



Review

Current Acquaintance on Agronomic Biofortification to Modulate the Yield and Functional Value of Vegetable Crops: A Review

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Abstract: Fresh vegetables and fruits have always been the mainstays of good nutrition as providers of fiber, beneficial phytochemicals (such as vitamins and phenolic compounds), and minerals. Today and in the future, biofortification is a promising strategy to increase the concentration of these compounds. Considering the importance of minerals in human health, the enrichment of fresh produce for consumption has been considered through specific agronomic approaches. This review discusses, in detail, the latest findings on vegetable agronomic biofortification, aimed at increasing the concentration of crucial minerals, such as iron (Fe), zinc (Zn), iodine (I), selenium (Se), molybdenum (Mo), and silicon (Si), in edible portions, focusing on the direct and indirect effects of this strategy. Although agronomic biofortification is considered a feasible technique, the approach is complex due to the many interactions between the microelement bioavailability for both plants and consumers. Therefore, the effects of biofortification on human health and the influence of beneficial and antinutritional compounds were discussed in detail to analyze the advantages and disadvantages of this practice.

Keywords: human diet; minerals; phytochemicals; trace elements



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1. Introduction

Currently, the global population is expected to increase from 7.99 billion in 2022 to 8.54 and 9.74 billion by 2030 and 2050, respectively. Concomitantly, agriculture is vulnerable to existing worldwide emergencies such as climate change [1,2] and pandemics [3]. Pandemics intimidate comprehensive human lifecycles and fitness, which will be supplementary deteriorated by increasing hunger and undernourishment caused by a disorder in the food supply chain, mostly in emerging countries. This situation is intensifying the challenges for international food security [4]. Human malnutrition has a severe socio-economic impact, particularly in those countries where people cannot eat a balanced diet (developing and underdeveloped counties). Although several studies have been conducted, a huge unit of the population still cannot access or afford a satisfactory quality diet, which determines malnourishment and/or undernutrition. Children are the most affected category to malnourishment; indeed, as reported by Pinstrip-Andersen [5], approximately 45% of children's deaths are caused by malnutrition, 22.2% are underdeveloped, and 7.5% are underweight for their statures. Nowadays, people eat diets rich in carbohydrates; however, the hidden hunger question perseveres, as we are incapable of satisfying micronutrient necessities [6]. Consequently, as appraised by the International Food Policy Research Institute, approximately 2 billion people globally are affected by mineral malnourishment (hidden

hunger). Since micronutrients play an imperative role in human health, their shortage causes several disorders, such as undergrowth and development and cognitive decline, increasing the risk of mortality. Thus, as reported by Jangir et al. [7], removing mineral malnourishment is needed to attain and maintain a healthy global population. Accordingly, among the 17 “Sustainable Development Goals” (SDGs), the global community promoted the SDG2 named “Zero Hunger” that aims to achieve a hunger-free world. In this scenario, biofortification of edible crops is one of the most promising, efficient, sustainable, and cost-effective strategies in combating mineral malnutrition in humans [8–12]. As testified by Pérez-Massot et al. [13] and Kyriacou and Roupael [14], biofortification is the procedure of enhancing the nutritional status of staple food crops by increasing the nutrient content or bioavailability either via agronomic approaches, conventional breeding, or biotechnological tools. Although the latter approach is the best long-term solution, it is the high costs and restrictive regulations prohibiting the use of GMOs in some countries around the world that are holding back their widespread adoption. In light of this, agronomic biofortification programs are the best option, as they would allow increasing concentrations of essential nutrients in the edible parts of plants [15].

This justifies the increasing focus on fortifying vegetable crops with micronutrients, which has stimulated research activity converging toward the production of efficient agronomic protocols. The aim of this review was to describe advances in agronomic biofortification of vegetables, with a focus on certain micronutrients, such as selenium (Se), molybdenum (Mo), silicon (Si), zinc (Zn), iron (Fe), and iodine (I), focusing on the impacts of this agronomic practice on human health.

2. Agronomic Biofortification

Since the 1960s, many countries have used NPK-based fertilizers to increase crop yield. This is essential for feeding a continuously growing world population and coping with increasing hunger in underdeveloped countries. However, it is well known that microelements, such as Zn, Fe, Mg, and Mo, have important functions both for plant growth and human health [16]. A major part of these micronutrients is easily accessible to plants and, consequently, become a component of the food chain. However, when plants cannot absorb micronutrients easily, they need to be incorporated into plants via agronomic biofortification programs [15]. Agronomic biofortification is the simplest method to enrich food crops of useful microelements [17–20]. Accordingly, agronomic biofortification is especially useful in developing countries as a strategy to increase plant performance and to boost the microelement concentration in tissues [15]. One of the benefits of this method is also the rapid plant response with the great bioavailability of the microelements supplied [21]. However, there are vegetables more reactive to agronomic biofortification (Table 1).

Table 1. Most suitable vegetable crops to agronomic biofortification ⁽¹⁾.

Microelement	Most Suitable Vegetable Crops for Biofortification
Fe	Rocket, red cabbage, and mustard microgreens
Zn	Rocket, red cabbage, mustard microgreens, broccoli, carrot, kale, and lettuce
I	Basil, cabbage, carrot, Chinese cabbage, cowpea, lettuce, mizuna, mustard, onion, potato, and tomato
Mo	Spinach and lettuce
Se	Basil, broccoli, carrot, chard, endive, garlic, Indian mustard, lettuce, onion, radish, spinach, and turnip
Si	Basil, chicory, mizuna, strawberry, and Swiss chard

⁽¹⁾ Data refers to enquiry on Scopus[®] accomplished in January 2023.

Vegetables are usually cultivated in high input agro-systems characterized by a high level of intensification of the production practices, and in which the amount of nutrients supplied depends on the use of techniques such as soil fertigation, soilless cultivation, seeds soaking, and foliar fertilization. These options represent different strategies to supply the

chosen microelement targeted in agronomic biofortification programs [22]. However, there are some considerations to be made for each of the above methods. If the microelement is supplied via the soil, the availability should be taken into consideration; consequently, the selection of the best mineral forms and of the optimal quantities have a crucial role [23,24]. Moreover, the soil tillage, texture, pH, and water management have a fundamental role on elements assimilation and bioavailability. A different approach to overcome the low availability of some microelements in the soil is the application of hydroponic cultivation techniques, in which macro- and microelements are supplied via a nutrient solution. In this regard, it was reported that hydroponic cultivation could be the best way to enhance the nutrient concentration in plant edible parts [25–27]. Indeed, as reported by Montesano et al. [28], an accurate control of plant nutrition ensures the biofortification success. In this case, the main limitation factor is the pH of the nutrient solution that should be measured and adjusted continuously to keep it in the optimal range for plants mineral absorption (5.5–6.5). However, in the phloem of most plant species, trace elements, such as Fe, Zn, Cu, Mo, and I, have low mobility, and elements like Mn and Ca are immobile [29]. Consequently, when a microelement is absorbed by the plants, but it is not efficiently translocated to the edible plant parts, a valid alternative is represented by foliar fertilization, which is also the best cost-effective approach [15,30]. Even in this case, there are some limitations due to some plant and climatic factors, including plant water status, air relative humidity, stomatal conductance, and plant species, which influence elements leaf absorption [31]. In Table 2, we reported the mean concentrations of Fe, Zn, I, Mo, Se, and Si in the most important vegetable crops pre- and after the biofortification treatments.

Table 2. Mean concentration of iron (Fe), zinc (Zn), molybdenum (Mo), selenium (Se), and silicon (Si) of the most consumed vegetables (potato, tomato, lettuce, carrot, and onion) pre- and post-biofortification ⁽¹⁾.

Vegetables	Fe (mg/kg dw)		Zn (mg/kg dw)	
	Non-Biofortified	Biofortified	Non-Biofortified	Biofortified
Potato	11	23	15	42
Tomato	448	656	15	30
Lettuce	180	400	145	220
Carrot	464	680	116.2	207.5
Onion	No data	No data	25.5	33.5
Vegetables	I (mg/kg dw)		Mo (mg/kg dw)	
	Non-Biofortified	Biofortified	Non-Biofortified	Biofortified
Potato	0.15	0.29	No data	No data
Tomato	0.03	0.23	0.02	0.07
Lettuce	20	780	50	580
Carrot	0.6	4.63	No data	No data
Onion	0.08	8.33	No data	No data
Vegetables	Se (mg/kg dw)		Si (µg/g dw)	
	Non-Biofortified	Biofortified	Non-Biofortified	Biofortified
Potato	5	27	26	50
Tomato	0.09	8.91	No data	No data
Lettuce	3	80	No data	No data
Carrot	2.21	10.97	No data	No data
Onion	0.03	9.96	No data	No data

dw: dry weight. ⁽¹⁾ Data refer to enquiry on Scopus[®] accomplished in January 2023.

As stated by Bouis and Saltzman [32], the combined application via soil and leaves is frequently the most efficient biofortification method, granting the best results in terms of micronutrient intake. Nevertheless, as previously said, agronomic biofortification can

be influenced by several factors. In this regard, it is important to underline that the administration of these microelements is very delicate. It is very easy to supply an overdose of the microelement, which can cause toxic effects to the plants with consequences on yield and quality of the crop. Accordingly, many studies have been carried out to determine the best dose for the crop, the best way of administration (through leaves or via the root system), and the optimal mineral form to increase the efficiency of the biofortification program.

3. Direct and Indirect Effects of the Most Common Microelements Used in Vegetables Biofortification Programs

Agronomic biofortification determines direct and/or indirect effects on crops. The direct effect is the increase of the microelement concentration in plant tissues, whereas the indirect effects are those involving plant performance (yield and quality). These two effects must be considered when an agronomic biofortification program is performed. The knowledge of the plant response to the microelement supply is a very crucial aspect for planning the dosages and the time of application. Moreover, knowing the direct and indirect effects of biofortification could be useful for setting specific productive results in terms of yield and quality, optimizing the biofortification process itself.

Among microelements, there are six of particular interest as they are very useful for human health: iron, zinc, iodine, molybdenum, selenium, and silicon. These six microelements are the most spread in agronomic biofortification programs.

3.1. Iron (Fe)

Iron (Fe) is the second most abundant metal present in the earth's crust, after aluminum. However, Fe solubility is very low, especially in alkaline and aerated soils. In this condition, ionic forms are present in low quantity due to the formation of Fe compounds such as hydroxides, oxyhydroxides, and oxides [33]. For this reason, when Fe is supplied to crops, it is preferred to use a chelate form, which protects the Fe ion from the oxidation and, consequently, from insolubilization [16]. In Figure 1, we reported the main Fe effects in plants.

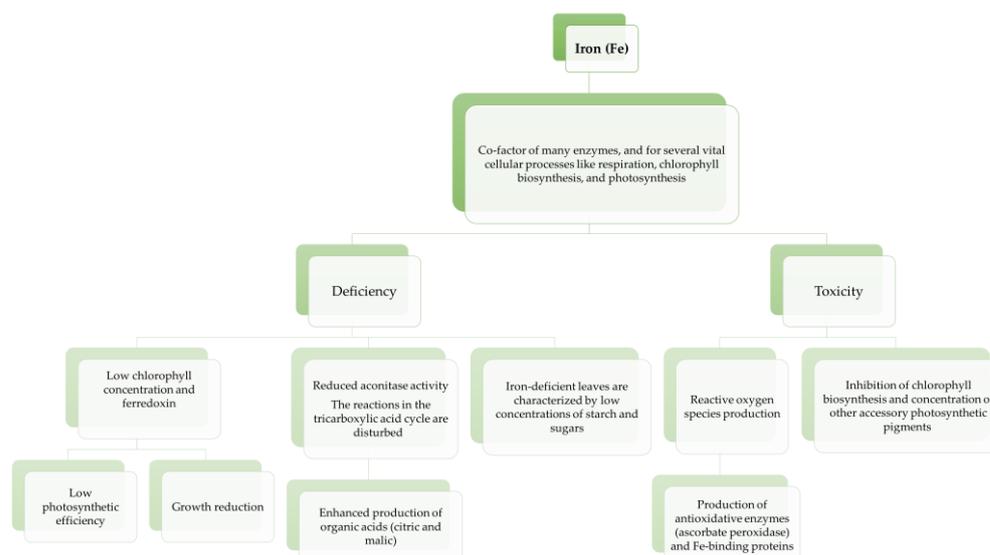


Figure 1. Main effects of iron (Fe) in plants.

Fe is considered an essential element for plant growth and development. Indeed, it is essential as a co-factor of many enzymes, and for several vital cellular processes such as respiration, chlorophyll biosynthesis, and photosynthesis. Even though Fe is very important to plants, it is estimated that about 30% of arable land did not have the optimal pH and aeration conditions to promote Fe-plant uptake [34]. After absorption, Fe

is transferred from roots to plant organs via the xylem, driven by the transpiration stream and root pressure, mainly in a citrate complex [34–37].

If the plant is under Fe-lacking conditions, its leaves suffer from chlorosis because, as previously said, Fe is necessary for chlorophyll biosynthesis and, consequently, for the photosynthesis itself. To overcome Fe deficiency, plants have developed various mechanisms. Indeed, it has been shown that the functionality of the peroxidase enzyme is highly reduced in plant roots suffering from Fe deficiency [38,39]. As consequence, hydrogen peroxide production is enhanced [38] and there is a build-up of phenolics compounds [16]. Some of these phenolics can efficiently chelate and reduce inorganic Fe (III) to promote plant Fe utilization and uptake efficiency [40]. This mechanism is called strategy-II and it is typical of graminaceous crops. On the other hand, non-graminaceous plants, such as tomato plants, developed another mechanism called strategy-I. In this case, plant cells release protons to enhance rhizosphere acidification and stimulate Fe (III) solubility [37].

Fe can be also supplied through the leaves. In this case it is important not to use Fe-EDDHA chelate for its photosensitivity [41].

Since the symptomatology caused by Fe deficiency is more severe on young leaves rather than on mature ones, young leaves are considered strong sinks and need more Fe than older ones.

Excess Fe (more than 500 mg kg⁻¹ of dry weight in leaves) causes toxicity and bronzing. Fe toxicity damage is usually linked to reactive oxygen species production and, consequently, to the production of antioxidative enzymes such as ascorbate peroxidase and Fe-binding proteins [42,43]. Indeed, Giordano et al. [44] reported that Fe supply at a concentration higher than 0.5 mM significantly reduced leaf area, fresh biomass, dry biomass, and radiation use efficiency of lettuce plants cultivated in a soilless system. Moreover, the application of high doses of Fe in the nutrient solution triggered an increase in the nitrate, ascorbic acid, and P content, while for K, Ca, and Mg, a reduction was recorded. Buturi et al. [45] stated that Fe application significantly reduced total dry biomass and increased dry matter content, chlorophyll, total phenols, anthocyanins, flavonoids, carotenoids, ascorbic acid, antioxidant activity, proline, and malondialdehyde of lettuce plants compared to the control. However, regarding the nutrient profile, Buturi et al. [45] found that Fe application significantly increased N, P, K, Ca, Mg, Fe, S, Zn, and B compared to the control. Fe can be supplied via the root or foliar spray. Lata-Tenesaca and co-workers [46], who investigated the effect of Fe application methods (via root or leaf) on nutritional quality and grain productivity of quinoa, demonstrated that the foliar application is more effective in increasing the Fe concentration in grains. Concomitantly, the foliar Fe supply reduced antinutritional compounds in quinoa plants compared to those supplied via the root system.

It is also reported that basil [47] is an Fe hyper-accumulator; however, there is no data on accumulator and non-accumulator vegetables.

3.2. Zinc (Zn)

Zinc (Zn) is the second most abundant transition metal in organisms after Fe, and the only one involved in all enzyme classes. It is reported that Zn is a component of carbonic anhydrase and an elicitor of aldolase, which takes part in carbon metabolism [48]. Furthermore, Zn is an essential compound of different biomolecules (e.g. lipids, proteins, and auxins co-factor) and, consequently, it plays a relevant part in plant DNA and RNA metabolism [49].

The primary contribution of Zn to the soil is from the weathering of parent rocks. Zn replaces Mg and Fe in rock-forming minerals [50]. Rocks include Zn in different forms such as sulphide, sulphate, oxide, carbonate, phosphate, and silicate [50]. Zn is absorbed by the plant roots in the form of Zn²⁺ ions or as organic acid chelate [51], then it is transported via the xylem into above-ground organs [52]. Zn transfer is performed by protein carriers of heavy metal, belonging to the ZIP group [53–55]. Zinc ions can be also transported via the

apoplast [56]. Moreover, plants can assimilate Zn through leaves; however, the process is not yet known [57]. In Figure 2, we reported the main Zn effects in plants.

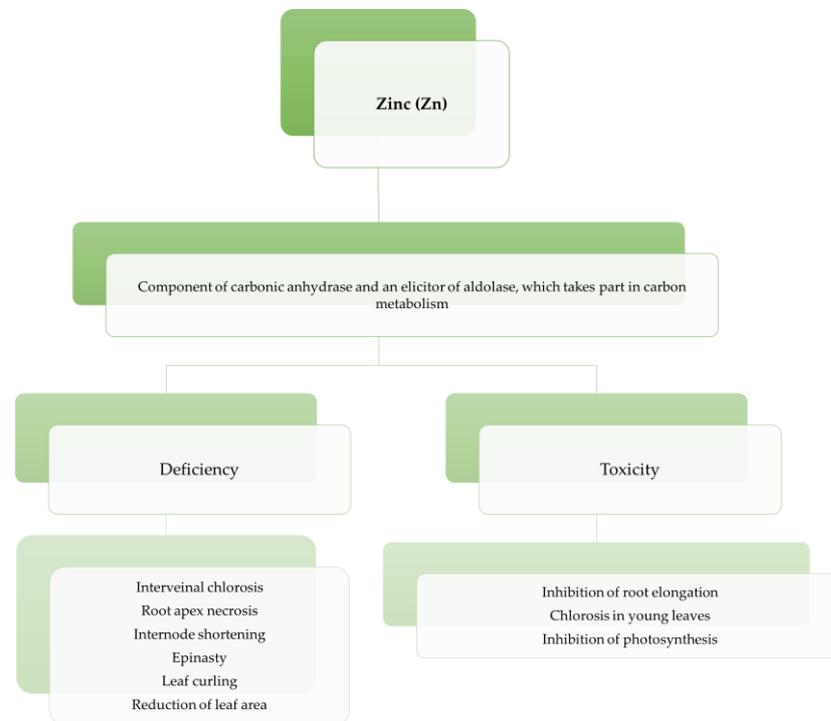


Figure 2. Main effects of zinc (Zn) in plants.

The first evidence of Zn essentiality was reported by Mazé [58] in maize, and by Sommer and Lipman [59] in barley and sunflowers. Since then, Zn deficiency symptoms have been reported in many crop species [16,60]. Plants affected by Zn deficiency show interveinal chlorosis, root apex necrosis, internode shortening, epinasty, leaf curling, and reduction of leaf area [61]. As stated by Marschner [16], the leaf Zn content required for a normal plant growth is about 15–20 mg kg⁻¹ of dry weight [16]. As reported by Wei et al. [62], the most efficient Zn chemical form is zinc sulfate (ZnSO₄).

Zn shortage is the most spread microelement deficiency, especially in soils with high pH [63,64]. About 33% of the soil cultivated in China and the most of those in Western Australia are characterized by Zn deficiency [61]. To overcome this worldwide spread of Zn deficiency, agronomic and genetic biofortification is often employed. In this regard, Hassan et al. [65] found that Zn-biofortification has a beneficial effect in enhancing the yield and quality in bread wheat, while its deficiency reduces the yield and deteriorates crop quality [66]. Moreover, there are reports that a satisfactory Zn supply can alleviate drought tolerance in various crops species [67–69]. Sago et al. [70] reported that leaf Zn applications significantly decreased the fresh and dry weight of lettuce shoots. Moreover, D’Imperio et al. [71] found no significant differences in microelements concentration of rocket and purslane between biofortified and control plants. Interestingly, Ciriello et al. [72] found that biofortification with Zn significantly reduced plant height, leaf number, leaf area, plant fresh biomass, total dry biomass, and root dry weight, and increased dry matter, some color parameters, lutein, β-carotene, and the overall antioxidant activity of sweet basil plants compared to the control. Nevertheless, deep information on drought stress tolerance induced by Zn supply is missing.

Zn toxicity in plants is less spread than Zn deficiency; however, it may occur in soils polluted by mining activities, treated with sewage sludge, and in soil artificially enriched with Zn, especially if they have a low pH [73]. Toxicity symptoms occur at Zn leaf concentrations higher than 300 mg kg⁻¹ of dry weight; however, toxicity limits can vary even within the same species. For example, among leafy vegetables, spinach and beet

are very sensitive because they have a high Zn uptake capacity [73,74]. The effects of Zn application depend, also, on the type of application (soil or foliar). de Oliveira et al. [75] and Shivay et al. [76] found that Zn foliar application is more effective than soil application in enhancing the Zn concentration in soybeans and chickpeas, respectively. Moreover, Yilmaz et al. [77] demonstrated that the combination of soil and foliar supply is the best application method to increase the Zn concentration in plant tissues.

Recently, nano forms of Zn have also been studied and applied in biofortification programs. This kind of form is preferred for the high uptake efficiency since it is more water soluble and easily at plants disposal. In this regard, Solanki and Laura [78] reported that granular Zn sulphate is less effective than the respective nano form. Indeed, the current efforts in Zn biofortification aim to decrease the Zn particle size and to, therefore, increase its uptake efficiency.

There is evidence supporting that spinach [73], beet [74], and pak-choi [79] are Zn hyper-accumulators.

3.3. Iodine (I)

Iodine (I) is an essential microelement for animals and humans but not for higher plants; however, it is implicated in some plant physiological and biochemical processes [80]. The soil encloses small amounts of I (5.1 ppm), and consequently, plants have low disposability of this microelement [81]. Therefore, I content in plants is inadequate for humans in relation to their dietary requirements and it needs to be implemented to the soil [82]. In this regard, the management of I as a fertilizer is the easiest method, because it tackles the I-deficiency in the soil (and consequently in human nutrition) [83]. Iodine can be found in the soil in organic or inorganic (iodate or iodide) forms. Plants can absorb I from the soil, but its mobility depends on pH, composition, texture, and redox circumstances [84]. A low I intake could be useful for plant growth; indeed, positive effects have been recorded in many horticultural crops such as tomato, cabbage, and strawberry [26,85]. However, it is important to remark that high I dosage could inhibit its absorption by roots and could also be toxic for the plant [26,85–90]. In this regard, it is crucial to remember that I is also registered as a herbicide for agricultural usage [80]. However, the toxicity of I depends on its form: iodate or iodide. Iodate (IO_3^-) is reduced to I^- and this can explain why it is less toxic for the plant as compared to iodide [88,91,92]. Moreover, iodate is also a substitute electron acceptor for the enzyme nitrate reductase [84]. Once I is absorbed by plant roots, it enters cells via specific carriers or channels [24,84]. Muramatsu et al. [93], who studied the effect of different I chemical forms in *Brassica rapa*, reported that I-biofortification via the iodide form was more efficient than the iodate form. These results were sustained by Incrocci et al. [94] on basil.

Inside the plant, I is transported via the xylem and its concentration decreases from the root to the leaves, stems, and fruits [84–96]. Nevertheless, the presence of a phloematic path has been reported in tomato and lettuce [89,97,98]. There are reports that I, at a low dosage, can enhance the antioxidant behavior of plants, with positive effects against abiotic stresses such as salinity or heavy metals [99,100]. Even though Sabatino et al. [101] found a decrease in the growth parameters of curly endive plants biofortified with I, they found that I biofortification at mild doses (250 mg L^{-1}) positively enhanced dry matter content, total phenolics, ascorbic acid, glucose, and Ca compared to non-biofortified plants. Moreover, Consentino et al. [102] reported that a I dose of 100 or 300 mg L^{-1} can positively affect the marketable yield, fruit dry matter, and ascorbic acid, whereas the biofortification had a negative effect on the soluble solids content of eggplant compared with the control. Lawson et al. [103] reported that, by studying soil vs. foliar I-application for field grown vegetables, foliar supply is preferred as it is inexpensive and showed better performance in terms of biofortification efficiency. This pattern of results was supported by Strzelecki et al. [104] in radish plants. Furthermore, Smolen et al. [105] investigated the type of I application in lettuce and found that only foliar nutrition with I significantly increased the accumulation of this element in plant tissues.

Zhu et al. [92] reported that spinach is an I-accumulator. Furthermore, Caffagni et al. [86] also observed that tomato and potato are I-accumulators. However, no acquaintance data is available on I hyper-accumulator terrestrial plants.

3.4. Molybdenum (Mo)

Molybdenum (Mo) is among the most important trace elements vital for plant growth and development. Mo can be usually found in soils at high levels ($0.2\text{--}6.0\text{ mg kg}^{-1}$) to sustain plant needs; it seems to be one of the rarest transition elements [106,107].

Plants absorb Mo as molybdate (MoO_4^{2-}), which is also the most common soluble form found in soils [108] and the most Mo efficient form used in agronomic biofortification programs (e.g. ammonium molybdate tetrahydrate or sodium molybdate). However, the molybdate form is not biologically active in plants as it is, but is as a pterin complex called molybdopterin, which generates the Mo cofactor (Moco) [109]. This cofactor is very important as it contributes to the active site of enzymes important for the cycles of nitrogen, carbon, sulphur, and hormone biosynthesis in plants [109–112]. The two most important enzymes related to Mo are nitrate reductase and aldehyde oxidase. Nitrate reductase is involved in the reduction of nitrate in nitrite, thus, in the case of Mo deficiency, nitrogen assimilation would be impossible [113]. Aldehyde oxidase participates in the biosynthesis of hormones, such as abscisic acid and indole-3-acetic acid, which are fundamental for the regulation of plant growth and development [114,115].

Moreover, the high importance of Mo is related to its function in the biosynthesis processes of chlorophyll a and b. Thus, a lack of Mo determines a reduction in the efficiency of chlorophyll synthesis and, consequently, negatively affects yield and quality of the product [116]. Plant Mo availability strongly depends on pH, with optimal values above 5 [117]. Mo deficiency symptoms occur in plants highly watered and cultivated in acidic soils. The indicators that underline the lack of Mo in plants can be hard to ascertain since, in some circumstances, they have strong similarities with the deficiency of nitrogen. Mo deficiency affects several plant characteristics, such as leaf morphology, fruit quality, growth, and development, and also interacts with the development of complete and fertile flowers [101]. Thus, fertilization with molybdate and pH adjustment can positively affect plant performance [107,118,119]. It is important to underline that a higher presence of Mo, like any other metal, can determine toxic effects, both in plants and animal organisms [120]. In Figure 3, we reported the main Mo effects in plants.

The positive effects of Mo-biofortification are largely documented. Dhaliwal et al. [121] found that Mo-enrichment significantly increases yield and growth traits of cowpea plants compared to the control (not biofortified). Moreover, Sabatino et al. [101] reported that Mo-biofortification had no effect on fruit weight, b^* color coordinate, and titratable acidity, whereas they found an increase in the total yield, marketable yield, aboveground biomass, plant height, polyphenols content, ascorbic acid, soluble solids content, nitrogen fruit content, and iron fruit content of biofortified plants compared to the control. Contrariwise, Moncada et al. [122] found that, in a hydroponic cultivation, Mo-enrichment did not influence yield and morphological traits of leafy vegetables. The same authors showed that Mo-biofortification is imperative for harvesting marketable plants and to boost ascorbic acid and overall nutritional quality, while decreasing nitrate concentration in leaf tissues. Interestingly, La Bella et al. [10] reported that Mo-biofortification significantly boosted plant fresh weight, plant height, stem diameter, ascorbic acid, polyphenols, carotenoids, and nitrogen indices of spinach plants compared to the control, whereas it has no significant effect on P, K, Ca, and Mg concentration. Regarding the effect of the type of application (foliar spray or soil), Mondy and Munshi [123] observed that the Mo concentration in potatoes was more efficiently increased in plots treated via foliar spray. Furthermore, Jena et al. [124], who studied the effect of soil and foliar application of Mo in green gram, found that yield attributes (indirect effects of Mo-biofortification) were significantly increased by the foliar spraying application.

Concerning the Mo accumulation capacity among vegetables, currently, no data are available.

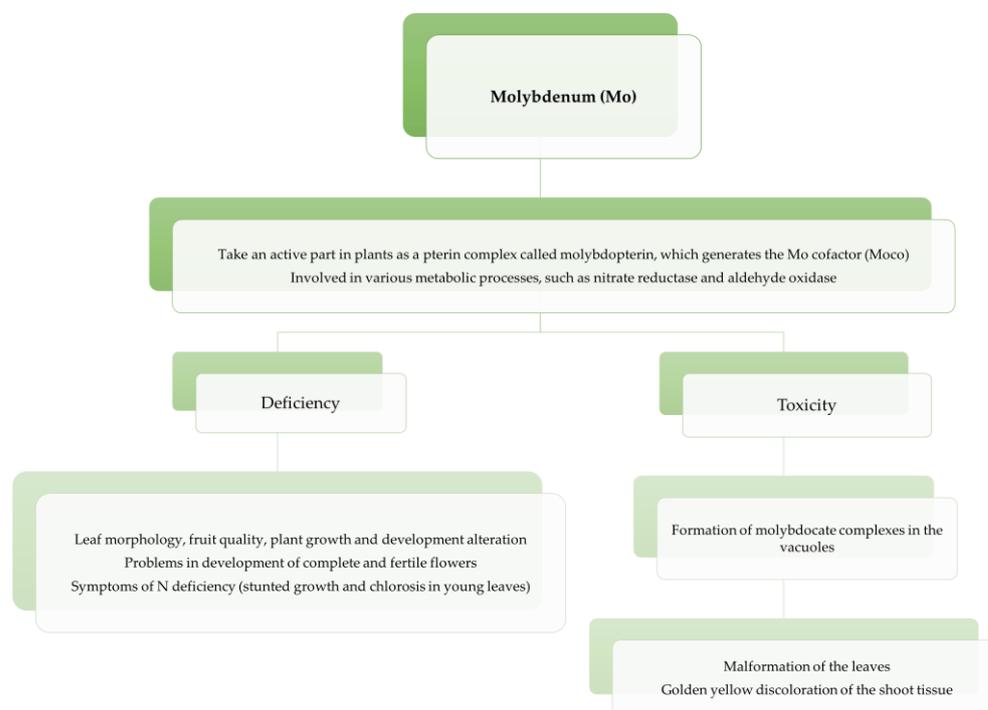


Figure 3. Main effects of molybdenum (Mo) in plants.

3.5. Selenium (Se)

Selenium (Se) is considered a trace element and a toxic metalloid, which is spread around the world in various quantities [125]. Since 1957, Se has been ascribed as an essential trace element for microbes, animals, and humans as it is a component of enzymes such as glutathione peroxidase, selenoprotein P, tetraiodothyronine, and thyroxine 5'-deiodinase [126]. Many authors reported that plants are the main Se source; accordingly, the interest in plant Se-biofortification has increased [127–129]. However, although Se is fundamental for humans, it is not so indispensable for the growth and development of higher plants [130].

As stated by Bodnar et al. [131], Se can be found in plants in organic and inorganic forms, whereas in nature, it is rarely found in elemental form and only exists as part of minerals [132]. Although Se is vital for microorganisms, animals, and humans [133], its essentiality for higher plants is uncertain. In this regard, it is important to underline that Se can be toxic for plants at high concentrations because it is chemically similar to sulfur and, replacing S in different amino acids, causes a wrong folding of the proteins and, consequently, malfunctioning of proteins and enzymes [134]. However, when Se is supplied in small quantities, it can be useful to improve plant growth and development and reduce the negative effects of abiotic stresses [135]. Consequently, the beneficial effects of Se application at low doses have been widely examined. Indeed, Pannico et al. [136] found that doses of 8 or 16 μmol of Se L^{-1} significantly increased the yield of coriander and tatsoi compared to the control (0 μmol Se L^{-1}). Moreover, Sabatino et al. [101] revealed that a Se dose of 4 μmol L^{-1} (via fertigation) or a dose of 8 μmol L^{-1} (via foliar spray) significantly boosted the yield parameters of curly endive plants compared to the control. Accordingly, Puccinelli et al. [137,138] and Nascimento et al. [139] found a significant enhancement of the head fresh weight of Se-biofortified lettuce and rocket, respectively. However, Abdalla et al. [140] found that Se-biofortification did not significantly increase the yield and mineral profile of two genotypes of lettuce, whereas Pannico et al. [141] found a slight reduction of yield of biofortified lettuce and an increase of phenolic acids and anthocyanins.

Interestingly, Puccinelli et al. [138] reported a significant increase in antioxidant capacity and flavonoid concentration in sweet basil and lettuce plants enriched with Se. Concomitantly, the same authors reported that Se-enrichment at 3 mg/L, supplied in form of sodium selenate, significantly decreased the nitrate concentration of lettuce plants, whereas it has no effect on sweet basil. Thus, as shown by these studies, Se-biofortification has a positive effect on production quality traits.

The supply of this microelement via fertigation or foliar spray is a very effective way to increase its concentration in plant tissues and to overcome the inadequate availability. Plant roots can uptake Se in different forms, such as selenate, selenite, selenium dioxide, or nano forms [142]. Among the aforesaid chemical forms, selenate is one of the most efficient [16]; however, nano forms are particularly appreciated due to low toxicity and high efficiency; they are partially water soluble, highly stable, rapidly converted into selenite and organic forms, and highly bioavailable [143].

After the absorption, Se is carried through the plasma membranes of root cells via sulphate (selenate) or phosphate (selenite) transporters [61,128,144,145]. In root cells, selenite is quickly converted into organo-selenium, whereas selenate is transported via the xylem to the shoot, where it is integrated as organo-selenium and reallocated within the plant following the same pattern of sulphur [61,128,146]. Methylated forms of Se-containing amino acids and peptides demonstrate the highest anticarcinogenic activity [147]. This is the reason why plants capable of producing such compounds as a result of biofortification, such as *Allium* and *Brassica*, are especially valuable. In this regard, studies highlighted the function of plants as the main dietary source of this element; thus, there was an up-surg-ing effort to increase the Se concentration in plants used for human diet [129–131,148,149]. Se-biofortification efficiency is also affected by type of application. In this respect, Sabatino et al. [150], who investigated the impact of Se-biofortification and type of application (foliar vs. fertigation) in a hydroponic system on curly endive growth, yield, and quality, found that Se applied via fertigation is a more efficient method for Se implementation. Contrariwise, Shalaby et al. [151], by studying the effect of Se-enrichment via foliar and soil application in lettuce grown in salt affected soil, found that foliar supply is more effective in increasing the Se concentration in plants tissues. Thus, these contrasting results could be attributed to the different cultivation systems (soilless vs. soil).

Regarding Se accumulation ability, several authors [144,145,152–156] found that vegetables belonging to the *Fabaceae*, *Asteraceae*, and *Brassicaceae* families are Se hyper-accumulators. However, White [145] stated that plants with a tissue Se concentration ranging from 100 to 1000 mg kg⁻¹ dry matter are Se-accumulators, whereas plants with a tissue Se concentration below 100 mg kg⁻¹ dry matter are Se non-accumulators.

3.6. Silicon (Si)

Silicon (Si) is one of the most abundant mineral elements present in the soil. Si has several environmental roles with complex functions in plants, such as facilitating relationships with the natural environment and other organisms [157–159].

Si build-up differs considerably according to plant species, ranging from 0.1 to 10% of dry weight [160]. Plants can be grouped depending on the Si concentration in tissues as accumulator, intermediate, or excluder categories [120,161]. As reported by Takahashi et al. [162] and Richmond and Sussman [163], these differences are ascribed to the various ways of Si uptake (active, passive, and rejective). Moreover, these differences are also determined by the ability of the plant root to absorb Si [117]. At pH values lower than 9, Si is taken by plant roots in form of silicic acid [Si(OH)₄], which is an uncharged monomeric molecule that depends on Si specific influx and efflux transporters [164]. Furthermore, Si can be supplied via foliar spray, and it is absorbed via cuticular pathways, stomata, and trichomes [165]. Buturi et al. [15] declared that silicate (e.g., potassium silicate and sodium silicate) are the most efficient Si chemical forms for the biofortification of vegetables.

Although Si is not considered a fundamental element for plants, it is helpful for plant growth and development, particularly under stress conditions [158,166,167]. Si promotes seed germination of various crops under drought stress conditions thanks to its ability to increase antioxidant defense and reduce oxidative stress [168–171]. Moreover, Si supply can increase plant biomass and the yield of several crops under drought stress. This positive effect can be ascribed to the modulation of root architecture (length, surface area, and volume), plant height, and dry matter [172–174].

The direct and indirect effects of Si-biofortification can vary largely, thus many studies have been conducted. Montesano et al. [28] reported that green bean plants biofortified with Si did not display a difference in yield, number of pods, and mean dry matter percentage compared to the control. Conversely, Valentinuzzi et al. [175] found a reduction in shoot and root fresh weight, leaf area, average yield per plant, average of berry per plant, and average berry weight of strawberry plants biofortified with Si compared to the control. Moreover, Hidalgo-Santiago et al. [176] found that Si-application boosts growth parameters in water stress conditions, and concomitantly, the biofortification reduces lipid peroxidation, H₂O₂ levels, proline accumulation, and protects photosynthesis performance. Da Silva et al. [177] underlined that Si-biofortification can also be useful to combating Ca deficiency in lettuce plants. The same authors found that Si-supply can increase ascorbic acid, total phenols, carotenoids, efficiency of photosynthesis, fresh and dry matter production, both in Ca deficiency and sufficiency circumstances. Contrariwise, D’Imperio et al. [178] showed that Si-supply has no effect on the yield and leaf area of chicory plants grown or not under saline stress, whereas it has a positive effect on K, Cu, and Fe leaf concentrations. Moreover, concerning the relationship between type of application and Si-enrichment effectiveness, Pilon et al. [179] reported that Si applied via soil prompted an accumulation of this element in all potato plant organs, whereas Si foliar application significantly increased the Si concentration only in tubers and roots. Thus, it seems that Si foliar application could be an efficient method for Si-implementation; however, further studies are necessary [180].

Hoffmann et al. [181] observed that cucumber is a Si accumulator species, whereas tomato is a non-accumulator. Li [182] also declared that lettuce, bok choy, and basil are Si non-accumulators.

3.7. Joint Biofortification of Vegetables

The agronomic biofortification of vegetables with multiple elements is particularly attractive, as the biofortified plants may exhibit simple or combinatorial effects of the elements supplied. Particularly, the combined application of Se and I may have potential benefits for farmers [183]. In this respect, Golob et al. [184], who investigated the impact of the combined effect of Se and I enrichment in pumpkins, found that Se and I joint biofortification enhanced the seeds germination and increased the Se concentration in sprouts. Furthermore, Germ et al. [185] found that the combination of Se and I increased backwheat microgreens yield and Se content by 50–70% and 50%, respectively, compared to Se and I alone. Germ et al. [186], by studying the impact of different forms of Se and I in chicory plants, also reported that I (in both forms: iodide and iodate) applied together with selenite increased the Se uptake, whereas when I was combined with selenate, Se uptake was reduced. Smoleń et al. [187] found that the combined application of Se and I significantly enhanced the I concentration in carrots. There is evidence that when *Brassica oleracea* var. *gongylodes* is biofortified with Se and I, Se has an antagonistic effect on I accumulation, although this multiple biofortification is feasible for human nutrition [188]. Sahin [189], testing the combined effect of I, Se, and Zn biofortification in a soilless lettuce crops, found that the synergistic effect of these three microelements significantly boosted Se, Zn, S, Si, barium (Ba), lanthanum (La), lead (Pb), and titanium (Ti), whereas it decreased the Fe, manganese (Mn), cobalt (Co), nickel (Ni), and bromine (Br) concentration. There is also evidence that the mutual application of I, Fe, and Zn has no significant effect on essential element concentrations, excluding calcium (Ca), sodium (Na), and Si concentrations in tomato fruits [190]. Furthermore, Golubkina et al. [191], who studied the interactive effect

between Se and I joint biofortification and microbial biostimulant application (arbuscular mycorrhizal fungi) on yield and quality traits of chickpea seeds, found that the Se and I joint biofortification effects were enhanced by the biostimulant application. Although the results of these experiments provide new insights, additional studies are required to improve knowledge of the interactive effects of multiple microelements supply on vegetable crops.

3.8. Microgreens Biofortification

Microgreens are a relative new type of horticultural product, which is often appreciated by consumers thanks to the high nutritional and nutraceutical properties [192]. They are vegetables grown until the cotyledonary or 1–2 true leaf stage and are consumed raw. According to recent studies, microgreens enclose a higher quantity of beneficial compounds than the relative mature vegetables [136]. Currently, there is an upsurging interest in the enrichment microgreens with trace elements to increase their nutraceutical value. According to Di Gioia et al. [193], Zn and Fe biofortification increases the yield and the micronutrient concentrations in *Brassicaceae* microgreens. Pannico et al. [136] found that Se application significantly boosted the yield, phenolic components, and Se concentration of various microgreens (coriander, green basil, purple basil, and tatsoi). Moreover, Puccinelli et al. [194] reported that Se-biofortification significantly improved the chlorophyll and flavonoid content, as well as the Se concentration, in three wild species (*Rumex acetosa* L., *Plantago coronopus* L., and *Portulaca oleracea* L.) cultivated as microgreens. Newman et al. [195] found that sodium selenate application significantly increased antioxidant capacity, total phenols, and the overall mineral profile, including Se concentration, in culinary herbs microgreens (*Allium fistulosum* L., *Ocimum basilicum* L., and *Coriandrum sativum* L.). A similar pattern of results was found by Mezeyová et al. [196], who investigated the effect of Se-supply on quantitative and qualitative traits of mizuna, arugula, green basil, cress, and radish. Although recent studies have been conducted on Fe, Zn, and Se microgreen biofortification, limited information is available on I, Mo, and Si microgreen implementation; thus, further research efforts are required.

4. Effects of Biofortification on Human Health

Malnutrition is a world issue that significantly affects health, and is related to the economic situation of the countries [197]. There are two billion people worldwide in middle- and low-income countries where the most consumed low-cost food is the staple and where the diet is poor [198]. Women and children are much more affected by malnutrition compared to men. The cause for malnutrition is an unvaried diet poor in quality. About one-third of the global population is affected by malnutrition due to micronutrient deficiency. The deficit of micronutrients, such as Se, Mo, Zn, Fe, and I, rapidly compromise health status and is one of the main causes of the well-known ‘hidden hunger’ in underdeveloped countries [199,200]. The hidden hunger can occur without a deficit in macronutrients and, therefore, in energy intake but instead as a result of consuming a nutrient-poor diet. The hidden hunger due to the absence of minerals is responsible for the deaths of over one million children each year.

In 1984, to avoid Se-deficiency in the Finland population [201], Se in the form of sodium selenate (15 mg Se/kg) was applied as fertilizer. The dietary intake of Se increased from 0.04 mg to 0.08 mg, and the Se plasma concentration increased from 0.89 mol/L to the optimal level of 1.40 mol/L. The real impact of this practice on human health in Finland was difficult to appreciate in consideration of the absence of deficiency diseases. However, a reduced risk of the occurrence of both cardiovascular diseases and cancers was observed.

Food industries are looking for new food components to ameliorate the status of nutrition [106,202] and/or to prevent the occurrence of diseases related to nutritional deficiency. In fact, as we state, a prevalent problem in undeveloped countries is the lack of micronutrients such as minerals and vitamins. This is called hidden hunger [203]. Scientific evidence has suggested the recommended daily allowances (RDA) and daily

tolerable upper levels (UL) for each microelement; we report the RDA and UL values for the microelement disserted in the current review in Table 3.

Table 3. Recommended daily allowances (RDA) and daily tolerable upper levels (UL) for iron (Fe), zinc (Zn), iodine (I), molybdenum (Mo), selenium (Se), and silicon (Si).

Microelement	RDA	UL
Fe	8–18 mg [204]	45 mg [204]
Zn	9–14 mg [204]	40 mg [204]
I	150 µg [204]	1100 µg [204]
Mo	120–240 µg [205]	600 µg [206]
Se	55 µg [204]	400 µg [204]
Si	Not established	1700–1750 mg [207]

A diet lacking micronutrients (selenium, iron, zinc, iodine, molybdenum) compromises both the cognitive and physical capacity of a large part of the population in underdeveloped nations. Chronic micronutrient deficiencies are responsible for about 7% of the diseases. Among the minerals, it was reported that the lack of iron alone is responsible for about 15% of these diseases [208]. A non-balanced diet, moreover, compromises many aspects of children’s development and impaired growth [209–211]. The chronic deficiencies of minerals depend on the type of food. In fact, the absence of nutrient dense foods or nutrient losses due to poor diets are responsible for the large occurrence of infections. In addition, the metabolic requirements for micronutrients change depending on the time in life. For example, the requirement for micronutrients is higher during menstruation in women of reproductive age, and during pregnancy and lactation. It is also high during early development. The World Health Organization (WHO) and the Food and Agriculture Organization of the United Nations (FAO) have adopted strategies to improve the intake of important micronutrients through food biofortification. It is a cost-effective strategy and a safe approach to improve diets, prevent disease, and control micronutrient deficiencies [212]. Moreover, as physically active people need adequate supplementation [213–215], biofortification could be an option. Unfortunately, studies on the impact of vegetable biofortification on human health are limited. Studies, for example, have been conducted using an experimental model, the *Gallus gallus*. In this experimental model, the consumption of biofortified food with zinc and iron was able to impact the composition of the microbiota. An increase in the population of bacteria that produced the SFCAs was observed, while the population of pathogenic bacteria was reduced [216]. Fe biofortified carioca beans (*Phaseolus vulgaris* L.) [217,218], Fe biofortified wheat (*Triticum aestivum*) [219], and Zn biofortified wheat [220] were used. This experiment demonstrated that Fe and Zn biofortified food provides several health benefits to the host by improving the bacterial profile, which leads to a healthier gut. Another study has looked at the possible health effects of foods biofortified with Si. This paper investigated the effects of bone mineralization of biofortified leafy vegetables with silicon (five different types) with respect to silicon in tablets. They found that biofortified purslane and Swiss chard increased bone formation markers [221]. These results suggest the potential application of consumption of fortified foods in different targets of human physiology, including bone metabolism. In fact, in consideration of the close relationship between the gut and bone [211,214], nutrition with mineral fortified foods could be a new way to counteract disease by a natural approach.

Food biofortification with iodine is also of interest because salt iodization is insufficient in ensuring adequate iodine intake in the population. In this respect, Mottiar and Altosaar [222] reported that non-organic I is volatile and often lost during transport, storage, and cooking. Agronomic biofortification of food crops, especially staples such as cereals, which are consumed widely, may be an effective component of a food system strategy to reduce Se and I malnutrition, to reduce associated I-deficiency disorders (IDD) and hypothyroidism, as both I and Se, when taken adequately, are essential for thyroid health [183]. In a recent clinical trial, a population of healthy people consumed curly endive

leaf biofortified with I for 12 days; whole-body homeostasis was not affected, suggesting that the consumption is safe, but there was an increase in the concentration of I in urine and a systemic increase in Ca, vitamin D, and K [8]. Mo is one of the micronutrients essential for maintaining the health of the human body. A clinical trial conducted for 12 days in a population using lettuce biofortified with Mo, reported reduced fasting glucose, insulin, insulin resistance, and increased insulin sensitivity in healthy people. Thus, in general, it was able to improve glucose homeostasis [223]. Moreover, supplementation with Mo-enriched lettuce in physically active people significantly improved Fe homeostasis by increasing non-binding hemoglobin and transferrin saturation [9]. These studies suggest that thanks to biofortification, it is possible to enhance the levels of nutrients essential to human health in crops. However, further studies on the impact of these micronutrients, including the levels they reach in the urine and serum, following human consumption are required.

5. Regulating Causes: Antinutrients and Promoters

Mendoza [224] reported that phytate and tannins, present in plant tissues, are restrictive factors for Fe, Zn, and Ca intestinal absorption. In this regard, Lin et al. [225] stated that tannin concentrations in comestible plant tissues differs significantly among varieties. Consequently, breeding activity to reduce concentrations of these antinutrients seems practicable. Furthermore, Jin et al. [40] and Murgia et al. [226] testified that phytic acid is considered an antinutrient since it can diminish human intestinal intake through chelating Fe. However, in plants, phytic acid accomplishes crucial biological functions (Figure 4). Contrariwise, there are several organic components that elicit the absorption of essential elements [227]. In this respect, ascorbate (vitamin C), β -carotene (provitamin A), protein cysteine, and various organic and amino acids are considered elicitors for human essential elements intake (Figure 5). However, an extensive intraspecific discrepancy in both vitamin C and β -carotene concentrations in vegetables was reported [228].

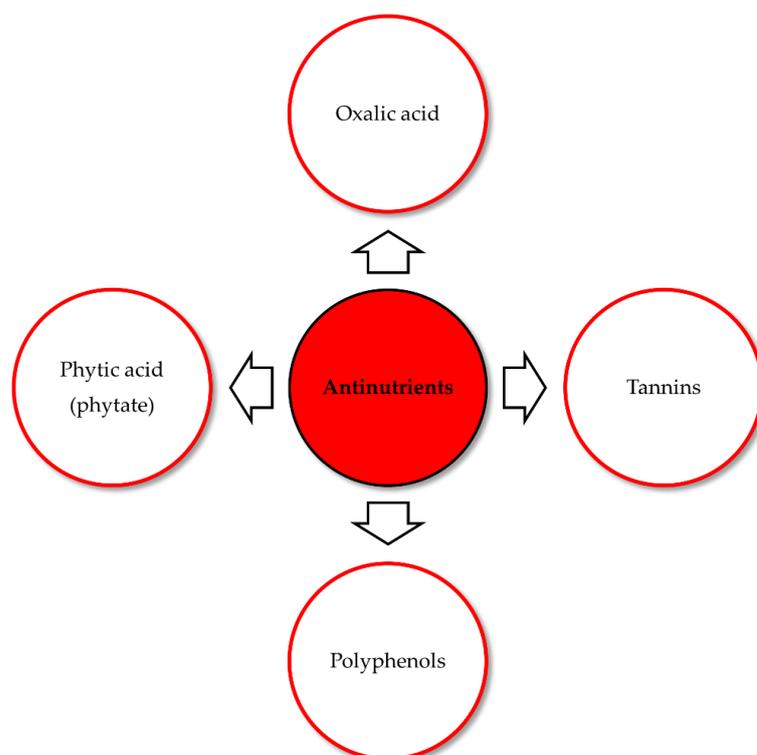


Figure 4. Antinutrients for human essential elements intake.

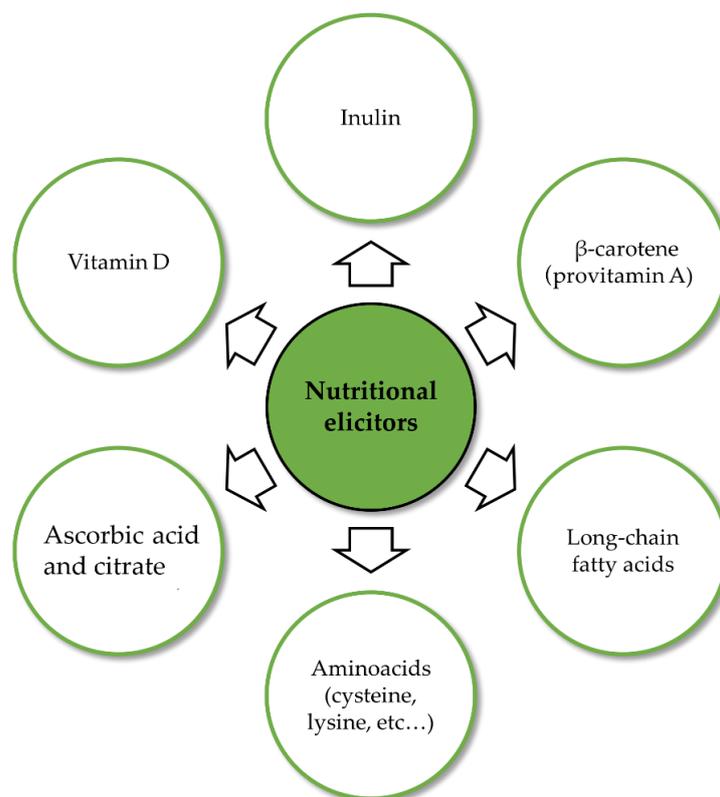


Figure 5. Elicitors for human essential elements intake.

6. Conclusions and Future Perspectives

Although the main purpose of current agriculture is to push crop productivity to the maximum, many disease conditions that plague human health are related to mineral and nutritional deficiencies. Overcoming this deficiency is precisely why the agricultural sector is increasingly interested in biofortification practices. Mineral-dense vegetable crop production merits a noticeable resonance in the current and coming years. Since the horticultural sector is characterized by a high rate of genetic turnover and considering the long time required for genetic improvement activity, agronomic biofortification, although it includes costly experimental actions, is an efficient approach to improve leafy and fruiting vegetables. However, several issues remain to be addressed, such as the bioavailability of minerals, the indirect effects from biofortification in terms of crop yield and quality, and the high cost of some specific chemical formulations, as well as the ecological impact of innovative agronomic practices.

As reported in this review, there are encouraging findings on the biofortification of different microelements in leafy and fruiting vegetables as they improve the human diet. However, the outcomes are not wholly coherent. Specifically, successful biofortification programs must consider the strong influence of different pre-harvest factors, so it is impossible to formulate universal protocols.

Considering this and regardless of scientific approach, the forthcoming accomplishments should be scheduled in a wider perspective to connect farmers, buyers, extension specialists, agronomists, nutritionists, and educators, assuming methodologies with the final intent to positively influence the human diet.

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