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Chapter

Plant-Based Foods Biofortified with Selenium and Their Potential Benefits for Human Health

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Abstract

Selenium (Se) is essential for humans. This element is present in more than 25 proteins related to redox processes, and its deficiency is related to the onset of chronic diseases. One way to incorporate Se into the human diet is by consuming plant foods rich in Se. Crop fortification with Se can be achieved through the agronomic practice of biofortification. This chapter discusses dietary sources of inorganic Se (selenate and selenite), organic Se (selenocysteine, selenomethionine, and methylselenocysteine), and bioactive compounds provided by consuming the edible parts of plants as a result of agronomic biofortification. The benefits to human health from consuming selenium-enriched crops due to their biological functions such as antioxidant, anti-inflammatory, and anticarcinogenic are also presented. The intake of Se-enriched plant foods is a growing trend. In addition to providing the daily dose of Se, these Se-enriched vegetables are a functional food option that improves human health due to their content of phytochemical compounds.

Keywords: biofortification, inorganic Se, organic Se, bioactive compounds, antioxidant, anti-inflammatory, anticarcinogenic

1. Introduction

Selenium (Se) is an element that is required in trace amounts and has an essential role in human metabolism, growth, and hormonal balance [1]. In humans, 25 selenoproteins have been reported and classified into six functional groups (proteins involved in Se transport, selenocysteine synthesis, protein folding, hormone metabolism, redox signaling, and reductase/peroxidase activity) [2]. Although most selenoproteins are related to protection against oxidative stress, others are involved in phospholipid biosynthesis and calcium signaling [2]. Selenium has also been reported to intervene in health through epigenetic processes, modulating DNA methylation and histone acetylation [3].

Meanwhile, Se deficiency can lead to human health problems ranging from endemic cardiomyopathy (Keshan disease), endemic deforming osteoarthropathy (Kashin-Beck disease), male infertility, prostate cancer, cystic fibrosis, muscular dystrophy and impairment of the immune system, and reducing defenses against infectious viral diseases (influenza, hepatitis, HIV or SARS-CoV-2) [4].

Selenium is characterized by its ability to transition to different oxidation states. In nature, Se has five oxidation states (+6, +4, 0, -1, and -2) and different selenate (Se^{+6} , SeO_4^{2-} , Se (VI)), selenite (Se^{+4} , SeO_3^{2-} , Se(IV)), elemental Se (Se^0), and selenide (Se^{2-}) forms, in addition to its organic forms such as selenocysteine (SeCys), selenomethionine (SeMet), and methylselenocysteine (MeSeCys) [3, 4]. These forms of Se are commonly found in traditional dietary supplements, along with selenized yeast rich in SeMet. Meanwhile, Se in proteins is found in the form of the amino acids SeCys and SeMet [3].

Although Se is an essential element for humans, its biological activity and bioavailability depend on a number of factors such as chemical form, accessibility, solubility, digestibility, the amount ingested, and physiological state of the organism, as well as the presence of other components in the diet [3]. Studies have revealed that the organic forms of Se are less toxic and are absorbed more efficiently than the inorganic forms of Se. Of the latter, Se^{+4} is more toxic than Se^{+6} [3]. In turn, Niedzielski et al. [5] indicate that organic Se compounds have a higher bioavailability and are assimilated in ranges of 85–95% when it comes to food/supplements, whereas inorganic selenium has an absorption range of 40–50% during human intake.

The recommended dietary allowance of Se for humans depends on gender, age, pregnancy, lactation, dietary intake, and geographical location. The United States (US) Department of Agriculture indicates a dose of 55 $\mu\text{g}/\text{day}$ as the recommended daily allowance (RDA), while the European Food Safety Authority (EFSA) indicates an RDA of 70 $\mu\text{g}/\text{day}$ for men, 60 $\mu\text{g}/\text{day}$ for women, and 75 $\mu\text{g}/\text{day}$ for lactating women, being a more specific dose. Meanwhile, the US Institute of Medicine expert panel determined the tolerable upper limit (UL) at 400 $\mu\text{g}/\text{day}$ and the no-observed-adverse-effect level (NOAEL) at 800 $\mu\text{g}/\text{day}$ [3]. Finally, the International Food and Nutrition Board suggests an average daily intake of 40–70 $\mu\text{g}/\text{day}$ for men, 45–55 $\mu\text{g}/\text{day}$ for women, and 25 $\mu\text{g}/\text{day}$ for children [3]. Therefore, it is important to maintain a balance in the daily dose of Se, since doses higher than 1.2 mg/day can cause toxic effects and lead to neurophysiological alterations (confusion, memory loss, dizziness, irritability, fatigue, anxiety, anger, insomnia, depression, or headache), eye problems, skin lesions, or hair and nail loss [3, 4].

The production of Se-enriched plant foods can be an alternative to the consumption of biofortified vegetables to reduce Se deficiency, thus preventing and treating several diseases that threaten human health [6]. In recent years, Se biofortification has emerged as an effective strategy to increase the Se content in crops and thus improve its availability in the edible parts of cultivated plants, allowing this trace element to enter the food chain and strengthen human health.

2. Agronomic biofortification

For the agronomic biofortification of Se in plants, research has been generated in terms of concentration, type of plants, dynamics and different forms of Se in the soil, type of crops, application methods, and lately its nanotechnological use in agriculture. Se biofortification consists of a process to increase the bioavailability of Se, in plants consumed during human intake, without compromising crop yields [7]. This strategy can be achieved by agronomic techniques or through gene targeting [8]. The main agronomic methods for Se biofortification are foliar applications and soil applications, with foliar spraying of Se being the most efficient because this prevents selenate leaching and selenite fixation in the soil [9]. Selenite and selenate are the two inorganic

forms of Se that are mainly used as fertilizers for the exogenous application of Se to plants. Currently, there are other agronomic techniques for Se biofortification such as Se-enriched nutrient solution in hydroponics and seed soaking, among others [8, 10].

2.1 Selenium biofortification in hydroponic systems

The technological approach of soilless cultivation seems to be a key factor for strict control of crop conditions and observation of the effect of Se in a biofortification strategy. Through this system, with the joint addition of Selenium (Se) + Iodine (I), there was an activation of the biosynthesis of organic forms of Se. In leaf vegetables such as lettuce, it was shown that the application of Se + I, with a low dose of salicylic acid, increased the sugar content in leaves and improved the concentration of macro- and micronutrients in roots (P and Mn) [11, 12]. The addition of 5 μM Se to the nutrient solution could be considered a high concentration but at the same time safe for human and plant health as it stimulated lettuce growth and yield and increased the content of phenolic compounds [13]. Under hydroponic conditions, supplying Se to the nutrient solution delayed and reduced the toxic effects of cadmium (Cd) on bell pepper plants [14]. In another study, humic/fulvic acid mixture plus root application of Se in the nutrient solution reduced the harmful effects caused by Cd toxicity in broccoli plants; furthermore, improvements in growth rate and reduction in Cd transport from leaves to inflorescence were observed [15]. Selenium appears to positively affect cell membrane stability in cucumber plants exposed to Cd, as Cd accumulation in roots was reduced [15]. In addition, selenoproteins act as antioxidant agents in plant metabolism, increasing the activity of enzymatic and non-enzymatic compounds that together act against reactive oxygen species (ROS) and cellular detoxification [16].

2.2 Selenium biofortification in soil and foliar spray crops

The joint foliar application of Se + I is an interesting biofortification method, although this strategy presents some difficulties due to the toxicity of Se [17]. Although it is a very efficient method for product application, it was observed that foliar application of Se did not reduce the toxic effects of Cd on bell pepper plants; whereas, root application with nutrient solution proved to be a more effective method [14]. It is not recommended to apply Se to broccoli plants to mitigate the toxic effects of Cd, as this could further increase its toxicity [15]. Foliar application of a micronutrient mixture (zinc (Zn), iron (Fe), I, and Se) represented an effective strategy for wheat biofortification, without yield effects [18]. This micronutrient mixture also had beneficial effects on rice grain, as the Zn, I, and Se content was increased [19]. A high dose of Se (10 mg/kg) decreased grain yield and biomass in wheat. Whereas, Se (in the form of selenite) accumulated mainly in wheat grain and root, a higher accumulation in the form of selenate was found in leaf and straw [20]. Selenium is chemically similar to sulfur (S) and is taken up by plants through S transporters present in the root plasma membrane, metabolized by the S assimilation pathway, and volatilized to the atmosphere [21]. Plants can take up inorganic Se (selenate, selenite, or elemental Se) and organic Se (SeCys and SeMet); the forms and availability of Se will depend on soil type and pH [22]. For biofortification, it is necessary to consider many factors, the method of application, the timing of application, the pH of the mixture, and the concentrations, and to know the possible synergistic and antagonistic effects between the products to be applied [23].

It is also worth mentioning that there are new nanotechnological tools for agronomic biofortification. A study revealed that Se nanoparticles (SeNPs) could be used for Se supplementation, an essential microelement for humans. With the application of 4.65 $\mu\text{g}/\text{mL}$ SeNPs, the highest germination percentage was obtained in barley seeds [24]. A field experiment revealed that SeNPs improved growth parameters, carotenoid content, and insect control in sunflowers when 20 mg/L was applied [25]. SeNPs increased the activity of enzymes related to free radical scavenging; in addition, SeNPs showed excellent bioavailability, low toxicity, and high biological activity [26]. In tomato, Se application significantly favored the tomato fruit quality, including total soluble solids, soluble sugar, and titratable acid [27]. The use of Se-pelleted seeds has emerged as an interesting and viable alternative to increase Se supplementation in agricultural ecosystems [28].

3. Source of inorganic and organic selenium from the crop plant

Because organisms cannot synthesize Se, humans enter Se into their diet mainly through the intake of cultivated foods, so one strategy to increase Se content in crops and the human food chain is through agronomic biofortification with Se. It is also important to understand the bioaccessibility of Se in the edible tissues of Se-enriched crops.

Selenoproteins are the form in which Se is present in the human body; for this purpose, Se can be ingested in organic and inorganic forms. Selenite and selenate (organic Se) and methionine (organic Se) are considered highly bioavailable. Elemental Se is classified as difficult to be absorbed by the gastrointestinal tract. In addition, organic Se from food intake is considered relatively safe for the human body, whereas inorganic Se ingested by chemical supplements has a narrow range between its therapeutic effect and its toxic potential [1].

One of the crops that stands out for its consumption throughout the world is wheat, which is also characterized by its ability to accumulate Se. In a study by Wang et al. [10], it was found that regardless of the method of biofortification (foliar or soil application) and the form of exogenous Se applied (selenite or selenate), the speciation of Se in wheat grains was the organic form (93–100%). Organic Se in wheat grains comprised 87–96% SeMet and 4–13% SeCys₂; whereas, the inorganic Se species was selenate (1–6%). The bioaccessibility of Se in white flour and whole wheat flour was also determined in this study. In the intestinal phase, 10–38% bioaccessibility was reported in white wheat flour and 9–34% in whole wheat flour, while in the gastric phase, Se bioaccessibility was similar between white flour (6–34%) and whole wheat flour (6–27%) [10].

Rice is considered the staple food for more than half of the world's population, making it a strategic crop for biofortification and Se intake. In an analysis of Se speciation in rice grains, where the application of selenite to the soil and by foliar spraying was evaluated, it was found that selenite was the dominant Se species ($\approx 42\text{--}73\%$), the inorganic Se species being the prevailing one in rice grains and the organic species being a smaller proportion. A strong influence of the biofortification method was also reported; root application of selenite favored the presence of seleno-amino acids ($\approx 38\%$), and foliar spraying induced the accumulation of selenite ($\approx 73\%$) and selenate ($\approx 15\%$) in rice grains [29]. Se speciation changed when dealing with brown rice grains biofortified with foliar application of selenite, where SeMet was the main metabolite identified in Se-enriched rice [30].

The third-most consumed crop in the world is potato. During the production of potato tubers, selenite or selenate was applied by foliar spraying during different stages of plant growth. The main organic Se species in potato tubers was SeMet (78.6% with selenite application and 52.3% with selenate), although the presence of SeCys₂ and SeMeCys was also detected. Selenate was the predominant inorganic Se species, and its proportion varied according to Se source (1.5% with selenite and 31.9% with selenate) [9].

Se biofortification has also been studied in other cereals such as maize, in legumes such as cowpea, as well as in other crops such as groundnut. These crops had a high proportion of organic Se (>90%), indicating that the plants were highly efficient in converting inorganic Se to organic Se. SeMet was the dominant organic Se species in all three crops with proportions of 92.0% in maize, 63.7% in cowpea, and 85.2% in groundnut. SeCys₂ was also identified (7.1% in maize, 2.1% in cowpea, and 10.4% in groundnut). Cowpea grains stood out from the other two crops for their MeSeCys content (31.7%). As for inorganic Se species, the proportion was 2.7% selenate in cowpea and 2.1% selenite in groundnut. Gastrointestinal bioaccessibility was also determined in this work, and a range of 66.6–78.2% was found for the three crops, with no differences among the three types of grains enriched with Se [31].

In peanut, foliar and soil application (root irrigation) of selenite was evaluated, and the main Se species in peanut protein were determined. The major organic Se species was SeCys₂ (65.3%), followed by MeSeCys (13.9%); the inorganic form of Se was selenite and accounted for 11.7% of the total Se compounds. The organic Se content in peanut was about 86.3%. This crop efficiently absorbed and transformed selenite into organic Se sources [32].

The ability of strawberry plants to absorb and biosynthesize inorganic Se into seleno-amino acids has also been studied, with foliar application of selenite being the best biofortification treatment compared to other Se sources such as selenate or SeMet applied in root irrigation. In strawberry fruits, 86% of the total Se content is identified, and 16% corresponds to two unknown Se species. Of the identified Se species, 45% corresponds to SeMet, 20.7% to MetSeCys, 5.8% to SeCys, 5.6% to selenite, and 6.6% to selenate [33].

In the case of vegetables such as lettuce, four Se species were detected, SeMet, SeCys, selenite, and selenate. The proportion of these species was a function of the Se source used in biofortification. With selenate application, the proportion of SeMet, SeCys, and selenite was 51%, 4%, and 45%, respectively. Meanwhile, with selenite treatment, 90% of SeMet, 10% of SeCys, and no record of inorganic Se was obtained, indicating that all the supplemented selenite was converted into organic Se. In edible lettuce shoots, regardless of the source of Se applied, the proportion of organic Se was higher than the proportion of inorganic Se [8].

Sprouts are seedlings from seeds, which, after germination, are consumed with fresh vegetables. These types of plant foods are gaining interest because they may contain more bioactive compounds than seeds and can be enriched with Se. In the case of soybean sprouts, two Se sources (Se nanoparticles (SeNPs) and selenite) and two concentrations were evaluated. With the application of SeNPs, five Se species were identified in soybean sprouts, the organic Se species SeMet (55–71%), SeCys₂ (6–17%) and MeSeCys (6–14%) as well as the inorganic Se species selenite (2%) and selenate (11.5–15%). Whereas, in selenite-enriched soybean sprouts, SeMet species predominated (71.5–89.1%), followed by SeCys₂ (4.5–14.4%), MeSeCys (4.2–10.4%), and selenite (2.3–3.7%) [34].

Crop	Edible plant	Selenium (Se) speciation in crops		Reference
		Inorganic Se	Organic Se	
Wheat	Grain	Selenate: 1–6%	Selenomethionine (SeMet): 87–96% Selenocysteine (SeCys): 4–13%	[10]
Rice	Grain	Selenate: ≈15–18% Selenite: ≈42–73%	≈8–37%	[29]
Maize	Grain		SeMet: 92% SeCys: 7.1% Methylselenocysteine (MeSeCys): 0.9%	[31]
Cowpea	Grain	Selenate: 2.7%	SeMet: 63.7% SeCys: 2.1% MeSeCys: 31.7%	
Groundnut	Grain	Selenite: 2.1%	SeMet: 85.2% SeCys: 10.4% MeSeCys: 2.2%	
Papa	Tuber	Selenate: 1.5–31.9%	SeMet 50–80%	[9]
Peanut	Grain	Selenite: 11.7%	SeCys: 65.3% MeSeCys: 13.9%	[32]
Strawberry	Fruit	Selenite: 5.6% Selenate: 6.6%	SeMet: 45% SeCys: 5.8% MeSeCys: 20.7%	[33]
Lettuce	Shoot	Selenite: 0–45%	SeMet: 51–90% SeCys: 4–10%	[8]
Soybean	Sprouts	Selenite: 2.1–3.7% Selenate: 11.5–15%	SeMet: 55.1–89.1% SeCys: 4.5–17.3% MeSeCys: 4.2–13.9%	[34]

Table 1.
The proportion of Se species in edible organs of different crops biofortified with Se.

Plants have the ability to uptake and metabolize Se, which makes them ideal Se sources for daily dietary Se supplementation. Many crop plants have been shown to have a high capacity to convert inorganic Se into organic Se. In plants, Se species are related to the type of crop; thus, different crops may have different inorganic or organic Se species (**Table 1**). The organic Se species are seleno-amino acids such as selenocysteine (SeCys) and selenomethionine (SeMet), which in turn can give rise to methylated SeCys (MeSeCys) and methylated SeMet (MeSeMet). These organic forms of Se have bioactive properties that benefit human health as anticarcinogens and in the regulation of inflammatory processes.

Recently, the amount of research on Se biofortification has focused on crop production; of these, cereals are the ideal crops for Se biofortification due to their high

consumption worldwide. However, the cultivation of hydroponic vegetables, such as lettuce, and the production of sprouts are also excellent options because they have a short production cycle, are easy to handle, have fresh taste characteristics, and can be eaten fresh or cooked [8]. These vegetables along with fresh fruits, such as strawberries, can frequently be found in the diet of people around the world. To date, there has been a great diversity of Se-enriched plant foods that can be ingested to supplement the Se required by the human body to maintain or improve health.

4. Secondary metabolites derived from Se biofortified crops

Phytochemicals or secondary metabolites have no recognized role in the vital processes of plants but are important in their interaction with the environment. From the point of view of human health, there is extensive evidence of the diverse biological activities presented by the different classes of phytochemicals, which include antioxidant, anti-inflammatory, antimicrobial, antitumor, and immunomodulatory, among others. Therefore, in recent years, there has been growing interest in the consumption of vegetables rich in these bioactive compounds for the prevention of chronic diseases and the regulation of oxidative stress [35]. The production of these phytochemicals can be elicited in response to biotic (bacteria, fungi, viruses) and abiotic (drought, salinity, heavy metals, UV radiation) stress factors.

In several studies, it has been observed that biofortification with Se is useful to increase the content of this trace element in the edible parts of plants as well as improves their nutraceutical value through the accumulation of biocompounds. In addition to the beneficial health properties, these phytochemicals also provide fruits and inflorescences with their organoleptic properties, such as lycopene in tomato, capsaicin in chili, and glucosinolates in broccoli.

The application of Se in foliar form, as a soil amendment, in the irrigation solution, or in hydroponics has a positive effect on the accumulation of phenolic compounds, terpenes, capsaicinoids, and glucosinolates. The accumulation of phenolic compounds in response to Se has been extensively evaluated, in some plant species, by determining their total content and in others, by identifying some compounds individually, in different plant organs (**Table 1**). In bean grains, root irrigation application of 5 and 10 μM Na_2SeO_3 increased the content of total phenolic compounds and total flavonoids differentially among common bean varieties [36]. In lettuce leaves, the tentative identification and quantification of caffeoylquinic and dicaffeoyltartaric acids, as well as glycosylated derivatives of quercetin and cyanidin, was carried out. From a concentration of 0.04 mg/L Na_2SeO_4 , an increase in the response of these phytochemicals was observed by electrospray ionization mass spectrometry (ESI-MS) [6]. In basil leaves, increases in the content of different phenolic acids (gallic, chlorogenic, coumaric, rosmarinic acids) were achieved with the application of 50 mg/L SeNPs, but in the case of caffeic acid, a positive response was only observed at twice the concentration [37]. The use of Se nanomaterials as a base fertilizer in soil for lettuce cultivation induced increases in the abundance of quercetin (2.9-fold), rutin (2.7-fold), and coumarin (2.4-fold) [38]. In jalapeño pepper fruits, the content of phenolic compounds and total flavonoids increases as higher Na_2SeO_3 concentration is applied and correlates with the observed antioxidant capacity [39]. Selenium, in the form of Na_2SeO_4 , also stimulated the production of phenolic compounds, flavonoids, and anthocyanins, as well as the expression of biosynthetic enzymes (phenylalanine ammonium lyase and chalcone synthase) in Indian mustard leaves [40]. In

microgreens biofortified with Na_2SeO_4 , the most abundant phenolics are chlorogenic acid and rutin (coriander), caffeic acid hexoside and kaemferol-3-O (caffeoyl)-sophoroside 7-O-glucoside (tatsoi), and chicoric and rosmarinic acids (basil) [41].

In broccoli florets, the Se source is important in the induction of these phytochemicals, obtaining positive effects on the production of phenolic acids with the lowest doses of Se yeast, while Na_2SeO_3 had similar effects only with the highest doses (Table 2). In contrast, flavonoid content increased with the highest Na_2SeO_3 concentration but did not undergo any modification when the organic Se source was applied. In the case of glucosinolates, both Se sources induce their accumulation [42].

Induction of secondary metabolism by Se can be carried out by increasing the content of this element in the same vegetative organ (direct) or even in an indirect way. Se accumulation in broccoli florets as the dose of Na_2SeO_4 (applied to roots) increases causes contrasting effects on two classes of phytochemicals; at the intermediate concentration evaluated (0.4 mmol/L), Se induced glucosinolate production and reduced flavonoid content [44]. Similarly, in cauliflower, foliar application of Na_2SeO_4 results in the accumulation of this element in florets, inducing a higher content of carotenoids and phenolic compounds in two cultivars. The Graffiti cultivar accumulated twice as many glucosinolates as the Clapton cultivar at the 5 mg/L doses, identifying glucobrassicin, 4-hydroxy glucobrassicin, 4-methoxy glucobrassicin, and neo-glucobrassicin [45]. In tomato fruits, this direct induction of Se on flavonoid content is also observed, with no change in lycopene content [46]. However, with the foliar application of 1.5 mg/L Na_2SeO_3 , no changes in the accumulation of this trace element in jalapeño pepper fruits were recorded, but an increase in the content of flavonoid, phenolic compounds, and capsaicin was noted [39]. Therefore, it is relevant to carry out studies on the mechanism by which this trace element induces the synthesis of these bioactive compounds.

Plants are naturally exposed to several stress factors simultaneously. In this sense, some studies have evaluated the effect of Se in combination with other elements or stressors on the accumulation of phytochemicals (Table 2). In tea leaves, the enzymatic (SOD) and non-enzymatic (epigallocatechin and epigallocatechin gallate) antioxidant systems are activated in response to Se, which may be part of the strategy

Species	Plant part	Biofortification method	Bioactive compounds	Reference
<i>Phaseolus vulgaris</i> L.	Grains	Root irrigation every 15 d: 0, 2.5, 5, and 10 μM Na_2SeO_3 .	Total phenolic compounds and total flavonoids	[36]
<i>Lactuca sativa</i> L.	Leaves	Weekly foliar application for 3 weeks: 0, 0.04, and 0.5 mg Na_2SeO_4 /L	Phenolic acids, flavonoids, and sesquiterpene lactones	[6]
<i>Lactuca sativa</i> L.	Leaves	Soil amended with selenium nanomaterials: 0, 0.1, 0.5, and 1.0 mg /kg; and 0.5 mg SeO_3^{-2} /kg	Quercetin, rutin, caffeic acid, and coumarins	[38]
<i>Lactuca sativa</i> L.	Leaves	Nutrient solution: 0.5 mg Na_2SeO_3 /L + 5 mg KIO_3 /L	Phenolic compounds, phenylpropanoids, flavonols, and anthocyanins	[11]

Species	Plant part	Biofortification method	Bioactive compounds	Reference
<i>Ocimum basilicum</i> L.	Leaves	Foliar application: 0, 50, and 100 mg SeNPs/L	Monoterpenes, carotenoids, and phenolic acids	[37]
<i>Capsicum annuum</i> L.	Fruit	Foliar application every 15 d (6 times): 0, 1.5, 3.0, 4.5, and 6 mg Na ₂ SeO ₃ /L	Capsaicin, phenolic compounds, and total flavonoids	[39]
<i>Brassica oleracea</i> L.	Florets	Foliar application every 15 d: 0.1, 0.2, 0.4, 0.8, and 1.6 mg/L, Na ₂ SeO ₃ and organic Se.	Glucosinolates, phenols, and total flavonoids	[42]
<i>Brassica juncea</i> L.	Leaves	Amended soil: 0, 2, 4, and 6 μM Na ₂ SeO ₄ /kg	Total phenols, flavonoids, and anthocyanins	[40]
<i>Camellia sinensis</i> L. Kuntze	Leaves	Daily foliar application for 5 d: 0 y 2 mg Na ₂ SeO ₃ /L d + low T (4 °C).	Caffeine, gallic acid, and flavonoids	[43]
<i>Coriandrum sativum</i> L., <i>Ocimum basilicum</i> L., <i>Brassica rapa</i> L. subsp. <i>narinosa</i>	Microgreens	Daily nutrient solution: 0, 1.5, and 3.0 mg Na ₂ SeO ₄ /L, 12 d coriander and 19 d basil.	Carotenoids and phenolic compounds	[41]
<i>Brassica oleracea</i> L.	Florets	Root irrigation every 15 d: 0, 17.3, 34.6, 69.2, 138.3, and 276.6 mg Na ₂ SeO ₄ /L	Glucosinolates and flavonoids	[44]
<i>Brassica oleracea</i> L.	Florets	Foliar application: 1, 5, 10, 15, and 20 mg Na ₂ SeO ₄ /L, three times (in weeks 2, 5, and 8).	Glucosinolates and phenolic compounds	[45]
<i>Solanum lycopersicum</i> L.	Fruit	Foliar application at the onset of flowering: 1 mg Na ₂ SeO ₄ /L	Lycopene and total flavonoids	[46]

Table 2.
 Bioactive compounds induced in edible parts with selenium biofortification.

to prevent oxidative stress generated by low-temperature stress [43]. In contrast, Se + I and Se + I + AS (0.1, 1.0, and 10.0 mg/L) combinations did not induce changes in the total contents of phenolic compounds, flavonols, phenylpropanoids, and anthocyanins in lettuce leaves [11].

These results place biofortification with Se as a promising agronomic strategy for obtaining functional foods.

5. Health benefits from the intake of biofortified crops with Se

One of the most recognized biological activities of Se is its contribution to antioxidant processes, as well as its role as a chemopreventive agent since an adequate intake of Se can reduce the risk of cancer. In addition, many plant foods contain compounds

Food plant	Effect on human health	Suggested mechanism	Reference
Rice	Antioxidant	Increased glutathione (GSH), ascorbic acid (AsA), and glutathione peroxidase (GSH-Px) activity	[29]
Soybean sprouts	Antioxidant	Increased vitamin C and GSH content. Increases in peroxidase (POD) and ascorbate peroxidase (APX) activity	[34]
Chickpea sprouts	Antioxidant	Entry into cells (Caco-2) to combat oxidative stress	[47]
Green tea	Antioxidant	Increased superoxide dismutase (SOD) activity and epigallocatechin gallate content	[43]
Tomato	Antioxidant	Increased vitamin C, E, and GSH content	[46]
Lettuce	Anti-inflammatory	Inhibition of inducible nitric oxide synthase (iNOS) activity. Increased quercetin content	[6]
Coriander and tatsoi microgreens	Anti-inflammatory	Increased rutin and kaemferol-3-O-(feruloyl) sophoroside-7-O-glucoside content	[41]
Peanut	Anticarcinogenic	Inhibition in the proliferation of Caco-2 and HepG2 cell lines.	[32]
Soybean sprouts	Anticarcinogenic	Increased isoflavones content	[34]
Broccoli sprouts	Anticarcinogenic	Increased glucorapinin and glucoerucin content, precursors of anticancer compounds	[48]
Chickpea sprouts	Anticarcinogenic	Increased GSH-Px and thioredoxin reductase (TrxR) activities. Overexpression of Fas protein	[49]

Table 3.
Effect of Se-enriched plant-source foods on human health.

with important biological activities for disease control. Thus, research has shown that the biofortification of crops improves the antioxidant, anti-inflammatory, and anticarcinogenic properties of edible parts of plants (**Table 3**).

5.1 Antioxidant activity

In addition to providing organic Se species and bioactive compounds, biofortification with Se provides plant foods that benefit health through ingestion of edible parts with antioxidant capacity. Root application of selenite increased 85.9% glutathione (GSH) content, 39.2% ascorbic acid (AsA), and 186.0% glutathione peroxidase (GSH-Px) enzyme activity, indicating that Se biofortification increases the antioxidant capacity of rice grains [29]. Similarly, in soybean sprouts enriched with Se (selenite and SeNPs), an average 3-fold increase in vitamin C and 38% increase in GSH content were reported, as well as an increase in the activity of the antioxidant enzymes catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), and ascorbate peroxidase (APX). Higher activity of POD (72–176% higher activity) and APX (2.5 times higher than the control) enzymes was highlighted in soybean sprouts enriched with 100 μ M selenite and SeNPs [34]. Selenium treatments improved the antioxidant properties of soybean sprouts, so

their consumption could improve human health. It is important to highlight the benefits of vitamin C, which is recognized as an excellent antioxidant that protects plants from ROS and plays a vital role in the human body. In another study, it was found that the protein fraction from chickpea sprouts, enriched with Se (2 mg selenite/100 g of seeds), had a significant increase in cellular antioxidant activity (CAA). The highest percentage of CAA was detected in peptides <10 kDa with Se supplementation ($59.11 \pm 2.06\%$), a CAA value equivalent to that of SeMet, SeCys, or selenite. The antioxidant activity assay indicated that Se species entered cells (Caco-2) at supranutritional doses, exerting different mechanisms to combat oxidative stress, those mainly related to redox cycles such as cell signaling, DNA stability, cell cycle genes and proliferation, reduction of the inflammatory response, caspases-mediated apoptosis, angiogenesis, and osteoclast inactivation [47]. The antioxidant activity of selenoproteins was a function of their Se content.

In green tea plants, induction of SOD activity and an increase in the content of epigallocatechin gallate (EGCG, 15.1%) and other catechins in response to Se application resulted in a reduction in the content of hydrogen peroxide (H_2O_2 , 31.6%) and malondialdehyde (23.9%) [43]. The latter is a good indicator of lipid peroxidation. In addition to its antioxidant and chelating properties, EGCG has shown therapeutic potential as an anti-inflammatory, antibacterial, and antiviral, as well as for cancer prevention [50], which associates with numerous health benefits. In broccoli, the antioxidant capacity induced with Se biofortification depends on the cultivar, highlighting the 40% increase in Graffiti, while in the cultivar Clapton, only a 29% increase was recorded at the same concentration (5 mg $\text{Na}_2\text{SeO}_4/\text{L}$) [45]. Foliar application of Se also has an effect on antioxidant properties in tomato fruits, inducing vitamin C (1.3-fold higher than the control) and vitamin E (1.4-fold) production, as well as a 2-fold increase in reduced glutathione levels [46].

5.2 Anti-inflammatory activity

Se has been shown to have beneficial effects in the treatment of inflammatory diseases. Inflammation is characterized by the presence of pain, redness, swelling, and impaired function [6]. There are different markers that mediate immune cell recruitment and response to infection or injury. Among these, the enzyme inducible nitric oxide synthase (iNOS), responsible for the formation of nitric oxide (NO), plays an important role during the inflammation process. In this regard, Se was reported to modify the anti-inflammatory properties of lettuce plants that were grown under Se application, determined by inhibition of iNOS activity [6]. In addition, an increase in quercetin 3-O-(600-acetyl-glucoside) content was found. Quercetin and kaempferol are among the most common metabolites found in vegetables and fruits, which are considered to have high anti-inflammatory and antioxidant activity in *in vitro* studies [6]. It is important to note that biofortification with Se favors the synthesis of these compounds in different species, since in coriander and tatsoi microgreens, increases of 33 and 157% in rutin and kaempferol-3-O-(feruloyl) sophoroside-7-O-glucoside content are achieved at a concentration of 1.5 mg/L [41]. This induction of Se is carried out at the transcriptional level in broccoli, favoring the expression of genes of the phenylpropanoid pathway [44]. Caffeic acid is another secondary metabolite that is increased in lettuce plants biofortified with Se nanomaterials and is considered one of the bioactive compounds of propolis with antitumor and anti-inflammatory effects [38].

5.3 Anticarcinogenic activity

It has already been mentioned that one way to include Se in the human diet is through the consumption of cultivated plants enriched with Se. Therefore, Se intake is of vital importance both to cover nutritional demand and for the prevention of health problems such as cancer. A study evaluated the anticancer activity of Se-enriched peanut protein and found an inhibitory effect on Caco-2 and HepG2 cell lines. Furthermore, it was reported that peanut protein, obtained from Se biofortification, significantly inhibited cell proliferation in a dose-dependent manner, with a dose range of 15.6 to 250 $\mu\text{g}/\text{mL}$, with the 250 $\mu\text{g}/\text{mL}$ dose being more effective [32]. These studies provide solid information on the anticancer effect of Se-enriched peanut protein.

Secondary metabolites such as isoflavones have also been reported to have bioactivity for cancer prevention and treatment. In this regard, Rao et al. [34] found that selenite and SeNPs promoted the accumulation of total isoflavones in soybean sprouts. In addition to tasting good for direct and fresh consumption, soybean sprouts contain health-promoting substances such as vitamin C and isoflavones.

Another group of phytochemical compounds with important anticarcinogenic activity is glucosinolates. Brassicas are crops recognized as chemopreventive foods. Therefore, biofortification with Se during Brassica cultivation would be expected to increase the chemopreventive activity of the sprouts. In sprouts of three broccoli cultivars, enriched with selenate, glucoraphanin was found to be the dominant glucosinolate, accounting for 70% of the total glucosinolate content. Glucoraphanin is an aliphatic glucosinolate and is a direct precursor of sulforaphane isothiocyanate, which acts as a potent monoinducer of phase II-related enzymes during the inactivation of carcinogenic metabolites. Another aliphatic glucosinolate present in broccoli sprouts is glucoerucin, accounting for 14% of the total glucosinolate content, which is metabolized to the isothiocyanate erucin, considered an anticarcinogenic agent [48]. Therefore, broccoli sprouts could be considered an excellent source for the intake of isothiocyanate compounds for cancer prevention.

Se-enriched chickpea sprouts were found to be an important source of dietary Se and isoflavonoids with chemopreventive potential for the treatment of colorectal cancer. A diet enriched with a supranutritional dose of Se (2.29 $\mu\text{g}/\text{g}$ diet) in combination with isoflavonoids (2.34 mg/g) was tested on tumor growth of xenoplastic human colorectal adenocarcinoma cells in immunosuppressed mice [49]. The diet promoted cell apoptosis through overexpression of cell surface death receptor (Fas). In addition, an increase in GSH-Px and thioredoxin reductase (TrxR) enzyme activity was observed; as well as an increase in cholesterol, triglycerides, and low-density lipoprotein cholesterol, resulting in a significant decrease in tumor cell growth [49]. These types of studies indicate that ingestion of chickpea sprouts enriched with Se can contribute to reducing cancer cell proliferation.

6. Conclusions

Agronomic biofortification is becoming the most widely used strategy for Se supplementation of plant foods because it is a relatively simple agronomic practice to operate and because of its high availability. The distribution of organic and inorganic Se species is a key factor to consider in the biofortification process. There are a large number of cultivated plants that have the ability to convert inorganic Se (mainly selenate or selenite) into organic Se (SeCys, SeMet, or MetSeCyt), representing an excellent metabolic mechanism for obtaining Se-rich foods.

Selenium applied in different forms enhances the accumulation of phytochemicals with antioxidant, anti-inflammatory, antimicrobial, and antitumor properties in different edible plant species, highlighting the advantages of incorporating biofortification with Se in the production chain of foods rich in bioactive compounds, which is a desirable feature in the food industry due to the positive impact on human health. Therefore, it is imperative to elucidate the mechanisms by which this trace element induces the production of these biocompounds in plants in order to optimize this strategy.

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Conflict of interest

The authors declare no conflict of interest.

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