

Review

Roles of selenium in mineral plant nutrition: ROS scavenging responses against abiotic stresses

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ARTICLE INFO

Keywords:

Abiotic stress
Antioxidant metabolism
Food security
Biofortification
Hidden hunger
Selenium

ABSTRACT

Agronomic biofortification of crops with selenium (Se) is an important strategy to minimize hidden hunger and increase nutrient intake in poor populations. Selenium is an element that has several physiological and biochemical characteristics, such as the mitigation of different types of abiotic stress. Selenoproteins act as powerful antioxidants in plant metabolism through the glutathione peroxidase (GSH) pathway, and provide an increased activity for enzymatic (SOD, CAT, and APX) and non-enzymatic (ascorbic acid, flavonoids, and tocopherols) compounds that act in reactive oxygen species (ROS) scavenging system and cell detoxification. Selenium helps to inhibit the damage caused by climate changes such as drought, salinity, heavy metals, and extreme temperature. Also, Se regulates antenna complex of photosynthesis, protecting chlorophylls by raising photosynthetic pigments. However, Se concentrations in soils vary widely in the earth's crust. Soil Se availability regulates the uptake, transport, accumulation, and speciation in plants. Foliar Se application at the concentration 50 g ha⁻¹ applied as sodium selenate increases the antioxidant, photosynthetic metabolism, and yield of several crops. Foliar Se application is a strategy to minimize soil adsorption and root accumulation. However, the limit between the beneficial and toxic effects of Se requires research to establish an optimal dose for each plant species under different edaphoclimatic conditions. In this review, we present the compilation of several studies on agronomic biofortification of plants with Se to ensure food production and food security to mitigate hidden hunger and improve the health of the population.

1. Introduction

According to FAO (2017), there are about 2 billion people with nutritional deficiencies in the world. The nutritional deficit is caused by the production of staple foods in soils with low mineral availability. The deficiencies caused by the lack of Fe, I, Se, Zn, and vitamin A are currently the ones that cause the greatest concern regarding human health, especially in developing countries (White, 2016).

Edible vegetables enriched in selenium (Se) can be a safe way to combat Se deficiency in humans. However, most soils are considered poor in Se, and nutrient absorption depends on several factors that reduce their incorporation (Yang et al., 2019). Agronomic biofortification is an agricultural practice used to enrich food production with nutrients, such as Se, to increase food intake by the population (Reis et al., 2017; Adebayo et al., 2020).

Soil or foliar application of fertilizers containing Se can increase the its concentration in the edible parts of plants (Oliveira et al., 2019; Reis

et al., 2019; Reis et al., 2020). Selenium is considered a beneficial element for higher plants, enhancing the antioxidant metabolism, photosynthesis, secondary metabolites and carbohydrates in plant leaves (Andrade et al., 2018). Se application at low concentration enhance photosynthesis in plants due to increase protection of antenna complex. Silva et al. (2020) observed that foliar application of Se induced the conversion of chlorophyll *a* into chlorophyll *b* and also increased carotenoids and pheophytin concentration in cowpea plants. In addition, these authors also observed that Se-fertilized plants showed an enhanced antioxidant metabolism by the increasing of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) activity. These enzymes are responsible to scavenge reactive oxygen species (ROS) protecting plant cell membrane against oxidation (Reis et al., 2017; Lanza et al., 2021). Combined effects of photo-protectant pigments biosynthesis and enhanced antioxidant metabolism induced by Se are the main physiological mechanisms on the photochemistry of photosynthesis boosting photosynthetic

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<https://doi.org/10.1016/j.plaphy.2021.04.026>

Received 28 February 2021; Accepted 22 April 2021

Available online 29 April 2021

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performance in several plant species (Feng et al., 2013; Silva et al., 2018, 2020; Lanza et al., 2021). Also, synergistic and antagonistic relationships of Se with other nutrients favor plant nutrition and mitigate abiotic stresses such as drought, high temperatures, salinity, and heavy metals (Guerrero et al., 2014; Gupta and Gupta, 2017).

According to Hartikainen et al. (2000), Se has a wide antioxidant capacity due to the promotion of selenoproteins such as glutathione peroxidase, which act to combat ROS promoted in plant osmotic imbalance under stressful situations. It may be an osmoprotective strategy to mitigate the harmful effects of abiotic stresses such as drought (Rady et al., 2020), salinity (Habibi, 2017), heavy metals (Shekari et al., 2019), temperature (Seliem et al., 2020) and excess of light (Jaiswal et al., 2018).

Excess Se can be toxic to plants and humans (Gouveia et al., 2020; Martens et al., 2015). Selenium toxicity is characterized by the presence of chlorosis in plant leaves, and hormonal changes in the human body (Vinceti et al., 2018; Lanza et al., 2021). The determination of ideal doses and sources of Se is extremely important to ensure the food security of the population through the consumption of legumes (Silva et al., 2018; Reis et al., 2019), cereal (Lara et al., 2019; Reis et al., 2020), fruits (Deng et al., 2019), vegetables (Tian et al., 2018), and even medicinal plants used as herbal medicines (Stonehouse et al., 2020). Most of the studies on agronomic biofortification with Se were performed with rice and soybean plants. Further studies on agronomic biofortification of vegetables and fruits with Se are needed in order to diversify human diet and deliver Se at safety concentration to the population.

This review compiles the most recent discoveries about Se in plants, analyzing its reactions in different plant species and their interactions with abiotic stresses.

2. Se distribution in the soil, plant, atmosphere, and human health

Selenium concentration generally ranges between 0.01 and 0.20 mg kg⁻¹ in most non-seleniferous soils (Yang et al., 2019). Thus, many factors can affect the content of Se in different foods, including different rates of absorption by plants, which may be related to the type of plant species, soil, pH, microbial activity, precipitation, and some other biogeochemical parameters (Reis et al., 2017).

The biogeochemical cycle of Se is based on its availability to plants by removing the available element from the soil, and consequently the absorption in their tissues and translocation to the edible parts of plants. There is also the possibility that Se can be converted into volatile metabolites and enter the atmosphere, being able to return to vegetables through the leaf surface. Anthropogenic activities are a major source of Se availability in the atmosphere, such as burning fossil fuels and forest fires (Terry et al., 2000; Combs, 2001; Gupta and Gupta, 2017).

The antioxidant role of Se helps to improve the immune system of patients, minimizing the risk of infections, protecting the body against the action of molecules that damage metabolic functions, and mainly helping to fight free radicals and prevent cardiovascular diseases (Adebayo et al., 2020). Recently, adequate levels of Se have been associated with reduced mortality risks from the coronavirus disease pandemic (COVID-19), where Se status was higher in patients who survived SARS-CoV-2 infection (Moghaddam et al., 2020).

The distribution of Se in soils around the world is highly variable, with poor soils in Se (0.01–0.2 mg kg⁻¹) or seleniferous soils (ranging 3–100 mg kg⁻¹) (Chauhan et al., 2019). Brazil is a country with a vast territorial extension and wide biodiversity, reflecting variation in Se concentration ranging from 0.002 to 0.65 mg kg⁻¹ (Reis et al., 2017). In China, it is indicated that 72% of the continent suffers from Se deficiencies, where the levels of 0.10–87.3 mg kg⁻¹ found in soils, associated with average intakes below 10 µg day⁻¹, inducing an increase in cardiovascular diseases and osteopathic (Lin et al., 2017).

Africa is estimated to have 28% Se deficiency in its total area, and

studies carried out on the African continent also highlight that Se deficiencies found in the population also involve socio-economic factors, where a large part of the Se sources are found in foods with high added value such as meat, nuts, and seafood. A large part of Africa continent feeds primarily on vegetables, such as rice, corn, potato, and cassava, the low Se levels in the soils are combined with the increase in cases of infection and low immunity in Africa countries (Ligowe et al., 2020).

According to Combs (2001), foods need to provide Se content greater than 40 µg per day. Selenium is used as a cofactor for antioxidant enzymes, and values below than 70 µg per day reduce the risks of severe diseases, such as cancer. However, high Se intake can cause toxicity in humans and animals. A study conducted in Brazil induced children to eat 15–30 g of Brazil nuts (three to six nuts), which is the amount allowed by public health policies. However, the results of Se concentrations found in plasma and urine were above the allowed, with 155.3 µg day⁻¹ for the city of Macapá and 44.4 µg day⁻¹ for Belém (Martens et al., 2015). On the other hand, in India, it has been found that consumption of food grown in seleniferous soils causes dystrophic changes in the nails, hair loss, strong odors, dysfunctions in the liver, kidney, and pancreas (Vinceti et al., 2018).

3. Uptake, transportation, and accumulation of Se in plants

In nature there are organic and inorganic forms of Se. The elemental bioavailability has a direct influence on the absorption and translocation of Se in plant species. The inorganic forms most found in soils are selenate and selenite (Deng et al., 2019). Several studies demonstrate the efficiency of application of both forms via soil and report that the best form of application to increase the Se content in grains is selenate, indicating that selenite is more adsorbed on soil particles (Deng et al., 2019; Silva et al., 2019).

Hawrylak-Nowak et al. (2015) demonstrated that while selenite retained a high concentration in the roots (967.2 mg kg⁻¹ DW) and low in the shoots (120.6 mg kg⁻¹ DW). Selenate shows higher translocation from root to shoot compared to selenite. This happens because selenite is rapidly converted into organic forms like selenocysteine or selenomethionine in the roots.

Also, studies evaluating the absorption, translocation, and speciation of Se in wheat revealed by the analysis of plant tissues that plants supplemented with sodium selenate have primarily the same elemental shape in the xylem, while plants with the application of sodium selenite generated several compounds such as SeMet, SeOMet, and MeSeCys in the roots. In the same study, it was observed that plants supplemented with selenate or selenite have an inversely proportional relationship with sulfur (S) and phosphorus (P), respectively (Li et al., 2008).

Selenite plays the more hazardous role at higher concentrations (Reis et al., 2017). Se application as selenite source, Se concentration tend to accumulate mainly in roots due to rapid conversion into organic forms. Application of Se mix forms (selenite and selenate) has been applied in several types of plant species. Se mix solution exhibit similar effects to those observed for selenite, suggesting that the presence of selenite blocks selenate uptake (Guerrero et al., 2014). These authors observed that both Se forms together will probably reduce the higher toxicity attributed to selenate as the more available Se form in soils. The mechanism of Se uptake under these conditions is still unclear.

Studies on Se application mixed with biostimulant also has been performed. Plant biostimulants are used to enhance nutrition efficiency, abiotic stress tolerance and crop quality. Xiao et al. (2021) concluded that biostimulant have a key role increasing both the amount of grains produced per spike and their biomass without diminishing the total amount of Se and/or disrupting Se species present in the grain, which is the main objective of biofortification processes. These authors concluded that combination and synergistic action of different compounds of biostimulant, it is also probably due to the catalytic influence of molybdenum species from the biostimulant on the physiology of vegetal cells through the enhancement of the mitochondria activity.

3.1. Selenium supply by soil or foliar

Selenate is the main soluble form of Se in soils, and given its chemical similarity to S, it is transported to plants through sulfate transporters (SULTRs) present in the plasma membrane from root to leaves, and synthesized in plastids (Gupta and Gupta, 2017). Selenite is absorbed by phosphate transporters and aquaporins (OsNIP2; 1) (Zhao et al., 2010). According to Oliveira et al. (2019), selenate has greater mobility within the plant, in contrast to selenite, which is more concentrated in the root system instead of being transported to the shoots due to the rapid transformation into organic forms of Se.

The reduction of selenate occurs through a series of consecutive steps that convert selenate > selenite > selenide > Secys. Fig. 1A illustrates the scheme of the metabolic reduction of inorganic forms of Se and its conversion to organic forms from the soil. Selenate is converted to selenite through the enzymes ATP sulfurylase (APS) and APS reductase (APR). Then, selenite becomes Se^{2-} through the enzymes sulfite reductase, glutathione, or glutaredoxins. The Se^{2-} , in turn, is converted to SeCys by coupling with O-acetylserine (OAS) in the presence of a cysteine synthase enzyme. The last stages of synthesis are responsible for the formation of elementary Se, methyl-selenocysteine (Me-SeCys), and selenomethionine (SeMet), the latter being responsible for the origin of selenoproteins (Schiavon et al., 2017). In plants, selenoproteins act in the transport of Se and regulation of cellular redox balance, the main example of this class being glutathione peroxidase (Malik et al., 2011).

Scientific advances point to problems in Se supplementation via soil, indicating that the element is not efficiently absorbed by plants and indicating economic losses with the application (Deng et al., 2019). Selenate is more absorbed by plants than selenite. Selenite is strongly adsorbed on soil components such as Fe/Al oxyhydroxides, having low mobility in the soil (Lopes et al., 2017).

Foliar Se application provides the deposit of droplets containing elements on the leaves, which in turn allows entry through the various physiological barriers of the plant. The main pathway for nutrients to enter the leaves is through a passive process due to difference in concentration, which occurs on the external surface, where there is a higher concentration of solute, towards the internal, with a lower concentration of solutes, through the aqueous pores present in the cuticles, proceeding to the mesophyll cells through specific transporters (Yang et al., 2019).

Although entry through leaf cuticles is the process with the highest absorption capacity. According to Wang et al. (2016), elementary particles can also enter plants through trichomes, stomata, stigma, and

hydathodes. The cuticles have limitations regarding the size of the particles, and the entry through the stomata depends on stomatal permeability, and as a consequence of the opening and closing of the stomata, in addition to the hydraulic conductivity of the cells. (Yang et al., 2019).

4. Physiological and biochemical roles of Se in plants: antioxidant metabolism responses

Plants subjected to high-stress intensities produce high amounts of ROS, which can appear as a superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl free radical ($\text{OH}\cdot$), singlet oxygen ($^1\text{O}_2$), methyl radical ($\text{CH}_3\cdot$) and lipid peroxidation free radicals ($\text{LOO}\cdot$, $\text{ROO}\cdot$) (Feng et al., 2013).

Overproduction of ROS cause peroxidation of membrane lipids, and one of the main meters is through the quantification of malondialdehyde (MDA), which is a widely used marker of oxidative lipid damage caused by environmental stress. Also, antioxidant enzymes such as catalase (CAT, EC: 1.11.1.6); glutathione reductase (GR, EC: 1.6.4.2), and ascorbate peroxidase (APX, EC: 1.11.1.11) are other useful markers to assess the fight against oxidative stress in plant metabolism as illustrated in Fig. 2 (Silva et al., 2018).

Several studies demonstrate the ability of Se at low concentrations to improve plant defense systems by detoxifying intracellular free radicals, and increasing enzymatic and non-enzymatic activity, which can help plants eliminate ROS and prevent oxidative stress (Schiavon et al., 2017; Silva et al., 2018).

According to Silva et al. (2020), Se can mitigate oxidative stress by regulating ROS, acting in the following ways: (1) stimulation of O_2^- dismutation into H_2O_2 , (2) regulation of enzymatic and non-enzymatic antioxidant systems, (3) direct extinction of ROS through Se species, and (4) regulation of photosynthetic complexes.

Non-enzymatic molecules act in minimizing ROS and are also important for preserving the cellular redox state, being of the type: glutathione (GSH), ascorbate, phytochelatin (PCs), proline, flavonoids, alkaloids, and carotenoids (Foyer and Noctor, 2012).

The two amino acids produced in Se biosynthesis via the S assimilation pathway are selenocysteine (SeCys) and selenomethionine (SeMet). Cysteine is a component of glutathione (GSH), a central molecule in plant responses to various types of stress, while Met is a precursor to aliphatic glucosinolates, which are compounds involved in plant-pathogen/herbivore interactions (Schiavon et al., 2017).

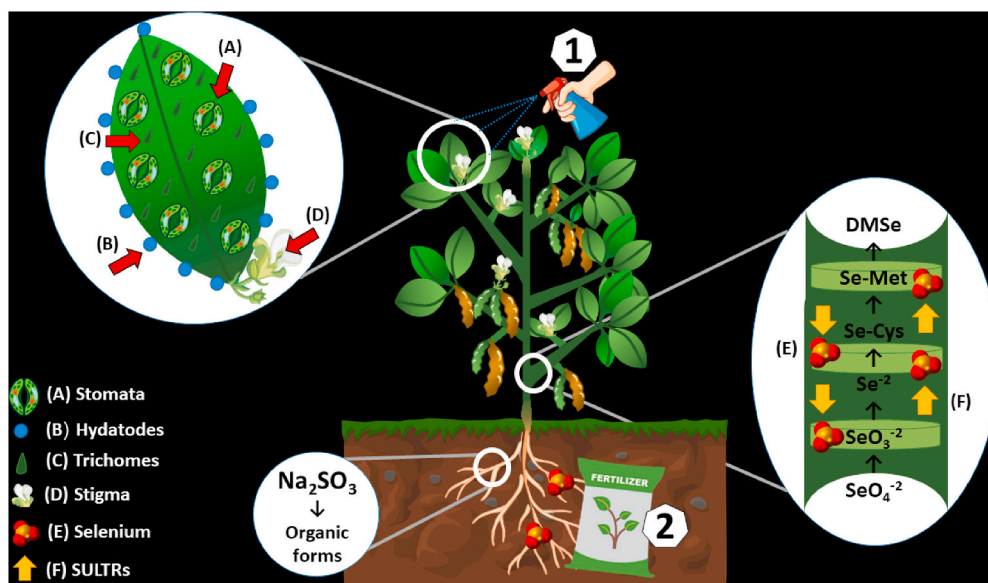


Fig. 1. Selenium uptake and assimilation mechanisms by plants: (1) Foliar selenium application, (2) Selenium application via soil.

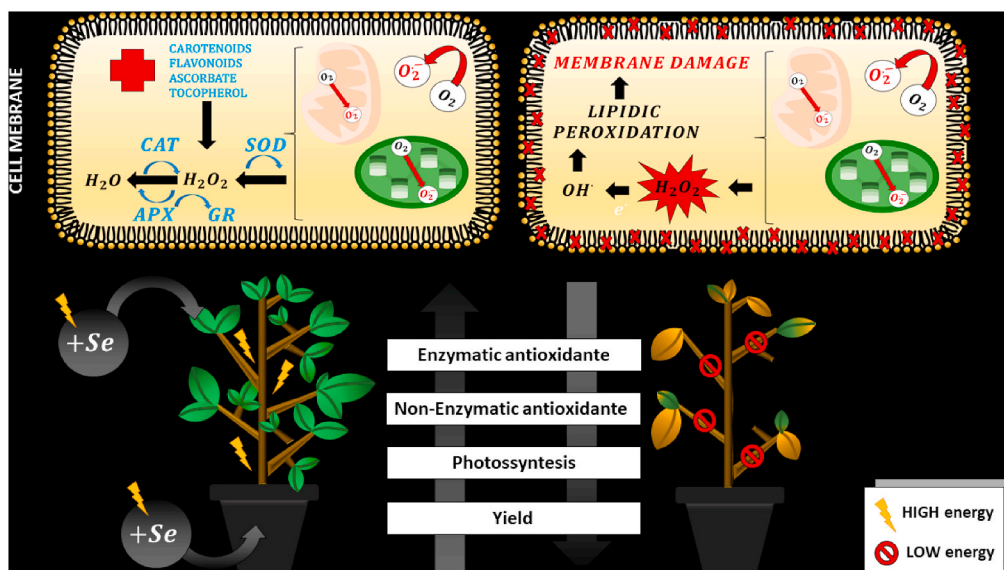


Fig. 2. Selenium role in antioxidant metabolism (enzymatic and non-enzymatic) as a mitigator factor of abiotic stress and ROS scavenging system.

According to Hunter (2014), the antioxidant capacity of Se is incorporated into the mechanism of glutathione peroxidase (GSH) in the reduction of hydrogen peroxide through the use of ascorbate (AsA). The GSH-Px enzyme is considered a key that can be strongly activated by Se in several plants exposed to different environmental stresses (Feng et al., 2013). The increase in GSH-Px, which is a sequester of H_2O_2 and lipid hydroperoxides, results in a reduction in the formation of superoxide anions (O_2^-) among oxygen species (Hartikainen et al., 2000).

High stressful conditions can induce a significant reduction in the levels of GSH, and consequently the enzyme GSH-Px, making it viable via ascorbate-glutathione cycle, and it is necessary to use antioxidant enzymes to reestablish the metabolism, as occurs with SOD activity (Hartikainen et al., 2000). Optima levels of Se primarily induce antioxidant activity through spontaneous reduction of O_2^- by GSH-Px. However, under severe stress, high levels of ROS will be produced, requiring specific enzymatic activities, such as SOD, and subsequently of other enzymatic and non-enzymatic antioxidants (Feng et al., 2013).

4.2. Selenium against lipid peroxidation: non-enzymatic antioxidants

In addition to being a component of the non-enzymatic process of ROS elimination, the forms of ascorbate (AsA) in plants suggest a multitude of benefits, such as accumulation of secondary metabolites, growth control, sugar increase, and control and pathogens (Foyer and Noctor, 2012). Selenium application at low concentration increase AsA accumulation, resulting in high elimination of H_2O_2 through various reactions such as maintenance of reduced α -tocopherol, zeaxanthin biosynthesis, reduction of the state of prosthetic metal ions, and maintenance of activity of antioxidant enzymes (Foyer and Noctor, 2012; Hasanuzzaman et al., 2019).

According to Hartikainen et al. (2000) tocopherols, popularly known as vitamin E, can eliminate the radicals of lipid peroxide ($LOO\cdot$), in addition to their performance in cooperation with Se to positively influence the detoxification of O_2^- . Thus, the main antioxidant function of vitamin E is to protect the phospholipid bilayer of the cell membrane, preventing lipid peroxidation (Hunter, 2014).

Carotenoids can directly eliminate free radicals and extinguish species of O_2^- (Hunter, 2014). In plants, carotenoids participate in the maximum photochemical efficiency of PSII, indicating their photoprotective action during photosynthesis (Habibi, 2017). For human health, lycopene and β -carotene are considered major natural antioxidants, acting as inhibitors of the most important carotenoids and acting

as inhibitors of O_2^- and protecting cells against free radicals (Moral-es-Espinoza et al., 2019).

Selenium application affects the metabolism of nitrogen biosynthesis, proteins, and amino acids, and, in particular, the amino acid phenylalanine which is a precursor to phenolic compounds, such as flavonoids (Golubkina et al., 2018). Flavonoids have been widely recognized as beneficial antioxidants due to their ability to capture free radical ions and protect plants from the adverse effects of abiotic stress (Chauhan et al., 2017; Jaiswal et al., 2018).

Oliveira et al. (2019) concluded that increasing proline content is a process that plants use to adapt to abiotic stress, reducing excess free radicals. Thus, several studies claim that proline can be used as a strategy to maintain the fluidity of the membrane during water stress (Rady et al., 2020). Or, also, act as a stress signal, or as a metal chelating osmolyte (Dai et al., 2020).

Sugars are used as biomarkers of ROS, and in large quantities, can influence the increase in cytosolic H_2O_2 , but in ideal doses, it works to combat oxidative stress, mainly through the pentose phosphate (PPP) pathway. Selenium also increases a very important element of analysis, especially for fruits, which are total soluble solids (TSS), and which are composed of sugars, playing an important role in metabolism, photosynthesis, and carbohydrate production (Golubkina et al., 2018; Gouveia et al., 2020).

4.3. Selenium against lipid peroxidation – enzymatic antioxidants

Superoxide dismutase (SOD) can be considered the first enzymatic barrier against oxidative stress by the O_2^- dismutation reaction to form O_2 and H_2O_2 . Thereafter, the H_2O_2 can be quickly converted to H_2O and O_2 by the direct or indirect action of enzymes such as catalase, guaiacol peroxidase (GPX), ascorbate peroxidase (APX), guaiacol peroxidase (GPOX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and glutathione S-transferases (GST) and non-enzymatic antioxidants that are ascorbic acid, glutathione, carotenoids, tocopherols, proline, glycine betaine and flavonoids (Schiavon et al., 2017; Xie et al., 2019).

Specifically, CAT is an enzyme that accelerates the breakdown of H_2O_2 to H_2O and O_2 due to the high affinity with this substrate. While APX uses ascorbate as an electron donor to reduce H_2O_2 to H_2O and O_2^- . Thus, the GR maintains an intracellular reduction state by converting glutathione disulfide (GSSG) to reduced glutathione (GSH) (Reis et al., 2017; Silva et al., 2018).

4.4. Selenium in chlorophyll and photosynthesis

Selenium application at low concentration can improve the photosynthetic process by increasing the production of chlorophyll (Ashraf et al., 2018; Hemmati et al., 2019; Seliem et al., 2020), stomatal conductance (Bian et al., 2020; Elkelish et al., 2019; Oliveira et al., 2019), and internal CO₂ concentration (Zhang et al., 2020).

The benefits of Se in photosynthesis may be related to its relationship with the Fe–S complex in chloroplasts, which have a vital role in the electron transport chain, making the high excitations of electronic levels have enough substrates to remain organized. This process helps to reduce the generation of ROS, mainly O₂⁻ and H₂O, in plants subjected to stress (Feng et al., 2013).

When plants are subjected to environmental stress, their chloroplasts are damaged, leading to the interruption of photosynthesis. However, adding appropriate levels of Se can reduce damage to chloroplasts and increase the content of chlorophyll and other photosynthetic pigments that act as non-enzymatic antioxidants, such as carotenoids (Hasanuzzaman et al., 2019). Chloroplasts and peroxisomes are the main generators of ROS in the presence of light, while mitochondria are the main sources of ROS production in dark conditions (Xie et al., 2019).

Studies conducted by Silva et al. (2020) suggest that Se application promotes a rearrangement of the antenna complex to improve energy uptake and protect the system against oxidative stress, with the application of selenite providing greater production of Chl b, while selenate provides greater production of carotenoids. According to Mittler (2002), antioxidants influence the molecular mechanisms to regulate the photosynthetic apparatus and the antenna complex according to the quality and intensity of the light, and may even promote the suppression of photosynthesis. In the chlorophyll cycle, the proportion of chlorophylls can change to stabilize the antenna system, given that each photosynthetic component can absorb light in a different spectrum, and therefore, plants can use Se as a precursor of this system of adaptation to stressful situations (Chauhan et al., 2017).

Photosynthetic pigments act as protectors of light capture, preserving chlorophylls, which are the central molecules of photosynthesis, from undergoing disruption and degradation of their structures. The synthesis of these metabolites (anthocyanin, ascorbates, and carotenoids) provides that plants can carry out their photosynthetic cycle, and provide the plant with the energy necessary to complete its life cycle. Being that these results are seen in the increase in the synthesis of sugars and carbohydrates, proteins, and consequently crop yield (Saleem et al., 2020; Schiavon et al., 2020).

5. Selenium as mitigation of abiotic stresses

Plants are sessile beings that are exposed to various stresses from the environment, such as salinity, drought, contrasting temperatures, concentrations of toxic elements, and excess light. Vegetables express complex strategies to release damage and return to their homeostasis as a way of mitigating stress (Xie et al., 2019). In the following section, the role of Se as a mitigator of different abiotic stresses will be specifically addressed (Table 1). Physiological and biochemical responses to each abiotic stress-promoting source in plants will be discussed.

5.1. Drought

Plants have physiological mechanisms to acclimate to water stress or even to resist periods of water deficiency, such as stomatal closure. This process is responsible for reducing the rate of CO₂ assimilation and the stomatal conductance (Gs) that is directly linked to the degradation and fragmentation of chlorophyll, caused by the overexpression of the enzyme rubisco (Andrade et al., 2018). Antioxidants, such as Se can protect chloroplasts and increase chlorophyll content, regulate redox reactions, and stimulate the action of antioxidant enzymes (Rady et al., 2020).

However, the availability of nutrients for plants under water restriction is another challenge to be overcome, since, under conditions of drought stress, the roots are unable to absorb many nutrients from the soil due to the decrease in root activity, which is associated with the decreased movement of water towards the roots and the slower ion diffusion (Andrade et al., 2018).

Rady et al. (2020) demonstrated that the application of 20–40 mM of selenate to tomatoes subjected to irrigation with only 60% of soil water retention capacity resulted in a significant increase in photosynthesis quantification parameters, such as the efficiency of photosystem II (Fv/Fm), the rate photosynthetic (Pn), and the SPAD index, which is relative to the chlorophyll content present in the leaves. Also, Se induced an increase in non-enzymatic antioxidants (water content, lycopene, total soluble sugars, proline, AsA, GSH, and α-tocopherol) and enzymatic (SOD, CAT, and APX), resulting in a decrease in O₂⁻, H₂O₂, and MDA.

Canola submitted to severe water deficit stress during the development stage showed a reduction in plant size (Table 1), while Se application at the dose 30 g L⁻¹ as sodium selenate increase plant height, number of pods and seeds, the weight of 100 seeds, seed yield and seed oil yield. This result is explained by the increase in photosynthetic efficiency (chlorophylls a and b) and of substances such as proline (Hemmati et al., 2019).

Cucumber seeds treated with sodium selenite demonstrated the narrow limit between the benefits and toxicity of Se and its influence on the generation of ROS (Table 1). Selenium application at low concentrations (1 and 5 μM) increases the antioxidant capacity through the action of the enzymes SOD, CAT, and APX, and reduces the ROS (O₂⁻, H₂O₂, OH⁻ and MDA), while Se in high concentrations (10 μM) increases lipid peroxidation (Jóźwiak and Politycka, 2019).

Exogenous Se application as a mitigator for water deficit stress in plants demonstrates to be a great commercial strategy. The treatment with 100 mg L⁻¹ of Se as sodium selenate increased molecules such as chlorophylls, carotenoids, phenols, and SeMet, and provided an increase in the antioxidant capacity of extra virgin olive oil (Table 1), by increasing oxidative stability of the product, favoring shelf life for commercialization (D'Amato et al., 2018).

5.2. Salinity

According to Ashraf et al. (2018), the use of mineral elements is an approach widely used by researchers to improve tolerance to salinity in crops. In the studies conducted by these authors, foliar application of 20 and 40 mg L⁻¹ of Se as sodium selenate decreased the accumulation of toxic Na⁺ in different parts of the plant regulating important physicochemical attributes under salinity (Table 1). These results suggest that Se reduced Na⁺ due to the compartmentalization of Na⁺ in vacuoles, as well as increasing the bond with the cell wall.

Regarding stomatal opening, treatments of 1–25 μM Se as sodium selenite in corn exposed to 100 mM NaCl resulted in an increase in stomatal conductance, transpiration rate, and, consequently, photosynthetic efficiency (Table 1). The increase in carotenoid levels may also be related to better absorption and regulation of antenna complex, leading to a reduction in lipid peroxidation (Jiang et al., 2017; Silva et al., 2020).

High concentrations of Na⁺ have an antagonistic relationship with the ions K⁺ and Ca²⁺ causing an imbalance in cell homeostasis, nutrient deficiency, oxidative stress, delayed growth, and cell death (Yu and Assmann, 2016). For wheat exposed to 100 mM NaCl, the treatment of 5 μM of Se as sodium selenate provided a reduction of Na in plant tissues, and an increase in K, Ca, and N, reflecting an increase in seed yield (Elkelish et al., 2019).

Elkelish et al. (2019) observed that the increase in the levels of non-enzymatic antioxidants (AsA GSH, phenolic compounds) and the accumulation of osmolytes (proline, sugars, and K⁺) besides acting in the fight against ROS, and the fight against lipid peroxidation, also act in

Table 1

Effect of Se application on ROS scavenging system and yield of crops in response to abiotic stresses.

Abiotic Stress	Species	Trial	Stress	Se doses/source	Yield	Non-enzymatic antioxidants	ROS scavenging system	Conclusion	Reference
Drought	<i>Oryza sativa</i> L.	Greenhouse	–50 kPa	0.5–2.0 mg kg ⁻¹ Na ₂ SeO ₄	↑ Plant height	–	↑ SOD, ↓ H ₂ O ₂	The antioxidant capacity of Se in rice under water deficit minimizes damage to productivity by increasing photosynthetic capacity and reducing lipid peroxidation.	Andrade et al. (2018)
Drought	<i>Brassica napus</i> L.	Field	Irrigation and development stage	30 g L ⁻¹ Na ₂ SeO ₄	↑ Plant height, number of pods and seeds, 100 seeds weight, seed yield and seed oil yield.	↑ Proline and relative water content	–	The interference of parameters under drought stress may have been generated by the increase in ROS, and the application of Se was useful to reduce harmful effects.	Hemmati et al. (2019)
Drought	<i>Cucumis sativus</i> L.	Hydroponics	Total water deficit after 96h of Se treatment	1–10 μM Na ₂ SeO ₃	–	↑ Water content	↑ APX, POD and SOD, ↓ O ₂ ^{•-} , H ₂ O ₂ , OH [•] and MDA	Se at lower concentrations (1 and 5 μM) increased antioxidant capacity and reduces the ROS, while Se at higher concentrations (10 μM) enhances lipid peroxidation.	Józwiak et al. (2019)
Drought	<i>Olea europaea</i> L.	Field	Total water deficit and 110 m ³ ha ⁻¹	100 mg L ⁻¹ Na ₂ SeO ₄	↑ Dry, fresh weight and oil content	↑ Carotenoids and Phenols	–	The application of Se can increase the nutritional properties, increasing antioxidant compounds and providing longer shelf life.	D'Amato et al. (2018)
Drought	<i>Solanum lycopersicum</i>	Greenhouse	100 and 60% Soil field capacity	20–40 mM Na ₂ SeO ₄	↑ Number of leaves, dry and fresh weight	↑ Water content, lycopene, total soluble sugars, proline, AsA, GSH and α.TOC	↑ SOD, CAT, and APX, ↓ MDA, H ₂ O ₂ , and O ₂ ^{•-}	The supplementation of Se in the soil is more efficient to increase the enzymatic and non-enzymatic antioxidants and minimize the effects of drought stress through antioxidant metabolism.	Rady et al. (2020)
Salinity	<i>Zea mays</i> L.	Greenhouse	4 dSm ⁻¹ NaCl	20 and 40 mg L ⁻¹ Na ₂ SeO ₄	↑ Dry and fresh weight	↑ Total soluble proteins, phenolics and flavonoids	↑ CAT, POD, SOD, ↓ MDA and H ₂ O ₂	The antioxidant action of Se in salinity stress depends on the form of application, low doses and vegetative stage, promoting a reduction in lipid peroxidation, increased photosynthetic capacity and Na inhibition.	Ashraf et al. (2018)
Salinity	<i>Triticum aestivum</i> L.	Greenhouse	100 mM NaCl	5 and 10 μM Na ₂ SeO ₄	↑ Length, fresh and dry biomass	↑ Carotenoids, proline, soluble	↓ Proline oxidase and ↑ γ-glutamyl	Low concentration Se (5 μM) was shown to be	Elklish et al. (2019)

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Table 1 (continued)

Abiotic Stress	Species	Trial	Stress	Se doses/source	Yield	Non-enzymatic antioxidants	ROS scavenging system	Conclusion	Reference
						sugars and water content.	kinase, SOD, CAT, GST, APX, GR, ↓ H ₂ O ₂ and MDA	beneficial in increasing non-enzymatic antioxidants and reducing ROS, and therefore, minimizing the deleterious effects of salt stress.	
Salinity	<i>H. annuus</i> L.	Greenhouse	15 dS m ⁻¹ NaCl	5 mg kg ⁻¹ Na ₂ SeO ₄	↑ Dry weight	↑ Carotenoids and Anthocyanin	↑ GPx, ↓ H ₂ O ₂ and MDA	Se minimizes oxidative damage caused by salt stress by increasing photosynthetic parameters, inhibiting Na translocation and reducing oxidative stress.	Habibi et al. (2017)
Salinity	<i>Solanum lycopersicum</i> L.	Greenhouse	50 mM NaCl	1–20 mg L ⁻¹ Nano-Se	↓ Plant height, number of leaves and ↑ Number of fruits,	↑ Flavonoids, Phenols, Lycopene, and β-carotene, titratable acidity, soluble solids ↓pH	↑ APX, GPX, CAT, SOD	Nano-Se increased the enzymatic activity and resulted in the improvement of the photosynthetic capacity of the plants, in addition to increasing the antioxidant compounds.	Morales-Espinoza et al. (2019)
Salinity	<i>Zea mays</i> L.	Growth chamber	100 mM NaCl	1–25 μM Na ₂ SeO ₃	↑ Dry Weight	↑ Carotenoids	↑ SOD, CAT, APX, ↓ Lipidic Peroxidation	Low Se treatment activated the antioxidant defence system, preserve the chloroplasts ultrastructure promote alleviate ROS damage, and reduced Na concentration.	Jiang et al. (2017)
Heavy metals	<i>Oryza sativa</i> L.	Hydroponics	25 μM NaAsO ₂	5–25 μM Na ₂ SeO ₃	↓ Plant Growth	↑ Carotenoids and phenolic compounds	↓ SOD and CAT ↑ GPX, GR, APX, POD, ↓ O ₂ ^{•-} , H ₂ O ₂ and MDA,	Se supplementation ameliorated As toxicity in rice plant by reducing As accumulation and by retrieving As induced nutrient deficiency.	Chauhan et al. (2017)
Heavy metals	<i>Cucumis sativus</i> L.	Growth chamber	25 and 50 μM CdCl ₂ ·2.5 H ₂ O	5 and 10 μM Na ₂ SeO ₄	↑ Fresh weight	↑ Phytochelatin and carotenoids	↓ MDA	Treatment with Se can relieve the toxicity of Cd and its destructive physiological effects on plants, however, depends on the proportion of these two elements in the nutrient solution.	Hawrylak-Nowak et al. (2014)
Heavy metals	<i>Brassica campestris</i> L.	Hydroponics	1 mg L ⁻¹ K ₂ Cr ₂ O ₇	0.1 mg L ⁻¹ Na ₂ SeO ₃	↑ Increased the total length, surface area, volume and tip numbers	–	–	Se application reduced Cr uptake and increasing the negative effects of Cr toxicity.	Zhao et al. (2019)
Heavy metals	<i>Brassica napus</i> and <i>Brassica juncea</i>	Growth chamber	50 μmol L ⁻¹ CdCl ₂	3 μmol L ⁻¹ Na ₂ SeO ₄ , Na ₂ SeO ₃ and Se-Met	↑ Dry Weight	–	↑ CAT and ↓ SOD, POD, ↓ H ₂ O ₂ and O ₂ ^{•-}	Cadmium stress was combated by the application of Se by reducing reactive oxygen	Zhang et al. (2020)

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Table 1 (continued)

Abiotic Stress	Species	Trial	Stress	Se doses/source	Yield	Non-enzymatic antioxidants	ROS scavenging system	Conclusion	Reference
Heavy metals	<i>Cucumis sativus</i> L.	Hydroponics	20–25 mM CdCl ₂ and 60–100 mM PbCl ₂	4–8 mg L ⁻¹ Na ₂ SeO ₃	↑ Fruiting, accelerated flowering, number of fruits, fruit length and diameter, single fruit weight and total yield.	–	–	species by increasing antioxidant activity and photosynthesis. The application of Se relieves the symptoms of stress by cadmium and lead, increasing the fruit productivity parameters.	Shekari et al. (2019)
Temperature	<i>Valerianella locusta</i> L.	Greenhouse	35/22 °C day/night	50 mg dm ⁻³ Na ₂ SeO ₄	↑ DW	↓ Proline	↓ APX ↑ GPX, CAT, GSH, ↓ H ₂ O ₂	Foliar Se treatment was more efficient than soil application, and Se efficiently alleviated HS-induced disorders in the metabolism.	Hawrylak-Nowak et al. (2018)
Temperature	<i>Fragaria</i> × <i>ananassa</i>	Growth chamber	0 °C (6–12 h)	2.5–10 mg L ⁻¹ Na ₂ SeO ₃	–	↑ Ascorbic acid	↓ APX, GR, and MDHAR, ↑ SOD, CAT, POD, DHAR, ↓ MDA, and H ₂ O ₂	Se applications significantly alleviated the adverse impacts of chilling stress on changes in stomatal conductance and intercellular CO ₂ concentration.	Huang et al. (2018)
Temperature	<i>Zea mays</i>	Hydroponics	24–44 °C	5–15 μM Na ₂ SeO ₃	–	–	↑ SOD, APX, GR, MDHAR, DHAR, GPX, and ↓ POX and TBARS, ↑ O ₂ ^{•-} and H ₂ O ₂	Se can control the production and quenching of ROS.	Yildiztugay et al. (2017)
Temperature	<i>Chrysanthemum morifolium</i> Ramat.	Greenhouse	37.3–41.6 °C	50–200mg nano-Se L ⁻¹	↑ Number of opening flowers, plant height and weight	–	Low Se ↓POX, CAT and ↑ PPO, Low Se ↑ H ₂ O ₂ and ↓ electrolyte leakage	The application of Nano-Se has the ability to protect flowers from the negative effects of thermal stress, providing the activation of the antioxidant system and ensuring the functioning of the photosynthetic apparatus.	Seliem et al. (2020)
Temperature	<i>Gossypium hirsutum</i> L.	Field	Heat imposed at squaring or flowering (±40 °C)	50–150 mg L ⁻¹ Se	↑ Seed cotton yield and fiber quality	–	–	There was a strong correlations of phenological and quality attributes with seed cotton yield with Se treatment.	Saleem et al. (2020)
Light	<i>Lactuca sativa</i> L.	Hydroponics	Fluorescent light, red LED light, blue LED, and mixed red and blue LED.	10 mmol L ⁻¹ Na ₂ SeO ₄ and 0.5 mmol L ⁻¹ Na ₂ SeO ₃	↑ Fresh and dry weight and length	–	–	Se forms has a strong interaction with the light spectra, and promotes influence on the Se accumulation and the regulation of nitrogen metabolism.	Bian et al. (2020)
Light	<i>Triticum aestivum</i> L.	Field	UV+ and UV-	10 mg L ⁻¹ Na ₂ SeO ₄	↑ Biomass ↓ Plant height	↓ Carotenoids and Anthocyanins	–	The combined treatment of UV light and Se promoted an	Golob et al. (2017)

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Table 1 (continued)

Abiotic Stress	Species	Trial	Stress	Se doses/source	Yield	Non-enzymatic antioxidants	ROS scavenging system	Conclusion	Reference
Light	<i>Brassica oleracea</i> L.	Growth chamber	CK:1R1B1G LED, 1R1B1G + Se, 1R1B + Se, 1R2B + Se, 2R1B + Se	100 $\mu\text{mol L}^{-1}$ Na_2SeO_3	↓ Hypocotyl Length, Fresh Weight and ↑ Dry Weight	↑ Carotenoids, Anthocyanins, Soluble sugar, Protein, Vitamin C, Total Phenolic Compounds, Total Flavonoids and Glucosinolate	–	increase in the defense metabolism of plants through the increase of compounds that absorb UV, light reflectance and transmittance, combating oxidative stress. The combination of Se with different light treatments has been shown to be effective in increasing the nutritional quality and protective compounds of broccoli sprouts for plants and humans.	He et al. (2020)
Light	<i>Glycine max</i> L.	Growth chamber (in vitro)	UVC-light (30 or 60 min)	5, 10 or 20 mg L^{-1} Na_2SeO_3	–	↑ Isoflavonoids, inhibition of nitric oxide production and Cellular antioxidant activity	–	Se stress increased the concentrations of isoflavonoids (glycitein and genistein) in soybean calluses, demonstrating higher levels of nitric oxide inhibition and cellular antioxidant activity.	Mata-Ramírez et al. (2019)
Light	<i>Triticum aestivum</i>	Growth chamber (in vitro)	Visible light and UV-B light	Seleniferous and nonseleniferous soil	–	↑ Phenolic content, flavonoids and DPPH radical scavenging	↑ SOD, CAT and ↓ POD, APX, GR, GPx, ↓ Lipid peroxidation	Se treatment increased different secondary metabolites in wheatgrass and protect against lipidic peroxidation.	Jaiswal et al. (2018)

the gene expression from vegetables, increasing Na^+ transporters to vacuoles, as a way to avoid excess salinity in the other parts of the plant.

The results found by Habibi (2017) suggest that Se decreases salt-induced damage by stimulating antioxidant activities. Sunflower seeds subjected to salt stress (15 dS m^{-1} NaCl) and treated with 5 mg kg^{-1} of Se as sodium selenate demonstrate an increase in carotenoids and anthocyanins, which are photosynthetic pigments that help in the capture and regulation of the apparatus photosynthetic. Consequently, there were several positive results of photosynthetic components, such as the increase in chlorophylls *a* and *b*, the efficiency of photosystem II (Fv/Fm), photosynthetic performance rate (PI), and the reduction of oxidative stress (H_2O_2 and MDA).

Another point raised in the literature is that under saline stress, in addition to biochemical modifications, plants can undergo morphological modifications, such as reduced leaf area, or biochemical, which can also be aggravated by harmful doses of Se. In this sense, the treatment of tomatoes with $1\text{--}20 \text{ mg L}^{-1}$ of Se as nano-Se source demonstrated that the nanoparticles present low risks of toxicity, and increase the antioxidant capacity of the element, as seen in the levels of flavonoids, phenols, lycopene, β -carotene, titratable acidity, and soluble solids (Morales-Espinoza et al., 2019).

5.3. Heavy metals

Plants can absorb elements from the soil, and assimilate them for use in their essential metabolic processes. However, this process does not have a specific selectivity, attributing to plants the risks of absorbing elements harmful to plant metabolism and human health. However, the biological activity of metal ions can be markedly affected by the presence of other ions in the root zone (Hawrylak-Nowak et al., 2014).

Chromium (Cr) mainly affects plant morphology, causing irreversible anatomical and ultrastructural changes and interfering with mineral nutrition. Pumpkins under Cr toxicity (1 mg L^{-1} $\text{K}_2\text{Cr}_2\text{O}_7$) demonstrated that the application of Se at low doses (0.1 mg L^{-1} as sodium selenate) can reduce the Cr concentration in the roots (Na, Ca, Fe, Mn, Cu, and Zn), in addition to increasing the absorption of other elements, demonstrating that there was protection or regeneration of root system (Table 1) (Zhao et al., 2019).

Cadmium (Cd) is one of the most dangerous heavy metals due to its high toxicity, mobility, and availability to all living organisms. Vegetables like cucumber exposed to different levels of Cd (25 and $50 \mu\text{M}$) showed impaired water balance, mineral nutrition, photosynthesis, and respiration. However, treatment with Se (5 and $10 \mu\text{M}$) provided an increase in the fresh matter, chlorophylls, carotenoids, and phytochemicals, which are recognized by the ability to inactivate metal ions

(Table 1) (Hawrylak-Nowak et al., 2014).

The same effect of Se on Cd mitigation was seen by Zhang et al. (2020) for rapeseed (*Brassica napus*) treated with 50 $\mu\text{mol L}^{-1}$ of Cd, which is a Cd hyperaccumulator. The experiment focused on the speciation of Se (3 $\mu\text{mol L}^{-1}$ Na₂SeO₄, Na₂SeO₃, and Se-Met), and it turned out that the treatments were beneficial for photosynthesis (photosynthetic rate, stomatal conductance, internal CO₂ concentration, and respiration rate). Also, there was a reduction in H₂O₂ and O₂⁻ (Zhang et al., 2020).

The stress of arsenic (25 $\mu\text{M NaAsO}_2$) in rice plants was remedied with the application of 5–25 μM of Se. In addition, an increase in other nutrients (Mn, Fe, Co, Cu, Zn, and Mo) was provided, demonstrating benefits of Se on mineral nutrition of plants (Table 1). Also, Se was responsible for increasing the content of antioxidants, such as carotenoids and phenolic compounds, and consequently improving the photosynthetic apparatus. In this experiment, a reduction in SOD activity was observed, and an increase in enzymes involved in the ascorbate-glutathione pathway, suggesting that stress may have been alleviated through spontaneous stimulation mechanisms of O₂⁻ dismutation in H₂O₂ and through non-enzymatic antioxidants. These results were associated with the similar electronic configuration between arsenite (AsIII) and selenite (SeIV) and with the sharing of the common carrier for its absorption in plants (Chauhan et al., 2017).

5.4. Temperature

Each region of the planet has specific thermal characteristics, and as a consequence, plant species have created networks of adaptations over the generations to ensure crop yield. Temperature stress is one of the items of greatest concern for future projections, taking into account climate changes and the imbalances in ecosystems caused by anthropic action in recent decades (Bouis et al., 2019).

Vegetables are highly sensitive to high temperatures, requiring the management of ideal conditions for their growth and development. Foliar Se application in lettuce plants submitted to 35 °C, was more efficient than through the soil, increasing fresh matter, and antioxidant enzymes (GPx, CAT, GSH). In contrast, the reduction in proline levels indicates that Se did not exert its action through the increase in antioxidants, but again via the ascorbate-glutathione pathway (Hawrylak-Nowak et al., 2018).

Under cold stress, the application of 5 mg L⁻¹ Se in strawberry induced the antioxidant action by increasing enzymatic compounds, mainly SOD, and non-enzymatic compounds such as ascorbic acid. The treatment had a great influence on the photosynthetic processes, increasing the photosynthetic rate, chlorophyll content, and stomatal conductance (Huang et al., 2018).

Flowers are also species that are very sensitive to thermal imbalance, suffering losses in their production due to temperature fluctuations, and also requiring high nutritional control, being vulnerable to toxicity. Thus, the use of Nano-Se also demonstrates positive effects in the control of thermal stress, reducing lipid peroxidation through doses that ensure the benefits of Se, reducing the amount of application, but expanding the antioxidant capacity. The application of 150 mg nano-Se L⁻¹ in Chrysanthemum subjected to high temperature increased the activity of antioxidative enzymes, such as CAT and SOD, and increased the concentration of chlorophylls.

5.5. Light

According to Jaiswal et al. (2018), exposure to UVB stress accelerates the level of ROS and can cause oxidative damage to proteins, lipids, and nucleic acids in plants. In their studies, it was found that the cultivation of wheatgrass in soils with high concentrations of Se (seleniferous) induces plants to increase their ability to synthesize antioxidant compounds (phenolic compounds and flavonoids) as a way to mitigate excess light energy. Also, the high concentrations of Se induced a

reduction in lipid peroxidation through the action of the enzymes SOD and CAT.

Soybean plants has compounds that attribute antioxidant and anti-inflammatory characteristics to its grains, such as isoflavones (genistein, daidzein, and glycitein). However, under high intensity of UVB light changes in its biochemical and physiological routes. Therefore, the application of 5–20 mg L⁻¹ can mitigate the effects of excess light by increasing secondary metabolism compounds (Mata-Ramírez et al., 2019).

The increase in the amount of light energy acts directly on the photosynthetic mechanisms, overloading the complex antennas, and causing a disruption in the electron transport chain, generating the production of ROS and consequently damage to cellular components. The application of 100 $\mu\text{mol L}^{-1}$ If in broccoli treatments with different types of LED light it was responsible for reducing the levels of chlorophylls (a and b), in addition to photosynthetic pigments (He et al., 2020). This result may be associated with the regulation of the ability to capture light under stress (Chauhan et al., 2017).

6. Physiological roles of Se on crop yields: agronomic biofortification perspective

Functional foods contain nutrients and bioactive compounds that provide benefits to the human and animal organisms, and are used to combat pathologies and regulate metabolism, and can be included in diets such as fruits, vegetables, legumes, nuts, spices, olive oils, mustards, canola, and flaxseed (Tripathi et al., 2018).

However, according to Bouis et al. (2019), these foods are increasingly being threatened by the loss of biodiversity and poor population habits and emphasizes that agricultural foods have the function of providing the macro and micronutrients necessary to maintain life, support physical activity and achieve a healthy body composition.

The Codex Alimentarius indicates that the production of biofortified foods should not have Se levels greater than 0.3 mg kg⁻¹. However, diets with an intake of less than <50 $\mu\text{g day}^{-1}$ of Se are considered a nutritional deficiency (Reis et al., 2017). In the next section, the effect of agronomic biofortification with Se will be addressed in the main food classes that make up the food routine of the world population through the most recent research in the scientific scenario (Fig. 3).

6.1. Legumes

Legumes are great important food for humans and animals, providing high levels of protein, minerals, dietary fibers, and low levels of fats, and being an alternative for products with high added value, such as meat and seafood. This food class has consolidated its importance in combating the eradication of world hunger with the declaration of the United Nations General Assembly (UNGA) in 2016 with the establishment of the International Year of Pulses (IYP) (FAO, 2019).

Studies with cowpea have shown that foliar Se application at the dose 50 g ha⁻¹ is responsible for increase Se levels in shoots and grains, without causing symptoms of toxicity or causing oxidative damage in plant leaf cell (Table 2). Also, the intake of more than 50 g per day of biofortified cowpea with Se in the mentioned dosage can meet the recommended recommendation for adults (0.1 mg Se per day). This application limit also increases photosynthetic pigments, sugars and reduces oxidative damage (Silva et al., 2018, 2020; Lanza et al., 2021).

Dai et al. (2020) demonstrated that the application of Se in soybean plants at the dosages 0.5, 1.5, and 2 mg kg⁻¹ Se in the form of L-selenomethionine (C₅H₁₁NO₂Se) applied via soil, increased Se concentration in the grains by about 27 times, obtaining a maximum concentration of 0.23 mg kg⁻¹ of Se. The application also increased seed yield, content of photosynthetic pigments, proline and reduced significant damage. Hussein et al. (2019) did not describe the concentration of Se in his work with the application of nanoparticles, but highlighted the role of Se in the increase of fatty acids and proteins.

6.2. Cereals

Cereals are a food class widely used for human consumption, but with great emphasis on animal supplementation. However, over the years, cereal production is being affected by the environmental conditions of the main producing countries (Tripathi et al., 2018). According to FAO (2020), the consumption of cereals is expected to increase by 2.6% in 2020/2021 concerning the previous year, this increase is attributed mainly to the increase in the use of feed, especially corn and sorghum, and for the production of corn ethanol. Thus, strategies to increase cereal yield should be a necessity for the coming years.

The average consumption of wheat in Brazil is based on the product's derivatives, such as bread, pasta, and cakes, equivalent to a consumption of 60 kg year⁻¹, or 164 g day⁻¹ per person. Selenium application at the dose 21 g ha⁻¹ is the most suitable for biofortification of wheat, providing the grains with a grain concentration of 0.71 mg kg⁻¹ of Se. The stipulated dosage also favored the increase in seed yield, photosynthetic pigments, and carbohydrate metabolism (Lara et al., 2019).

Biofortification of rice with Se results in grains with higher nutritional quality (proteins, sugars, amino acids, nitrate, and ammonia), in addition to a significant increase in Se in grains. Considering that the average consumption of rice by the Brazilian population is 25 kg year⁻¹, that is, 68.5 g day⁻¹ per capita, the dosage of 25 g Se ha⁻¹ applied via foliar as sodium selenate was able to increase up to 50% the Se supply to meet the daily requirement, obtaining a value of 0.35 mg kg⁻¹ (Reis et al., 2018). Higher values of Se dosage for rice plants cause toxicity in rice plants (Gouveia et al., 2020; Reis et al., 2020).

Reis et al. (2018) elevated Se concentration in polished rice grains treated with soil fertilization, and estimated that agronomic biofortified cereal could increase the daily intake up to 66 µg/day based on consumption of rice in Brazilian population.

A single application of ⁷⁷Se to maize plants at the grain filling stage, provides a viable approach to Se biofortification (Ligowe et al., 2020). These authors find that application of 20 g ha⁻¹ Se produced sufficient grain Se enrichment in maize to provide the recommended dietary Se requirement. Given that applied Se remaining in the soil is not available for plant uptake beyond the growing season in which it is applied, seasonal application of Se would be required in order to continuously maintain recommended dietary Se intake. This could be achieved through adoption of Se fertilizer amendments to existing fertilizers.

6.3. Fruits

According to Bouis et al. (2019), the low consumption of specific food groups in the past reveals high indications of food malnutrition in the present, and the low consumption of fruits is reported as one of the limiting factors in human nutrition. Studies show that fruit biofortification, in addition to increasing nutritional levels, also adds several benefits to the commercial characteristics of foods, such as sweetness, firmness, pH and flavor (Zahedi et al., 2019).

The consumption of 150 g of fresh strawberries grown hydroponically and treated with 10 µM Se (Table 2) provides the human metabolism with 60 µg Se per day and provides a diet with a higher content of sweetness in the fruits and antioxidant compounds (flavonoids and polyphenols) beneficial to human health (Mimmo et al., 2017). Foliar Se application increased more than 70% of Se concentration in pear juice (Table 2), with the element mainly concentrated in the peel and juice, accounting for 41–58% and 31–48% of the total Se concentration of the fruit, respectively (Deng et al., 2019). For tomatoes, the application of 2 and 5 mg L⁻¹ Se provided a concentration of 24.5–35.8 µg g⁻¹ of Se (Table 2), revealing that the application of Se at low concentrations can improve harvest yield and fruit quality (Rahim et al., 2020).

6.4. Vegetables

According to Bian et al. (2020) supplementing vegetables with Se is a safe and effective way to combat Se deficiency in humans, as vegetables play an important role in the human diet. The application of 25 µM of Se in broccoli was able to increase 10–12 mg kg⁻¹ in its florets and 17–30 mg kg⁻¹ in the stems and leaves, indicating that in addition to being a vegetable highly consumed for its nutritional density (Table 2). Broccoli has high attractiveness because it is entirely used for consumption, and consequently has a larger area of Se supply (Tian et al., 2018).

Oliveira et al. (2018) report that consumption of 50 g of carrots biofortified with 50 µM L⁻¹ Se supplied via foliar application, corresponds to a daily intake of 105 µg Se, considering that the treatment concentrated about 14 mg kg⁻¹ of dry weight (Table 2). This application also favored increased carrot yield, titratable acidity, and reduced root maturation.

Selenate is the most efficient source for potato biofortification with Se in tropical conditions when supplied in low doses (Table 2). The application of 0.75 mg kg⁻¹ of Se via soil concentrated 5 mg kg⁻¹ of Se in

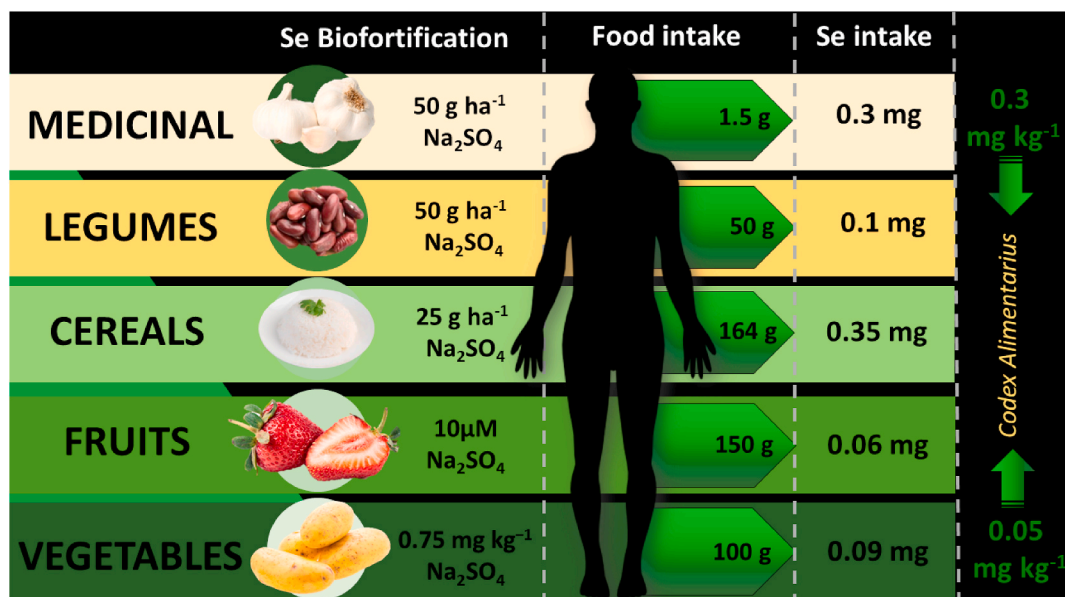


Fig. 3. Se intake in the human body. Maximum (0.3 mg kg⁻¹) and minimum (0.05 mg kg⁻¹) limit range of Codex Alimentarius for biofortified foods.

Table 2
Effect of Se application on mineral nutrition, antioxidant metabolism and yield of several types of plant species.

ID	Species	Trial	Se doses	Se source	Application	Se shoot*	Se edible part	Se roots*	Observation	Conclusion	Reference
Legume	<i>Vigna unguiculata</i> (L.) Walp.	Field	10–150 g ha ⁻¹	Na ₂ SeO ₄	Foliar	0.04–17 mg kg ⁻¹	0.04–10.4 mg kg ⁻¹	–	Above 50 g ha ⁻¹ resulted in visual symptoms of Se toxicity	The dose of 50 g ha ⁻¹ ↑ photosynthetic pigments and yield.	Lanza et al. (2020)
Legume	<i>Vigna unguiculata</i> (L.) Walp.	Field	50–1600 g ha ⁻¹	Na ₂ SeO ₃	Foliar	±0.01–100 mg kg ⁻¹	±1.5–12.2 mg kg ⁻¹	–	Concentrations higher than 50 g ha ⁻¹ caused leaf toxicity symptoms	The doses of 1200 and 1600 g ha ⁻¹ ↑ lipid peroxidation and ↓ total sugars, sucrose, and carotenoid concentration.	Silva et al. (2018)
Legume	<i>Vigna unguiculata</i> (L.) Walp.	Field	2.5–60 g ha ⁻¹	Na ₂ SeO ₃ and Na ₂ SeO ₄	Soil	Selenate (0.12–0.39) and Selenite (0.09–0.29 mg kg ⁻¹)	Selenate (0.09–0.67) and Selenite (0.09–0.32 mg kg ⁻¹)	–	The effect of Se application differed between source.	Both sources ↑ leaf sucrose and total sugars concentration in cowpea leaves (indicator of ROS scavenging).	Silva et al. (2020)
Legume	<i>Glycine max</i> (L.)	Greenhouse	0, 1.5 and 2 mg kg ⁻¹	L-selenomethionine (C ₅ H ₁₁ NO ₂ Se)	Soil	1.05–2.89 mg kg ⁻¹	0.08–0.23 mg kg ⁻¹	1.36–3.74 mg kg ⁻¹	Application of Se reduced Zn uptake from soil.	All treatments ↑ biomass, photosynthetic pigments, proline and ↓ MDA.	Dai et al. (2020)
Legume	<i>Arachis hypogaea</i> L.	Greenhouse	0, 20 and 40 ppm	N–Se	Foliar	–	–	–	The doses altered fatty acid composition and protein signatures.	The treatments ↑ yield components, seeds oil and antioxidant metabolism.	Hussein et al. (2019)
Cereal Crops	<i>Triticum aestivum</i> L.	Field	12–120 g ha ⁻¹	Na ₂ SeO ₄	Foliar	0.3–2.35 mg kg ⁻¹	0.6–2.86 mg kg ⁻¹	–	Increasing doses of Se did not influence S contents.	The dose of 21 g ha ⁻¹ ↑ photosynthetic rate, starch, total soluble sugars, reducing sugars, sucrose, and yield.	Lara et al. (2019)
Cereal Crops	<i>Oryza sativa</i> (L.)	Field	250–2000 g ha ⁻¹	Na ₂ SeO ₄	Foliar	–	±3.5–25 mg kg ⁻¹	–	Se accumulation occurred in the endosperm and aleurone/pericarp of the seeds.	All treatments ↓ yield and physiological seed quality.	Reis et al. (2018)
Cereal Crops	<i>Oryza sativa</i> (L.)	Field	10–100 g ha ⁻¹	Na ₂ SeO ₄	Soil	0.014–2.97 mg kg ⁻¹	0.099–2.16 mg kg ⁻¹	–	There was a high translocation of Se from leaves to grains.	All treatments ↑ Se concentrations in leaves and grains, and the concentrations of storage proteins in rice grains.	Reis et al. (2020)
Cereal Crops	<i>Oryza sativa</i> (L.)	Hydroponics	1.5 mM L ⁻¹	Na ₂ SeO ₄	Solution	±4.2–5.1 mg kg ⁻¹	–	±8.2–11 mg kg ⁻¹	The treatment cause visual symptoms of toxicity characterized as leaf chlorosis and necrosis.	The treatments ↑ leaf sucrose, total sugars, nitrate, ammonia, and activity of antioxidative enzymes.	Gouveia et al. (2020)
Cereal Crops	<i>Zea mays</i> L.	Greenhouse	1,2,4, 8,16, 32 mg kg ⁻¹	Na ₂ SeO ₄	Soil	95.4–318.4 mg kg ⁻¹	–	40.2–167.9 mg kg ⁻¹	Treatments above 4 mg kg ⁻¹ soil was toxic to maize plants.	Lower Se doses ↑ dry matter, chlorophyll, proline and activities of defense enzymes.	Sharma et al. (2018)
Fruit trees	<i>Coffea arabica</i>	Hydroponics	1.0 mmol L ⁻¹	Na ₂ SeO ₄	Solution	±200–383.27 mg kg ⁻¹	–	±500–849.92 mg kg ⁻¹	The treatment promoted root browning in all	The treatment ↓ photosynthetic pigments, antioxidant	Mateus et al. (2020)

(continued on next page)

Table 2 (continued)

ID	Species	Trial	Se doses	Se source	Application	Se shoot*	Se edible part	Se roots*	Observation	Conclusion	Reference
Fruit trees	<i>Fragaria ananassa</i>	Hydroponics	10 and 100 μM	Na_2SeO_4	Solution	10.48–125.08 $\mu\text{g g}^{-1}$ DW	3.95–46.04 $\mu\text{g g}^{-1}$ DW	19.02–174.42 $\mu\text{g g}^{-1}$ DW	genotypes and influence P and S contents in the shoots. There was involvement between phenolic compounds and Se supplementation, and alteration of secondary metabolites (cytokinin and amino acids). Se and N–Se controlled fruit cracking.	enzymes activities and \uparrow sucrose. Both treatments \uparrow mineral nutrient content (Ca, Mg, Mn and K), quality parameters, soluble sugars, organic acids (Citric and Malic). The dose of 2 μM (N–Se) increased chlorophyll content, yield, leaf mineral content (N, P, K, Ca, Fe, Zn), total sugars, phenolic compounds, antioxidants and anthocyanins. Selenate accumulate more Se in the fruit.	Mimmo et al. (2017)
Fruit trees	<i>Punica granatum</i>	Field	1–2 μM	Na_2SeO_4 and N–Se	Foliar	N–Se (2–2.5) and Selenate (1.5–2 $\mu\text{g g}^{-1}$ DW)	–	–		The dose of 2 μM (N–Se) increased chlorophyll content, yield, leaf mineral content (N, P, K, Ca, Fe, Zn), total sugars, phenolic compounds, antioxidants and anthocyanins.	Zahedi et al. (2019)
Fruit trees	<i>Pyrus communis</i> L.	Field	20–200 mg L^{-1} and different stages.	Na_2SeO_3 and Na_2SeO_4	Foliar	Selenite (0.63–7.85) and Selenate (0.72–8.92 mg kg^{-1} DW)	Selenite (7.04–27.30) and Selenate (61.77–127.32 $\mu\text{g kg}^{-1}$ FW)	–	Above 40 mg L^{-1} resulted in toxicity symptoms.	Selenate accumulate more Se in the fruit.	Deng et al. (2019)
Fruit trees	<i>Solanum lycopersicon</i> L. Mill	Greenhouse	2 and 5 mg L^{-1}	Na_2SeO_3	Soil	20.9–20.4 $\mu\text{g g}^{-1}$	24.5–35.8 $\mu\text{g g}^{-1}$	–	The solution doses did not interfere with the absorption of macronutrients.	The treatments \uparrow agronomic values.	Rahim et al. (2020)
Vegetables	<i>Cucumis sativus</i>	Hydroponics	Selenate (2–80) and Selenite (2–60 μM)	Na_2SeO_3 and Na_2SeO_4	Solution	Selenate (10.2–648.0) and Selenite (11.2–120.6 mg kg^{-1} DW)	–	Selenate (7.75–603.5) and Selenite (68.5–967.2 mg kg^{-1} DW)	There were symptoms of Se toxicity at the concentrations of 80 (Selenate) and 20 μM (Selenite).	Low doses of Se promoted \uparrow growth and \downarrow lipid peroxidation in roots.	Hawrylak-Nowak et al. (2015)
Vegetables	<i>Daucus carota</i> L.	Greenhouse	Soil (1.0 mg dm^{-3}) and Foliar (50 $\mu\text{M L}^{-1}$)	Na_2SeO_3 and Na_2SeO_4	Soil and Foliar	Selenate (± 10 –15) and Selenite (± 3 –19 mg kg^{-1})	–	Selenate (± 10 –15) and Selenite (± 7 –8 mg kg^{-1})	Foliar application of selenate was the most effective source and form of application.	Foliar application \uparrow dry mass, yield, titratable acidity and \downarrow root maturation.	Oliveira et al. (2018)
Vegetables	<i>Brassica oleracea</i> L.	Greenhouse	25 μM	Na_2SeO_4	Soil	± 17 –30 mg kg^{-1}	± 10 –12 mg kg^{-1}	–	The total amino acid levels were not significantly affected by treatment	The treatment \downarrow the secondary metabolism	Tian et al. (2018)
Vegetables	<i>Brassica juncea</i> L.	Field	50 mg Se L^{-1}	Na_2SeO_4	Foliar	8922 \pm 870 $\mu\text{g kg}^{-1}$ DW**	–	–	There was a synergism between Se and I that provided inhibiting nitrate accumulation.	The treatment \uparrow chlorophyll, carotene, ascorbic acid, flavonoids, total soluble solids, Al, B, and \downarrow Cd and Sr concentrations.	Golubkina et al. (2018)
Vegetables	<i>Solanum tuberosum</i> L.	Greenhouse	0.75–5.0 mg kg^{-1}	Na_2SeO_3 and Na_2SeO_4	Soil	Selenate (± 0.8 –5.63) and Selenite (± 0.5 –6.20 mg kg^{-1})	Selenate (± 5 –10) and Selenite (± 1.6 –5 mg kg^{-1})	–	In low doses selenate is the most efficient source	Low doses \uparrow production of tubers, Ca content and antioxidant system. High doses \downarrow production, S content,	Oliveira et al. (2019)

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Table 2 (continued)

ID	Species	Trial	Se doses	Se source	Application	Se shoot*	Se edible part	Se roots*	Observation	Conclusion	Reference
Medicinal	<i>Allium sativum</i> L.	Field	20 and 50 g ha ⁻¹	Na ₂ SeO ₄	Foliar and Soil	8.020–15.46 mg Kg ⁻¹	1.732–3.23 mg Kg ⁻¹	–	Foliar application was more positive than soil.	pH and peroxidase activity. The dose of 50 g ha ⁻¹ applied by leaf ↑ total phenolic content, total flavonoid content, and total antioxidant capacity.	Shafiq et al. (2019)
Medicinal	<i>Cannabis sativa</i> L.	Hydroponics	5–80 μM	Na ₂ SeO ₄	Solution	±8–200 mg kg ⁻¹ DW	±9–150 mg kg ⁻¹ DW	±12–80 mg Se kg ⁻¹ DW	The dose above 40 μM was toxic to hamp plants	In the mature plant stage the doses of 5–40 μM ↑ yield, plant height and photosynthetic performance	Stonehouse et al. (2020)
Medicinal	<i>Stevia rebaudiana</i> Bert.	Greenhouse	1–10 mg kg ⁻¹	Na ₂ SeO ₃ and Na ₂ SeO ₄	Soil	Selenite (11.4–96.7) and Selenate (77.9–415 mg kg ⁻¹)	–	–	Selenate and Selenite treatments did not affect the growth and shoot biomass	Stevia leaves fortified with 1 mg kg ⁻¹ of selenate can be used as sweetener for some drinks (water, coffee, and green tea).	Szarka et al. (2020)
Medicinal	<i>Ocimum</i> spp.	Greenhouse	50 g ha ⁻¹	Na ₂ SeO ₄	Foliar	–	0.370–0.823 mg kg ⁻¹ DW	–	The consuming of 9 g selenised basil seeds the daily recommended dose of selenium could be covered for human beings.	The treatment ↑ the content of selenium in basil seeds that is a source of polyphenols with multiple times higher antioxidant activity.	Mezeyová et al. (2020)
Medicinal	<i>Cordyceps militaris</i>	Greenhouse	5–40 μg g ⁻¹	Na ₂ SeO ₃ , Na ₂ SeO ₄ and Se-Met	Solution	–	Selenate (±17–130.9 40), Selenite (±22–125) and Se-Met (12–58 μg g ⁻¹)	–	The predominant Se species in Se-biofortified fruiting bodies were SeCys2 and SeMet.	The application of 40 μg g ⁻¹ as source of selenate and selenite ↑ the Se concentration in fruiting bodie.	Hu et al. (2019)

the tubers, being able to supply 90 µg of Se, considering the consumption of 100 g of fresh tuber (80% water), also, to increase the content of other nutrients, such as Ca (Oliveira et al., 2019).

6.5. Medicinal

Garlic (*Allium sativum*) is probably the most cited herb in the literature for medicinal properties (Tripathi et al., 2018). The biofortification of garlic with Se at the dose 50 g ha⁻¹ as sodium selenate can supply the daily Se intake in humans from the consumption of 16 g of biofortified bulb, and the dosage was able to generate a concentration of 3.23 mg kg⁻¹ in the edible parts (Table 2). Also, it was responsible for increasing the total phenolic content, total flavonoid content, and total antioxidant capacity (Shafiq et al., 2019).

Mushrooms, in addition to food interest, also have high value as a medicinal product, such as *Cordyceps militaris* which is one of the most popular edible and medicinal mushrooms worldwide, especially in Asian countries, given its pharmacological functions that affect the circulatory system and anti-inflammatory (Hu et al., 2019).

Cannabis sativa L. seeds is one of the functional foods of the century, and besides being associated with several medicinal benefits, it also has great potential for phytoremediation of soil elements, given its large accumulation of nutrients in its seeds and leaves. An experiment conducted in Colorado (USA) determined that the average dosage of sodium selenate could provide the recommended daily intake of Se (55–75 µg of Se) recommended through approximately 4 g of seeds. According to USDA, the daily recommendation for seeds is 30 g, which would provide an average of 450–750 µg of Se to human metabolism, which corresponds to the maximum allowed intake (Table 2). Another product based on *Cannabis sativa* L. seeds is beer, which, if produced based on biofortification, may offer 42 µg Se L⁻¹, which corresponds to 15 µg Se, about 25% of daily needs (Stonehouse et al., 2020).

Natural spices and sweeteners are also featured in medicinal plants and have a high capacity of biofortification with Se, which can be used as a food supplement. Szarka et al. (2020) noticed that the application of 1 mg kg⁻¹ Se in *Stevia rebaudiana* (Bert.) results in approximately 0.1 mg kg⁻¹ Se in water drinks, coffee, or green tea (Table 2). Stevia is commonly known as the level of sweetness provided by its leaves and is used as a substitute for conventional sugar, which is highly harmful to human health and well-being. Basil is also another element widely used in tropical cuisine, and the use of 9 g of basil seeds with the application of 5 mg m⁻² of Se can supply the recommended daily dose, while non-biofortified seeds should be consumed at an average of 120 g per person (Table 2). *Ocimum basilicum* also contains a significant amount of biological compounds with strong healing properties, and the application of Se was responsible for increasing the content of polyphenols and the antioxidant capacity.

7. Conclusion and future perspectives

Selenium is an element that has a wide cycle of action, influencing mechanisms in plants, humans, and animals, and presenting risks to these organisms both with their lack and excess. However, there is conclusive evidence that supplementation is safely possible, and that the benefits gained from the exogenous application of Se help in improving the nutritional quality of food, mitigating hidden hunger.

As perspectives, we show the improvements of used technologies help in the regulation of the limits between the toxic and the beneficial for the supplementation of plants, minimizing the necessary amount of application to reach the established daily consumption and the benefits for the plant metabolism. Foliar Se application at low concentrations can be used to improve the antioxidant (SOD, CAT, APX, GR) and non-oxidant (ascorbate, carotenoids, flavonoids, tocopherol) metabolism of plants to induce tolerance to abiotic stresses (drought, temperature, salinity and heavy metals). Studies are necessary to establish an optimal dose-response for different plant species in different edaphoclimatic

conditions aiming at agronomic biofortification.

Se roles on abiotic stresses such as drought, salinity, toxic elements (Al, Cd, As, Hg) are not fully understood (Ahmad et al., 2016; Handa et al., 2019; Arif et al., 2020; Ahmad et al., 2021; Hossain et al., 2021; Sheikhalipour et al., 2021). Further studies are needed to understand how Se control the mechanisms of genetic regulation and transport of these toxic elements to edible part of plants. Biofortification of plants with Se to avoid toxic elements accumulation in edible crops is essential to keep food safety in order to improve human health. Practice of agronomic biofortification with Se in plants can improve the nutritional and biochemical quality of agricultural products, enhance crop yield and can bring benefits to human health.

CRedit authorship contribution statement

Maria Gabriela Dantas Bereta Lanza: Conceptualization, Investigation, Methodology, Validation, Writing – original draft. **André Rodrigues dos Reis:** Conceptualization, Validation, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank FAPESP (São Paulo Research Foundation) for supporting this research with financial resources provided by process number 19/19114–2.

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