; Na ₂ SeO ₃ (5 μM), 30 days	Greater leaf area and more root growth	[45]
<i>Triticum aestivum</i>	Field		Increased plant weight and height	[27]

(Continued)

Table 1 (continued)				
Plant species	Experimental conditions	Se application (dose and form)	Positive outcomes of Se application	References
		Supplemented to the growing media; Se ⁶⁺ (0.4 mg kg ⁻¹ soil), 2 weeks		
<i>Vicia faba</i>	Plastic-made container	Added to the nutrient-solution; Na ₂ SeO ₃ (1.5 μM), 2 weeks	Improved shoot elongation and shoot fresh weight	[46]
<i>Zea mays</i>	Plastic-made container	Supplemented as spray; Na ₂ SeO ₄ (20 mg L ⁻¹), 10 days	Growth enhancements	[47]
<i>Solanum lycopersicum</i>	Plastic-made container	Added to the nutrient-solution; Na ₂ SeO ₃ ·5H ₂ O (10 μM), 21 days	Enhancements in root and shoot dry weights	[48]
<i>Brassica juncea</i>	Earthen pot	Supplemented to the growing media; Na ₂ SeO ₃ ·5H ₂ O (4 μM.Kg ⁻¹), 30 days	Growth enhancements	[49]
<i>Solanum lycopersicum</i>	Greenhouse	Added to the nutrient-solution; Na ₂ SeO ₃ or Na ₂ SeO ₄ (1 μM)	Improved shoot and root dry mass	[50]
<i>Melissa officinalis</i>	Greenhouse	Added to the nutrient-solution; Na ₂ SeO ₃ ·5H ₂ O (0.2 μM)	Growth enhancements	[51]

2.1 Benefits of Se for Plant Tolerance to Stress

Advancements in agriculture are frequently held back by the prevalence of abiotic stresses. Thus, scientists are continuously attempting to create modern techniques to combat the limits caused. Exogenous protectants are becoming more common for imparting stress resistance (Table 2). Selenium could indeed reduce the likelihood of membrane destruction by enhancing the photosynthetic machinery, increasing the direct quenching of ROS, and boosting enzymatic/non-enzymatic systems that promote plant-based defense through antioxidants (Table 2) [17]. Since Se can perform antioxidant roles in plants, while enhancing crop yield, it is capable of making plants tolerant to several types of abiotic stress. Through a chain of reactions and interactions, Se induces an increase in antioxidant activity and the defense system which strive to maintain plant physiological parameters in their normal state, resulting in a positive impact on crop yield. Several aspects of action by Se, however, remain unknown. Se causes cell death by increasing lipid peroxidation, α -tocopherol concentrations, and, in particular, GPX activity. Thus, systemic defense is strengthened to assist plants in mitigating the effects of ROS and reducing the amount of damage they cause (Fig. 2) [11]. Haghghi et al. [44] investigated Se-absorption and antioxidant-defense reactions in rice, discovering that a small amount of Se (5 mg kg⁻¹) increased the yield and growth of rice by contributing to the functions of glutathione (GSH), ascorbate (AsA), Peroxidase (POD), CAT, and SOD [52]. Under cadmium stress, adding Se (1 M SeO₄²⁻) to the nutrient solution of tomatoes enhanced their functions and antioxidative-defense enzymatics, such as APX (26%) and CAT (21%), thereby improving the ability of tomatoes to tolerate cadmium stress. The GSH biosynthetic pathway was also advanced by Se treatment (33%) [50]. In this regard, treating tomatoes with elemental Se (40 M) resulted in enhanced tolerance to drought and increased activities of SOD (56%), APX (44%), and CAT (27%) [53]. Tolerant plants, treated with Se, reportedly synthesized more antioxidants of the non-enzymatic type, such as α -tocopherol (36%), GSH (107%), and AsA (up to 131%).

Table 2: An overview of experiments aimed at finding appropriate doses of Se and rendering plants tolerant to stress. Each abbreviation is clarified in the text

Plant species	Type of stress	Se dose and form	Protective effects	References
	Salinity			
<i>Vigna unguiculata</i>	NaCl (50 mM)	5 and 10 μM Na_2SeO_4	Enhanced yield-related aspects, more growth and higher protein content	[54]
<i>Zea mays</i>	NaCl (100 mM)	1, 5 and 25 μM Na_2SeO_3	Enhanced salt-tolerance by causing changes in antioxidant activities, photosynthetic capacity, and Na^+ homeostasis	[55]
<i>Helianthus annuus</i>	NaCl salinity (15 dS m^{-1})	5 mg kg^{-1} as Na_2SeO_4	Enhanced activity of antioxidants, associated with a higher Na/K ratio for optimal photochemical performances	[56]
<i>Allium cepa</i>	Silt loam soil with salinity 8 dS m^{-1}	0.5 and 1 kg ha^{-1}	Maximum yield and enhancements in physiological and qualitative indices	[3]
<i>Zea mays</i>	Salinity (12 dS m^{-1})	20 and 40 mg L^{-1} Na_2SeO_4	A low dose of Se enhanced salinity-tolerance at the reproductive stage by counteracting oxidative stress and boosting the activity of antioxidants	[47]
<i>Triticum aestivum</i>	NaCl (100 mM)	5 and 10 μM Na_2SeO_4	A low dose (5 μM) of Se enhanced the plant tolerance to salt stress, reduced oxidative injury and boosted the activity of antioxidant enzymes	[16]
<i>A. sativum</i>	NaCl (30, 60 and 90 mM)	4, 8 and 16 mg L^{-1} Na_2SeO_4	A low dose of Se enhanced plant tolerance to salt stress and decreased oxidative injury by boosting the activities of antioxidants	[57]
	Drought			
<i>Brassica napus</i>	Polyethylene glycol, PEG (10% and 20%)	25 μM Na_2SeO_4	Increased antioxidant activities in plants	[58]
<i>Hordeum vulgare</i>	70% of field capacity (FC)	30 g Na_2SeO_4 ha^{-1}	Enhanced the production of biomass and boosted antioxidant activities	[59]
<i>Olea europaea</i>	80% and 25% of the substrate available water	50 and 150 mg L^{-1} Na_2SeO_4	Enhanced plant tolerance to drought by 9% and 13%, respectively, by protecting cells from oxidative injury and regulating the water status	[60]
<i>Z. mays</i>	PEG-6000 (25%)	5–15 μM Na_2SeO_3	A low dose of Se enhanced antioxidant activities, mainly GSH and AsA	[26]

(Continued)

Table 2 (continued)				
Plant species	Type of stress	Se dose and form	Protective effects	References
	Extreme Temperature			
<i>T. aestivum</i>	40% FC	Foliar spray of Na ₂ SeO ₄ (10 mL per pot)	Increased photosynthetic capacity, plant growth, RWC, and chlorophyll content. It boosted antioxidant activities	[13]
<i>S. bicolor</i>	High temperature (HT) (40°C/30°C)	75 mg L ⁻¹ Na ₂ SeO ₄	Improved POD and CAT activities by 26% and 24%, respectively. It reduced the amounts of malondialdehyde (MDA) and H ₂ O ₂ by 24% and 29%, respectively. It led to heavier and larger seeds, increasing them by 26% and 11%, respectively	[61,62]
<i>B. napus</i>	HT (38°C), 24 and 48 h	25 µM Na ₂ SeO ₄	Increased the amounts of antioxidants (GSH and AsA) and improved the activities of DHAR, MDHAR, GPX, GR, CAT, glyoxalase I (Gly I), and glyoxalase II (Gly II). It enhanced the amount of chlorophyll	[11]
<i>T. aestivum</i>	HT (38°C ± 2°C)	2 and 4 mg Se L ⁻¹ Na ₂ SeO ₄	Enhanced growth, reduced MDA and H ₂ O ₂ contents. It improved APX and CAT activities and increased the amount of photosynthetic compounds	[63]
<i>Cucumis sativus</i>	HT (40°C/30°C day/night), 40 d	8 µM Na ₂ SeO ₄	Decreased the H ₂ O ₂ (41%), O ₂ ^{•-} (54%), and MDA (54%). It increased the amounts of glycine betaine (GB), protein and total soluble sugars by 33%, 47% and 44%, respectively. It boosted antioxidant activity and led to more dry biomass (68%), more fresh biomass (75%), more fruits per plant (35%), heavier fruits (43%), longer fruits (40%), and bigger fruits in diameter (30%)	[64]
<i>Valerianella locusta</i>	HT (35°C/22°C day/night), 7 d	50 mg Se L ⁻¹ as Na ₂ SeO ₄ (foliar or soil)	Enhanced plant growth and reduced oxidative stress by heightened activities of CAT and guaiacol peroxidase (GPOX). It enhanced the GSH content and decreased the level of H ₂ O ₂ buildup, but had no effect on total phenolic content	[65]

(Continued)

Table 2 (continued)				
Plant species	Type of stress	Se dose and form	Protective effects	References
<i>C. sativus</i>	Chilling (10°C/5°C for 24 h, and then another 24 h at 20°C/15°C)	2.5–20 µM Na ₂ SeO ₄	Increased the biomass of roots and shoots. It increased the protein content and reduced the amount of MDA	[66,67]
<i>Fragaria</i> × <i>ananassa</i>	Chilling (0°C for 0, 6, or 12 h)	5 mg L ⁻¹	Increased photosynthetic rates, intercellular CO ₂ concentration, and stomatal conductance. It decreased the H ₂ O ₂ and MDA contents, but increased the antioxidant activity	[15]
Toxic metals/ metalloids				
<i>B. napus</i>	CdCl ₂ (400 and 600 µM), 14 d	Na ₂ SeO ₄ , (2 µM)	Decreased oxidative stress by modulating CAT, SOD, GPX, and APX activities; prevented Cd-induced alteration of DNA methylation	[68,69]
<i>Pteris vittata</i>	Na ₂ HAsO ₄ (150 or 300 µM), 10 d	Na ₂ SeO ₄ , (5 and 10 µM)	Reduced the buildup of As; boosted the antioxidants for defense via GSH and thiol	[70]
<i>L. perenne</i>	AlCl ₃ (0.2 mM), 20 d	Na ₂ SeO ₃ (1.0, 1.5, 2.0, 5.0, and 10 µM)	Improved POD activity and enhanced spontaneous dismutation of O ₂ ^{•-}	[42]
<i>B. napus</i>	CdCl ₂ (0.5 and 1.0 mM), 48 h	Na ₂ SeO ₄ (50 and 100 µM)	Reduced the MDA content; increased the MDHAR, APX, GR, DHAR, CAT, and GPX activities; increased AsA and GSH contents, as well as GSH/glutathione disulfides	[71]
<i>Oryza sativa</i>	CdCl ₂ (50 µM); 5, 10 and 15 d	Na ₂ SeO ₃ (10 µM)	Reduced Cd buildup in leaves, roots, stems, and grains; decreased ROS production; increased CAT activity	[72]
<i>O. sativa</i>	NaAsO ₂ (25 µM), 15 d	Na ₂ SeO ₃ (0, 5, 10 and 25 µM)	Reduced As accumulation and increased phenolic compounds	[17]

2.2 Benefits of Selenium for Plant Tolerance to Salinity

Salinity has an impact on agricultural output by impeding plant development and growth. The available literature contains many case studies on the significance of Se in mitigating the adverse effects of salt stress on plants (Table 2). However, there is a lack of sufficient information on how Se mediates the balancing mechanism of plant tolerance to excessive salt.

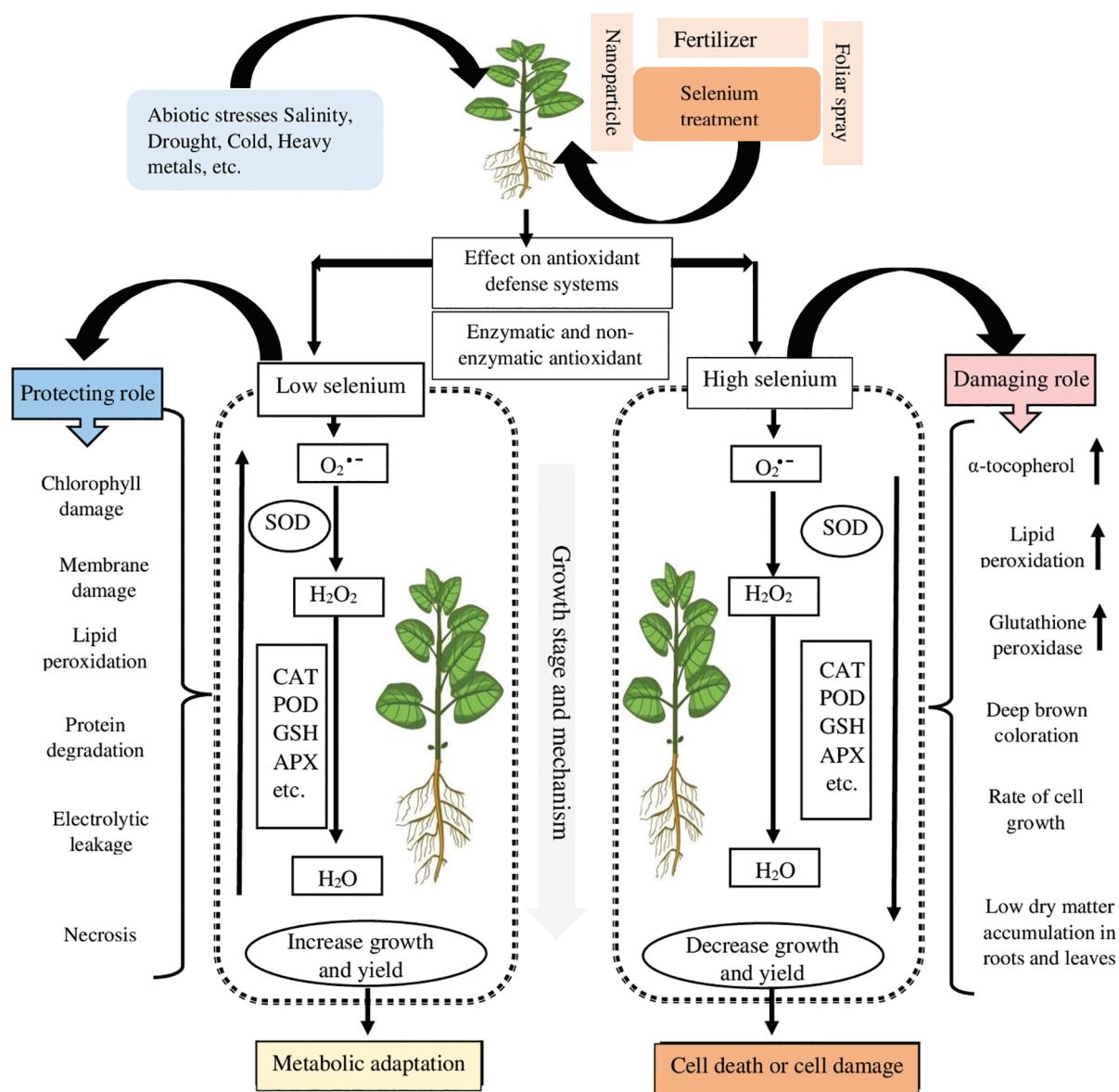


Figure 2: A schematic representation of how Se contributes to the defensive line of antioxidants against abiotic stress. Optimum doses of Se can enhance plant yield, growth, and health by assisting in ROS-scavenging and antioxidant activity, as evidenced by a dotted box illustrated above “metabolic adaptation”. On the other side of the spectrum, plants can grow less and produce smaller amounts of yield when Se is applied in high doses, resulting in less ROS-scavenging and a weakened antioxidant defense, as demonstrated by the dotted box on the right and the arrows that face downwards. In sum, low doses of Se have a protective role in the integrity of plants, whereas high doses are usually detrimental to plant health

2.3 Benefits of Selenium for Plant Tolerance to Drought and Extreme Temperatures

Numerous tests have been performed to investigate the effectiveness of Se in giving plants the ability to tolerate dry conditions (Table 2). Hasanuzzaman et al. [58] treated rapeseed seedlings with Se (25 μM ; Na_2SeO_4) as they were exposed to different drought intensities (10% or 20% PEG). Drought stress had

no significant effect on GSH, GSSG, H_2O_2 , or MDA accumulation in stressed plants that were treated with Se. Even so, at 10% PEG, there was a rise in the AsA concentration, as well as in the MDHAR and GR activities. Curiously, there were increases in glutathione S-transferase (GST), GPX, DHAR, and Gly I activities under both levels of drought stress, whereas the activities of CAT and Gly II declined [58]. A study on olive plants showed that foliar spraying with Na_2SeO_4 (50 mg or 150 mg Se L^{-1}) increased plant productivity and photosynthetic rates while retaining the RWC at a high level [60]. Particularly, Se promoted the activity of APX, GPX, and CAT, thereby preventing the peroxidation of lipids.

Selenium can inhibit ROS production, increase cellular viability, boost antioxidant activity, and uphold reproductive integrity *in vitro* and *in vivo* under extreme temperatures (Table 2). Malerba et al. [73] discovered that Se significantly improved cellular viability by partly preventing the cytoplasm from shrinking, reducing the $O_2\cdot$ output, and ameliorating the effects of heat shock (50°C, 5 min) by controlling the peroxidation of lipids in tobacco cell cultures. Since Se was observed to be involved in defending oilseed rape seedlings from oxidative stress, Hasanuzzaman et al. [11] showed that high temperatures (HT) at 38°C impacted the molecular participants of GSH-AsA biosynthesis, resulting in increased ROS generation [11]. Seedlings supplemented with 25 μM Na_2SeO_4 had more enzymatic activities and managed to accumulate more AsA and GSH. As a result, small supplements of Se caused greater tolerance to oxidative-stress caused by intermittent HT. In small amounts, Se (2 mg L^{-1} Na_2SeO_4) protected wheat from the damages of HT (38°C). As a spray treatment, Se increased crop growth, photosynthetic pigments, and the total amount of phenols [63]. The growth of cucumber seedlings, their photosynthetic activity and chlorophyll formation were suppressed by HT (40°C/30°C day/night), while the damage caused by oxidative stress became more prominent. However, the use of 8 μM Se at the flowering-initiation phase demonstrated higher photosynthetic rates, more osmolytes, and a greater level of antioxidant activity, thereby defending the crops against oxidative stress and bringing the possibility of optimal yields, compared to the case of untreated crops. Thus, the fruit weight and the total number of fruits per plant increased by 43% and 35%, respectively, in Se-treated crops, especially in comparison with HT-treated crops without the Se treatment [64].

Selenium partially helps protect crops from the effects of low temperatures (LT). A dose-dependent application of Se assisted cucumbers in becoming less prone to chilling-injury [74]. When exposed to LT, Se-treated cucumber plants showed resistance to the kind of oxidative stress that resulted from LT. Iqbal et al. [75] discovered that Se largely exerts its effects depending on the dose of the treatment, with a negative effect at larger doses. Responses of wheat seedlings to exogenous selenium supply under cold stress. They discovered that applying Se at 0.5 or 1.0 mg kg^{-1} enhanced chlorophyll content and seedling biomass, whereas its dose at 2.0 and 3.0 mg kg^{-1} enhanced the amount of chlorophyll only. Furthermore, the effectiveness of antioxidant activity varied in response to high or low levels of Se application, although it was reported that the 1.0 and 2.0 mg kg^{-1} dose was partly successful in mitigating the effects of LT on lipid peroxidation. Huang et al. [15] discovered that using Se treatments as a foliar spray reduced the adverse impact of LT on strawberries. In a time-dependent manner, while photosynthetic parameters were rendered suboptimal because of chilling-stress, and as the antioxidant activity of enzymes decreased, the role of supplementary Se (5 mg L^{-1}) improved the condition of LT-affected plants, compared to the control group.

2.4 Benefits of Selenium for Plant Tolerance to Toxic Metals/Metalloids

The physiological performance of various plants reportedly increased in response to Se application, as they demonstrated enhanced levels of resistance to toxic levels of metals and metalloids (Table 2). Se has reportedly protected plants by causing the roots to reduce their absorption of metalloids and metals that may become toxic, limiting the extent to which they are mobile in reaching aerial organs of plants [39]. When Se is added to heavy metal-containing media, it may come into contact with the subcellular

distribution and chemical variants of heavy metals that enter the roots and with the elements in the cellular walls of roots [76]. Surprisingly, Se creates an encouraging scenario for Fe absorption, invigorating the roots to absorb more of it, and, thus, providing more for the requirements of photosynthesis and chloroplast-driven processes [39]. Furthermore, when plants gain access to supplementary Se, they become more capable of synthesizing phytochelatin (PC) and compounds that can counter toxicity. Se can bind to other metals and form complex molecular structures that aid in the reduction of toxic symptoms caused by unwanted metals/metalloids [66]. In a relevant study, Se (2 μM) reduced the toxic effects of cadmium in oilseed rape by regulating, CAT, SOD, GPX, and APX activities and limiting the peroxidation of lipids [68]. In a report it was shown that Se had a significant role in reducing MDA-based substances, while enhancing the activities of MDHAR, APX, GR, DHAR, CAT, and GPX in plants, increasing the amounts of GSH and AsA, and leveling up the GSH/GSSG ratio in Cd-stressed oilseed rape [11]. Se contributes to the suppression of cadmium translocation, making it difficult for this element to reach the aerial parts of plants and hampering its bioavailability to plant cells [66].

Applying exogenous SeO_3^{2-} (5, 10, and 15 mg kg^{-1}) significantly reduced the accumulation of lead- and cadmium-based compounds in rapeseed, and, ultimately, hampered the mobility of these compounds in the xylem [77]. Furthermore, SeO_3^{2-} reduced the amount of oxidative damage caused by cadmium and lead, through the discouragement of ROS production and lipid peroxidation. In faba beans, lead-induced stress was countered by small supplementary quantities of SeO_3^{2-} (1.5 or 6 μM) [46].

According to Cartes et al. [42], SeO_3^{2-} has been effective in neutralizing the toxicity of aluminum (Al) in ryegrass roots. It was discovered that Se contributed to the increase in POD activity, along with greater $\text{O}_2^{\bullet-}$ dismutations into H_2O_2 , but it significantly reduced the output of thio-barbituric acid-reactive substances (TBARS). SeO_3^{2-} functioned as an efficient neutralizer of toxic metals by promoting the synthesis of GSH and thiols, while decreasing the peroxidation of lipids [42].

3 Se-Mediated Regulation of Gene Expression

As genes are regulated by transcription factors, they mediate adjustments and adaptability to various environmental variables. Throughout this context, plant cells respond to both external and internal signals via orchestrated signal perception and transduction systems that involve a variety of elements, the most significant of which include effectors, plant hormones, ionic transporters, Ca^{+2} , and kinases [25]. A transcriptional protein could indeed partly regulate transcriptions of downstream-genes, reconfiguring the growth of plants and biochemical reactions [25]. As a result, transcription factors make excellent target genes for orchestrating vital processes. The WRKY family of proteins both indirectly or directly participates in the down- or up-regulation of plant physiology and targets genes that are tasked with molecular defense at times of stress [26,27]. The transcription factor WRKY1 is responsible for the regulation of formative and stress-induced responses from gene clusters [25,28]. Among transcription factors, those of 4CL and PAL regulate catalytic reactions and synthesize important proteins when producing significant amounts of secondary-metabolites (SMs). Moreover, salicylic acid is a significant signaling agent generated by PAL's catalytic action [29]. Among the critical methods required for the control of gene expression is the regulatory oversight of the evolving environment of chromatin.

Throughout the gene-protein relationship, DNA fragments are methylated as a significant involvement in mediated functions, aiding in the reconfiguration of hetero-chromatin to euchromatin and translating them to a variety of molecular signals. High biological activities in plant extracts have indeed been credited to sophistication in the phytochemistry of plant cells that produce a plethora of valuable metabolic pathways for terpenoids and phenolic substances [30]. Using Se as a supplement reportedly resulted in linear upregulations of the WRKY1 gene. Similarly, the Se treatment significantly increased the transcription of 4CL and PAL gene clusters, as implicated in SMs production and charging the output of crucial SMs in plant defense, particularly salicylic acid which signals multiple reactions in the plant cell. The main

component of signaling pathways and events is a WRKY1 transcription factor, which is preceded more by regulatory oversight of downstream-defending genes assigned to disease prevention [13,25]. In this regard, WRKY1 has transcriptional elements that support pathways signaled by salicylic acid [41]. An overexpression of WRKY1 in grapevine tissues was reportedly attributed to upregulations of a gene family encoding jasmonic-acid and, as a result, an improvement in stress tolerance [41]. This gene also played a role in secondary metabolism (SM) and metabolic control [25]. One research, in particular, showed that using Se supplements ultimately induced a transcription factor aimed at bZIP and WRKY1 synthesis in peppers [10]. Similarly, exposing plant cells to Se was associated with a shift in the transcriptional template of the heat-shock factor [12]. In addition, while responding to the Se treatment, upregulations occurred in rosmarinic acid synthase (RAS) and hydroxyphenyl pyruvate reductase (HPPR) in lemon balm [78]. Numerous studies have identified Se-associated modifications in endogenous proteins as a critical contributing factor [3,10,15,42,78]. Low amounts of Se-induced nitrate reductase activity are substantial indicators of Se-induced modifications in metabolic activities, whereas high doses of Se disturbed nitrate-reductase activity, leading to proline absorption. In one study, Se was linked to changes in the functionality of nitrate-reductase [10,12,43,78]. The presence of proline was dynamically increased by Se supplements when used as sprays on lettuce foliage [10,15]. It leveled up nitrogen metabolic activity in lettuce by enhancing the functions of nitrate-reductase and the biosynthetic pathway of glutamate [43]. Changes in NO levels caused by Se have been linked to the functions of nitrate-reductase [44]. Se consumption altered the density-enhancing actions of catalase and peroxidase for the more efficient performance of antioxidants. The initiation of the antioxidant defense system by Se can be highlighted as a crucial system that contributes to more efficient safeguarding of crops against abiotic stressors [2,13,42]. Different forms of Se supplements have reportedly functioned as elicitors that facilitate higher levels of SM, as evidenced by an increase in the action of PAL enzymatic activity to synthesize phenylpropanoids, while being associated with an increase in the output of gene clusters that encode PAL and 4CL [2,10,12,78].

3.1 Regulation of Photosynthesis-Related Genes by Se

The most fundamental biological procedure in crops is photosynthesis. Se is capable of boosting antioxidant activity through enzymatic pathways, thereby helping plants defend themselves from stressful conditions. Enzymes of antioxidant capacity include, but are not limited to, peroxidase, catalase, glutathione peroxidase, superoxide dismutase, and ascorbate peroxidase [79–81]. Selenium-based compounds have been shown to stimulate biomass production and boost photosynthesis in lettuce and sorrel plants [82]. Of this kind, selenium-based compounds benefited the physiological aspects of barley and sorghum [61]. The normality of photosystem attributes was reportedly maintained by the application of selenium, protecting plants from the adverse effects of UV-B radiation and cadmium [83]. Selenium influenced the expression of photosynthesis-related genes. In potato leaves, selenite made a transient repression of genes encoding light-receptive compounds involved in photosynthesis [84]. From a perspective of proteomics, selenium treatments had a significant impact on rice crops, their primary metabolism, photosynthesis, and redox homeostasis. Selenium deficiency activated the anti-oxidative system, enhancing photosynthesis and primary metabolic activity. Applying high Se concentrations, on the other hand, harmed the photosynthetic apparatus, inhibited photosynthesis, and suppressed primary metabolic activity. Variations exist among the responsiveness of different genes to selenium [85]. Relevant research indicated that spraying amino acid, chelated-selenium on pears, grapes, and peaches increased their photosynthetic output. Precisely, the efficiency of PSII was enhanced by the application of supplementary Se which, in turn, promoted photochemical quenching [84].

Selenium-induced dysfunctions are likely to have adverse impacts on photosynthesis, suggesting preliminary causes of excessive ROS buildup and oxidative pressure [39]. However, regarding the anti-

phytotoxic roles of Se, Meeta et al. [86] discovered that 0.1–0.5 μM of SeO_3^{2-} reduced cellular levels of aminolevulinic acid (ALA) in maize foliage [86]. Relevantly, a decrease in chlorophyll content was significantly notable compared to the decrease in carotenoid compounds and ALA. Nonetheless, providing plants with more SeO_3^{2-} resulted in a reduction of ALA buildup in the presence and absence of light. Based on the available data on growth inhibition, chlorophyll decreased significantly in cucumber plants that faced Se-deficiency [87]. As a result, a decline in photosynthetic pigment concentration levels is viewed as a more prevalent response to the phytotoxic effects of high-dose Se, whereas leaf area and FW seem to be affected less intensely. Zhang et al. [88] demonstrated in an experiment that SeO_3^{2-} levels greater than $50 \text{ g}\cdot\text{ha}^{-1}$ decreased rice yields by affecting the photosynthetic integrity of plants while also disrupting their chlorophyll fluorescence [88]. With an abundance of Se-based supplements, the PSII was mostly suppressed because of abnormal changes in Fv/Fo and Fv/Fm ratios, resulting in a decrease in maximum quantum yield, a limited ability to uphold the normality of PSII functions, associated with a loss of thylakoid-membrane integrity [89]. Indicated ultrastructural adjustments, and chloroplast modifications, with a loss of appressed domains, due to the fact that toxic levels of SeO_4^{2-} destabilize chloroplasts [89]. In effect, electron transport chains are inhibited by such toxic levels. Cell size, cellular activity, and maintenance are all involved in rendering photosynthesis optimal. Compared to the regulation of plant development, the normality of photosynthetic activity is more susceptible to Se toxicity. Excess amounts of Se-based compounds can disrupt the appropriate ratios of necessary minerals in crops, thereby instigating unwanted fluctuations in the availability of nutrient contents in plant cells. Se ions can interfere with the regularity of nutrient levels, destabilizing the physiological functions that they control. The interplay between Se and essential elements is proportional, resulting in synergistic and antagonistic impacts. In maize, the application of SeO_3^{2-} (5–100 μM) led to high levels of calcium and phosphorus in the aerial parts of plants, whereas potassium was reduced [90]. Furthermore, Gui et al. [69] discovered that SeO_3^{2-} (10–100 mg kg^{-1}) suppressed the activity of roots in absorbing K, P, magnesium (Mg), copper (Cu), arsenic (As), and zinc (Zn) in Chinese brake fern (*Pteris vittata* L.). Se-based compounds reportedly altered the coefficients of permeability for certain ions, influencing their ability to cross membranes [91]. In contrast, some plant species cannot accumulate Se because Se-based amino acids fail to be replaced specifically with other viable Se equivalents. As a result, Se-susceptible crops incorporate Se into their protein structures, and, thus, render the proteins dysfunctional. In contrast, Se-tolerant species avoid incorporating Se into their proteins. Two amino acids are Se-based, i.e., selenocystathione and methylselenocysteine, which are normally not incorporated into protein structures in Se-susceptible species [92]. In Arabidopsis, the application of SeO_3^{2-} led to cellular membrane adjustments and regulatory changes in stomatal behavior. SeO_3^{2-} decreased the number of stomata in the leaves and instigated an intense condition of oxidative stress, as well as a medium degree of nitrosative stress [28]. *Brassica juncea*, on the other hand, responded to SeO_3^{2-} by opening the stomata and accumulating more pectin. As a result, the plants developed severe nitrosative stress and a medium level of oxidative stress. The authors proposed that resistance to SeO_3^{2-} partly emanates from the ability of plants to control oxidation processes. Kolbert et al. [93] demonstrated that the toxic effects of Se target crop proteomes, and, thus, result in the formation of not just oxy- and seleno-proteins, but nitro-proteins as well [93]. Crops that withhold Se-Cys from protein biosynthesis could indeed reduce Se-induced proteomic damages. Proteasome compounds are capable of removing old or deformed selenoproteins, nitroproteins, and oxyproteins.

3.2 Regulation of Phytohormones Biosynthesis Genes by Se

Se has key roles as a macronutrient in a wide range of organisms, although at high concentrations it can impede gene expression. While plants respond variedly to Se, supplementary amounts of Se are generally required to compensate for Se-deficient conditions. Other treatments may contribute to the cleaning up of Se-polluted soils. Plant hormones, e.g., salicylic acid, ethylene, and jasmonic acid, are tasked with

triggering Se resistance and, according to biochemical and molecular research, aiding non-accumulator crops in their tolerance to Se toxicity. Non-accumulator crops are plants that cannot accumulate Se; otherwise, they will suffer from physiological dysfunctions. As phytohormones are generated, tolerance to Se toxicity is aided by processes that enhance ROS scavenging, as well as phytohormones that coordinate an appropriate amount of Se-uptake. When Se-rich soils become saturated with moisture, selenate becomes more likely to permeate shallow aquifers [94]. High levels of Se absorption from the soil profile can sometimes be perilous for animals and humans if they regularly include Se-affected plants in their diet [95]. Due to the chemical similarity between sulfur (S) and Se, sulfate transporters in plant cells may take up Se along with S and, even worse, integrate Se into the structure of methionine (Met) and cysteine (Cys) analogs, as well as seleno-Met (SeMet) and seleno-Cys (SeCys) [96]. Substitutions of important S amino acids, i.e., Met and Cys in proteins, with Se-analogs, can become lethal to plant cells because they restrict S bridge forming and/or distort protein formulation [97]. A significant portion of studies on Se-resistance elaborated on how S interacts with Se when the former is metabolized in plants. Based on recent findings, Se induces responses in the defensive system, often reacting hypersensitively to abiotic and biotic stressors [98]. An interplay between several induced responses forms an integral part of Se-resistance in both accumulator and non-accumulator crops [99]. A complete evaluation of Se-receptive gene clusters in *A. thaliana*, a non-accumulator species, revealed the participation of defensive phytohormones in imparting Se-resistance to plants. In fact, transcriptome analyses have been aimed at recognizing selenate-receptive gene clusters. Treating plants with appropriate amounts of selenate increased the rates at which jasmonic acid (JA)- and ethylene-responsive genes were expressed [100]. Furthermore, extensive amounts of analyses on gene expression revealed that most of these responsive genes were induced in crops treated with selenate [98]. Specifically, Se-treated plants showed a greater level of induction for several genes, i.e., pathogenesis-related 4 (At3g04720, *PR4*), ethylene response factor 1 (At3g23240, *ERF1*), vegetative storage protein 1 (At5g24780, *VSP1*), plant defense in 1.2 (At5g44420, *PDF1.2*), JA-responsive gene (At3g16470, *JR*), and proteinase inhibitor 2 (At2g02100, *PIN2*) [98]. Furthermore, important enzymes were expressed in larger amounts by genes responsible for the synthesis of 1-aminocyclopropane-1-carboxylate synthase 6 (At4g11280, *ACS6*), S-adenosyl-Met synthase (At1g02500, *SAM*), and ethylene [101], in addition to allene-oxide synthase (At5g42650, *AOS*) and lipoxygenase 2 (At3g45140, *LOX2*) genes. These were reportedly involved in JA biosynthesis [98]. Relevant findings indicated that JA and ethylene production rates usually differ in response to Se-treatments. Exogenous selenite increased the accumulation of JA and ethylene molecules less significantly in a selenite-susceptible accession 'Ws-2', compared to a selenite-tolerant accession 'Col-0' [102]. Thus, it can be inferred that Se-tolerance can be induced with the help of JA and ethylene in non-accumulator plants. The role of JA and ethylene in Se-tolerance has been explored in non-accumulators while considering their biosynthetic pathway or signaling. Mutations were identified in the Se-tolerant accession 'Col-0', in its *acs6* locus which lacked ethylene-producing signs due to a mutation in the *ACS6* gene. Also, there were mutations in *ein2* which caused a lack in ethylene-signaling [103] and *jar1* which lacked the ability to synthesize standard JA after the mutation [104]. The above mutants seemed to be more susceptible to selenate and selenite, compared to the susceptibility of the wild Col-0 genotype [105]. In contrast, a test was conducted on 'Ws-2', as a susceptible accession, to determine whether cellular tolerance to selenite was restricted by smaller amounts of JA buildup and ethylene release. The results demonstrated that the provision of MeJA or 1-amino-cyclopropane-1-carboxylic acid (ACC, an ethylene precursor) increased cellular tolerance to selenite in the 'Ws-2' accession [98]. Such findings implied that ethylene and JA are able to contribute to Se-tolerance in plants. Some other defensive patterns reportedly involved phytohormones and salicylic acid (SA) which accumulated in selenite-treated *A. thaliana* [106]. Among the phenylpropanoids, the biosynthesis of SA is triggered by various biotic and abiotic stressors [107]. In *A. thaliana*, isochorismate-synthase 1 (*ICS1*) encoded an enzyme that limited the rate of SA biosynthesis [108]. Higher amounts of SA accumulated in plant cells and the *ICS1* gene was expressed

more in response to exogenous selenite. This was observed in the Se-resistant accession ‘Col-0’ and also in the Se-susceptible accession ‘Ws-2’ [109]. In some cases, mutations in *SID2* and *NPR1* genes have reportedly hampered the biosynthesis and signaling of SA, respectively [110]. Nonetheless, no significant variation was observed in selenite tolerance, compared to the non-mutant genotype, ‘Col-0’, which is an Se-tolerant accession. Even so, using SA on these plants made them more susceptible to selenite [109]. In comparison with the role of JA and ethylene, Se-tolerance is rather suppressed by accumulated amounts of SA in plants. The exact mechanism of SA’s negative impact on Se-tolerance still seems unknown, but an interplay among JA, ethylene, and SA signaling can be a plausible cause. In fact, relevant research on phytohormones revealed their effective role in relieving biotic and abiotic stress in crops, possibly through a mutually antagonistic or coordinated manner. Regarding *A. thaliana*, many recent genetic experiments have shown that SA can affect JA-signaling antagonistically. For example, *pad4* and *eds4* mutants lacked accumulated amounts of SA, and, thus, responded favorably to elicitors of gene expressions dependent on JA [111]. Mutations in several JA-signaling proteins, *suppressors of SA insensitivity2 (ssi2)*, *kinase4 (mpk4)*, and *coronatine insensitive1 (coi1)*, on the other hand, demonstrated that JA-signaling antagonizes the appropriate regulation of SA-related defense lines in *A. thaliana* [112]. Accordingly, SA is thought to suppress the action of ACC oxidase for the complete process in ethylene synthesis [113]. The suppression of SA signaling pathways via ethylene has been proven by transcriptome analyses and mutants that are not sensitive to ethylene [98]. Experimentally, enhanced Se-sensitivity can be associated with the existence of SA and could be mediated by the suppression of ethylene and JA-signaling pathways.

4 Selenium and Its Role in Secondary Metabolism

Many plants are known to synthesize and accumulate SMs throughout their life cycles. SMs are an indispensable group of compounds that counter pathogenic attacks. They are usually present in unique tissues and cells (e.g., epidermal cells and trichomes), and, thus, are known as phytoanticipins. Secondary metabolites are generated individually in response to the pathogenic presence and/or phytoalexins, the synthesis of which is induced by invading pathogens [114]. These substances defend against pathogenic microbes, viruses, herbivores (primarily insects), and other crops [115]. Understanding applicable pathways of biosynthetic mechanisms and the type of stimulation that determines their synthesis could be implemented in plant tissue culture and cellular metabolomics, primarily because Secondary metabolites have significant medical benefits [116]. Terpenes, plant volatiles, carotenoids, and phenolic substances include coumarins, tannins, flavonoids, and lignin. Together with sulfur- and nitrogen-containing substances (including cyanogenic glucosides, alkaloids, and non-protein amino acids or glucosinolate), they are major categories of Secondary metabolites in plants [117].

The Se/S quotients of shoots are mostly similar among angiosperms when tested under exactly equal climatic factors, and crops that accumulate an excess of S also accumulate more Se [118]. Secondary Se metabolite complementation and biosynthesis in plants appear to resemble aspects of S-based metabolites. Se could be found in a variety of Se-based SMs that result from SeMet and SeCys. Selenogluthathione seems to be a Se-metabolite with prominent roles. It is produced by the actions of glutamylcysteine synthetase and glutathione synthetase from SeCys, glutamate, and glycine [119], Se-allyl L-cysteine sulfoxide, compounds that result from SeCys directly or are generated by selenogluthathione indirectly in alliums [120]. Selenoglucosinolates can be found in tandem with Se-aglycons, generated by SeMet in brassicas species [121]. Surprisingly, despite the presence of Se-precursor compounds among the existing glucosinolate varieties synthesized by Brassicas, aromatic glucosinolates are derived from tyrosine and phenylalanine, while indolic glucosinolates are derived from aliphatic glucosinolate compounds, tryptophan, alanine, leucine, valine, and isoleucine [122]. With the presence of Se-metabolites, selenosugars are likely to be derived from cell walls in Se-treated crops [123].

5 Does Se Regulate Secondary Metabolites?

The effect of Se as a beneficial micronutrient on plants is dose-dependent. There are some literatures reporting protection role of Se for plants against abiotic stresses such as cold, drought and heavy metals [39]. A reduced amount of heavy metal absorption, detoxification, and chelation, along with a decline in ROS by antioxidant activity, are primary pathways in which Se mitigates the adverse effects of stress on plants [50]. Handa et al. [124] discovered that the application of Se assisted in crop health by restoring plant development and defense systems via improvements in SMs (Secondary Metabolites) against chromium toxicity in *Brassica juncea*. Additionally, using Se treatments on *Melissa officinalis* improved the ascorbic acid content, plant biomass, SMs content (e.g., caryophyllene oxide and caryophyllene), and proteins [51]. Nonetheless, whether Se has constructive effects depends on its dose, due to its ability to compete with sulfur, sometimes resulting in a decreased amount of sulfate absorption by plants, and partially due to the release of H₂O₂ [50]. Se was reportedly capable of ROS-scavenging via superoxide dismutase [125]. In spite of being a very simple molecule, H₂O₂ has a key role in cellular signaling, by oxidative modulation of the activity of redox sensitive proteins. It also affects the production of defensive secondary metabolites through the regulation of expression and activities of defense-related genes [126]. Changing H₂O₂ homeostasis, however, promotes hormone-related pathways for signaling and receptive patterns that distinguish changes in cells, allowing regular functions to be maintained in plant physiology. Phytohormones are important endogenous variables in cellular responses to stress [127]. There is limited knowledge of how Se can change the biosynthesis of phytohormones and secondary metabolites [127]. When small doses are applied, Se usually boosts the efficiency of antioxidants in non-accumulator crops. In this regard, using a moderate dose of Se (5 µM) on *Melissa officinalis* led to greater amounts of citral, z-citral, and geranyl acetate, whereas a low dose (0.2 µM) accelerated the synthesis of caryophyllene oxide in the essential oil. Also, the maximum amount of ascorbic acid occurred in response to this low dose [51]. Nitrogen-based compounds and their synthesis were affected by Se supplements that interacted with sulfur metabolism. Changes in nitrogen assimilation have significant implications for the biosynthesis of nitrogen-based compounds, including phenylpropanoids and alkaloids [118]. Se also increased the alkaloid content in *Astragalus verus* cells, thereby protecting cellular functions against stressors, although the increase in alkaloid content beyond a specific limit can indeed become problematic for cellular functions. Increasing the amounts of alkaloids in *Astragalus verus* cells, through a high-dose Se treatment, reduced plant longevity and biomass [128].

6 Conclusions and Prospective Outlooks

The impact of Se on crops changes from beneficial to toxic over a narrow concentration range, as reflected in plant growth and metabolism. There is much interest in the unique role of Se in counteracting the negative effects of various abiotic stresses in plants, rather than in its essentiality. Over the last three decades, substantial amounts of information have been obtained from examining the behavior of Se in crops, such as the patterns of uptake, assimilation, volatilization, toxicity, and tolerance. Even so, the processes through which Se counteracts stress remain unknown. To ensure that crops perform the most from Se application, appropriate amounts of Se form must be outlined for each stage of crop growth, species, plant size, method of application, the form of Se, and, most pertinently, the accumulation of Se. Tolerance to abiotic stresses can be improved by Se, although this requires precise evaluations to reveal the extent and manner of its effectiveness. While food products and fodders can be potentially biofortified with the application of Se, there is limited information on a few plants in this regard. Se toxicity is commonly linked to the synthesis of Se-based proteins, the production of ROS, and the oxidative stress that ensues, all of which lead to disruptions in plant physiology. Small doses of Se can boost the activity of antioxidants, thereby offering an intriguing area of research. Furthermore, finding the most appropriate dosages, researching Se-susceptible and Se-accumulator crops, and analyzing the dynamics of Se as an activator or inhibitor of biochemical pathways require extensive research. High Se levels in and around

hyperaccumulators harm Se-sensitive partners while simultaneously providing a niche for Se tolerant expert partners. The negative impacts on generalist herbivores and Se-sensitive plants benefit the plants by reducing herbivory and decreasing the amount of nearby vegetation. High Se concentrations in and around hyperaccumulators may have functioned as a selective pressure for the evolution of Se-tolerant herbivores, pollinators, detritivores, fungi, and surrounding plants. Similarly, the evolution of Se-tolerant herbivores and pathogens may have led to the evolution of Se hyperaccumulation to ever-increasing levels. The existence of a Se-tolerant that may aggregate Se to significant concentrations at different trophic levels most likely leads to Se transport in the local food chain and, eventually, Se cycling in the local environment. The entry point into this movement is the Se hyperaccumulator plants, which may play a major role. At the moment, nothing is known regarding the proportional role of terrestrial plants in global Se cycling.

Transcriptome analyses have shed light on how *Arabidopsis* plants respond to Se-induced stress and Se-tolerance. Jasmonic acid and ethylene usually serve as signaling agents that regulate plant tolerance to selenite. Se and phytohormone interactions are perceived to regulate genes that control the biosynthesis of S-based compounds, as well as the absorption of S and its assimilation. In turn, these factors affect plant development and growth under standard and stressful conditions. Several fields of omics, such as transcriptomics, genomics, metabolomics, and proteomics can offer a wide range of tools that can assist in determining the amounts of Se that are beneficial or harmful to each plant species. Furthermore, carrying out future research on ways to facilitate Se-mediated metabolic processes could add to our present understanding of Se-dynamics and help identify the correct Se-mediated stress response.

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