Review

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*Review*

# Future Food: The Possible Impact of Potato Biofortification on Climate Resilience and Space Food

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**Abstract**

This review examines the potential impact of potato biofortification on boosting climate resilience and enhancing the nutritional content of potato tubers to combat hidden hunger. It also explores future possibilities for biofortified potatoes as a food source during space travel or colonization. Widespread mineral deficiencies are prevalent globally, particularly in developing countries. Additionally, climate change could adversely affect potato production and soil nutrient absorption. In this context, developing breeding methods to develop cultivars that respond better to biofortification amid climate change is essential. These cultivars may be physiologically efficient at absorbing and transporting minerals into tubers. The review covers various approaches, including identifying germplasm accessions with enhanced micronutrient storage, understanding mechanisms of micronutrient uptake and translocation, and pinpointing genes related to micronutrient, oligopeptide transport, and lignads. It also discusses in vitro selection and screening of calli with improved capacity for micronutrient absorption and transport.

**Keywords:** germplasm; iron; metal transporter; somaclonal variation; translocation; zinc

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## 1. Introduction

Potatoes are the third most important food crop in the world, after wheat and rice. It supplies essential nutrients, including water, carbohydrates, vitamins, minerals, proteins, and fats. The potato is a staple food in almost every part of the world and relished by people of all ages in daily meals, snacks, and soups [1]. Moreover, it is also a crucial raw material for the industry to produce starch due to its high carbohydrate content [2]. The processed potato "milk" has been considered a cheap substitute for cow milk. The crop is consumed by large masses of the world's low-income population, who require substantial daily energy to sustain their lives. However, they often encounter significant deficiencies of vital minerals such as iron, zinc, vitamins, and iodine [3]. It is grown on an area of 16.8 million hectares. China is the largest grower and crop producer, accounting for approximately 93.4 million metric tons, equivalent to about 24% of world production[4]. The per capita consumption of potatoes was the highest in Belarus, at around 125 kg, followed by Ukraine and Kazakhstan. Large masses consume it daily as a vegetable slurry, soup, and fried and boiled foods. The micronutrient values may vary with environmental conditions and potato accessions. However, generally, the zinc (0.3 mg), iron (3.1 mg), folate (17 μg), calcium (30 mg), potassium (411 mg), sodium (12 mg), Vitamin C (10.9 mg), may be present per 100 g of potato serving[5]. These values indicate that potatoes are a rich source of potassium, while also containing trace amounts of other essential nutrients for the normal physiological functions of the human body [5].

Potatoes are served in various ways, including fried potatoes or chips, a favorite among children of all ages. The net worth of potato processed items (potato fries, starch) is approximately US$ 41

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billion, projected to reach around US$ 60 billion by end of 2025. It is also an essential part of local fried cuisines and other dishes consumed daily throughout the year. The consensus is that potatoes are the food of choice for low-income or impoverished people who rely on them for daily energy (390 kJ, $100^{-1}$ g of baked potato) in every corner of the world [2].

Global climate change has triggered severe environmental challenges, including drought, supra-optimal temperatures (such as chilling stress in winter and high temperatures during summer crops), frost injury, UV radiation, salinity, low soil fertility, diseases, and the accumulation of toxic chemicals like heavy metals and pesticides in the soil [6]. These factors threaten sustainable agricultural production and may also negatively affect tender crops. These environmental and biological stresses can impact growth and tuber formation, reducing crop yield potential by decreasing tuber size, tubers per plant, and photosynthate translocation [7]. Winter potato crops are often damaged by chilling temperatures and frost, necessitating low tunnels—a measure that increases production costs. Additionally, the crop requires loose, textured soil rich in organic matter and fertility, and is highly sensitive to salinity and alkalinity. An environmentally resilient crop can be achieved through both conventional and advanced breeding methods. Improving physiological functions, such as developing stronger root systems that can access water and minerals from deeper soil layers and increasing the translocation efficiency of minerals and food reserves, can enhance stress resistance. These improvements can also facilitate the breeding of tubers with enhanced mineral content, resulting from increased mineral uptake from the soil and the subsequent translocation of minerals into leaves and tubers.

## 2. Hidden Hunger

About 840 million people do not receive enough food to meet their daily energy needs [8]. At the same time, a large proportion of the world's population, exceeding 2 billion, suffers from micronutrient deficiencies despite having access to adequate food. The term "hidden hunger" is applied to this large proportion of the population, which generally resides in the developing world. It is an outcome when people feed themselves on a few food items and lack variety, which causes various diseases, including anemia, deformation of bones, blindness, goiter, and low fertility [9]. These large masses of the people, especially the children and women, are deficient in vital minerals such as iron, iodine, calcium, and zinc, vitamins, causing life-threatening diseases like anemia, malfunctioning glands, and a significant effect on the reproductive health of women. It is estimated that 1 in 2 pre-school-aged children and 2 out of 3 women of reproductive age may suffer from any micronutrient deficiencies [10].

As a non-grain crop, it is grown all year round, potatoes are a staple food of many nations, relished by people of all ages, including children and women. However, they are deficient in minerals (iron, zinc, and iodine) and vitamins like folate and β-carotene; thus, they are ideal for biofortification. Biofortification is a powerful tool for improving deficient minerals and functional molecules in crop plants through breeding and biotechnology [5]. The bred cultivars may be more efficient in absorbing and accumulating minerals in their targeted tissues, and thus could help manage input resources better than conventional cultivars. Additionally, with looming crises of drought, salinity, and heat stress, breeding populations that are physiologically efficient and developed with an idea of biofortification could also help improve climate resilience [11].

There are several benefits of targeting the potato crop for biofortification. The crop is adaptable to a wide range of environmental conditions and can meet daily energy requirements in a short span, compared to other cereal crops [12]. Several characteristics of this crop, including its adaptability to different systems, early maturity, and tuber formation under continuous light, make it an excellent candidate for exploration in space programs [13]. Various space agencies have also considered this crop for inclusion as space food, attracting significant scientific interest in using it to combat malnutrition in humans both on Earth and beyond. The limited availability of food and difficulties in producing highly nutritious crops during long space journeys could lead to diseases caused by malnutrition and increase the risk of hazardous cosmic radiation by lowering immunity and the lack

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of essential micronutrients needed as immunity boosters, which are important for activating DNA repair systems. Hence, the issue of hidden hunger or micronutrient deficiency could follow humanity beyond planet Earth and during the ongoing quest for space exploration.

Potato germplasm can also be selected to enhance the nutrient content of the tubers. However, the crop is polyploid with tetrasomic inheritance, which makes it difficult to breed using conventional methods. Additionally, the extent of genetic variation and heritability complicates selection through traditional breeding techniques. This review will examine progress in increasing micronutrients in potatoes, compare it with other field crops, and propose future strategies to address micronutrient deficiencies in potato crops.

### *2.1. Statistics of Micronutrient Deficiencies*

It has been reported that 37.5% of women and 17.5% of men suffer from iron deficiency. This deficiency is most prevalent in Western sub-Saharan Africa (47.4%), followed by South Asia (35.7%) and Central sub-Saharan Africa (35.7%) (Figure 1A) [14]. An inadequate diet is the primary reason for those experiencing micronutrient deficiencies. Approximately 3.5 billion people worldwide risk calcium deficiency due to poor dietary habits [15]. Calcium deficiency is associated with poor bone health and may also increase the risk of cancer, cardiovascular diseases, preeclampsia, and related complications [15]. These complications linked to calcium deficiency are major contributors to maternal morbidity and mortality. The prevalence of calcium deficiency is particularly high in Africa and Pakistan. Individuals with calcium deficiency may display symptoms of osteoporosis and uncontrolled blood pressure, which can lead to kidney and liver issues. The recommended daily calcium intake is approximately 1,000–1,300 mg, depending on the age group [16]. Zinc is the most important micronutrient, performing multiple functions in humans, and is vital for sustaining human life. It is the single most important micronutrient that performs more functions than any other micronutrient. It has catalytic, structural, and regulatory roles essential for gene expression and metabolism related to immunity and hormonal regulation. Its deficiency induces inhibition and stunting of growth in children and an increased risk of morbidity. The severe deficiency causes cognitive impairment, recurrent infections, and diarrhea [17,18]. It has been estimated that approximately 17% of the world's population is at risk of inadequate zinc intake. Among these populations, those in Asia and Africa are disproportionately affected, at 19% and 24%, respectively [19].

Iodine is another mineral considered deficient in approximately 35–40% of the world population. It is an essential component of thyroid hormones, thyroxine (T4) and triiodothyronine (T3), which play crucial roles in various physiological functions, including brain development, liver and kidney function, and metabolism, in children and adults [20]. Its deficiency causes goiter, affecting approximately 2.2 billion people worldwide. It is the leading cause of intellectual disability if the deficiency occurs during fetal development. Thus, it is essential for pregnant women and women of reproductive age. The intake of iodized salt has helped overcome iodine deficiency. However, 25% of the world population still encounters iodine deficiency. An adult human contains approximately 15–20 mg of iodine, most of which is accumulated in the thyroid gland. Adults require approximately 40 µg of iodine daily, which they obtain by consuming various foods. Animals, birds, eggs, seafood products such as shellfish, and dairy products like milk are rich in iodine. However, being an expensive commodity in poor and developed countries, the availability of this essential mineral through food is limited. The plants are also a good source of iodine, but the iodine content in the plants depends on the presence of this salt in the soil.

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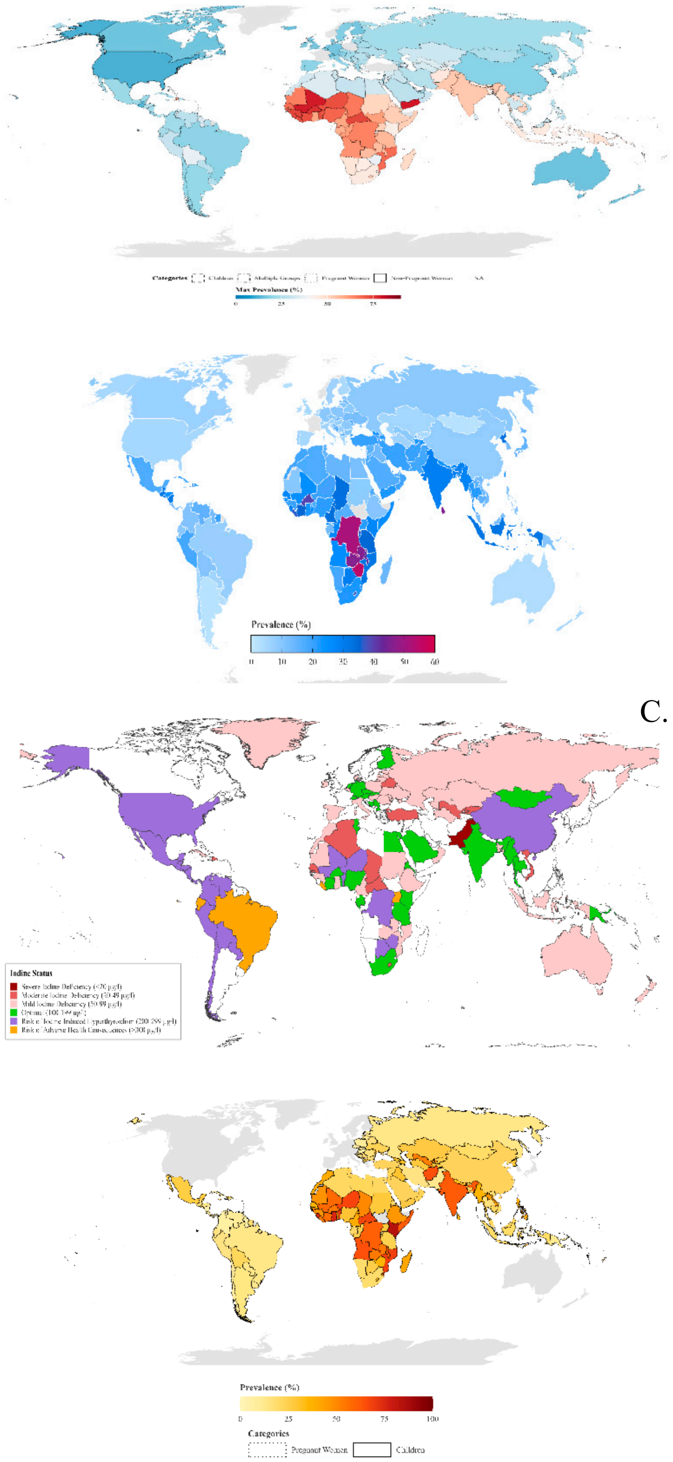


**Figure 1.** A. World anemia B. Zinc C. Iodine D. Vitamin A deficiency map based on various categories of children, pregnant and non-pregnant women. All maps were produced in the "R-program" using the library "tidyverse; Rnaturalearth", and function "ggplot2". Data were obtained from the WHO Global database for anemia and Vitamin A deficiency, while data for iodine deficiency were obtained from the link https://iris.who.int/bitstream/handle/10665/39840/9070785056_eng.pdf. The data for zinc deficiency was obtained from Wessells and Brown [21].

## 3. Environmental Stress and Nutrient Availability

It has been observed that tuber micronutrients were affected by the climatic conditions, genotypes and production system [13]. The bioavailability of minerals may be compromised by climate change, as it could reduce the availability of vulnerable food crops, like maize and potatoes.

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These crops are susceptible to environmental fluctuations, including high temperatures and water stress, which can threaten their survival and compromise the country's food security by potentially leading to yield failures or decreased food production. Moreover, abiotic stresses such as water scarcity or salinity hinder the absorption of essential minerals, leading to stunted growth and disrupting the micronutrient status of potato tubers. Soil pH is crucial for the absorption of $Zn^{2+}$ and $Fe^{2+}$ from the soil, with absorption increasing at more acidic pH levels. Under saline conditions, the Zn and Fe contents form insoluble complexes, rendering them unavailable to plants. To enhance mineral uptake, plant roots release organic acids, which facilitate the absorption of Zn and Fe. Water stress regimes significantly affect micronutrients like Mg, Fe, and Zn, with the highest contents observed under mild water stress (5.26, 0.75, and 0.14 mg $g^{-1}$), decreasing to 4.14, 0.46, and 0.05 mg $g^{-1}$ as water stress intensifies [22]. This represents a decrease of 21% for magnesium, 39% for iron, and 64% for zinc. The overall bioavailability of micronutrients may be even more significant when considering yield losses, suggesting that climate change could reduce the quantity of edible tubers and their nutrient content. Foliar application is recommended to mitigate the adverse effects of stress factors such as salinity. A foliar spray of ascorbic acid (200 mg $L^{-1}$) improved protein contents by 6 to 16% and starch contents by 13 to 19% in potato tubers grown in salt-affected soils [23]. A foliar application of 46.50 g $\cdot ha^{-1}$ silicon decreased $Fe^{2+}$ contents while increasing $Cu^{2+}$ and $Mn^{-}$ contents. A negative relationship was also noted between Fe and Si contents in potato tubers under drought stress [23]. Salinity and water stress conditions reduce the uptake of Fe and Zn, leading to key abnormalities such as stunted growth, reduced chlorophyll production, and impaired enzymatic activity. There is also a need to introgress salinity and drought stress tolerance genes. A gene with a putative function in enhanced mineral uptake from soil could improve the micronutrient status of tubers while mitigating the adverse effects of stress conditions. Engineered genes responsible for mineral uptake at low osmotic potential may enhance mineral absorption and induce tolerance by improving physiological functions. Mineral uptake under stress environments is hindered, but micronutrient translocation and distribution between vegetative organs, such as leaves, stems, and roots, increase at non-lethal high temperatures and $CO_2$ levels, even though further translocation into tubers remains unaffected during high temperature and $CO_2$ concentrations. This suggests that climate change may also impact the translocation patterns within plants [24]. To improve the nutrient balance within potato tubers and mitigate the suppressive effects of abiotic stress, foliar and soil amendments have been recommended to reduce the deteriorating effects of abiotic factors on the yield and quality aspects of potato tubers [25].

## 4. Status of Biofortified Crops

There are more than 400 biofortified cultivars of 12 different types developed through crossbreeding and selection, molecular breeding, or genetic engineering. These crops tend to accumulate several micronutrients at higher concentrations than conventional cultivars, addressing various nutritional issues, including Vitamin A, Vitamin E, iron, and zinc. The commercialization program for biofortified crops, led by the Global Alliance for Improved Nutrition (GAIN) and CGIAR HarvestPlus, has released biofortified crops in six countries in Asia and Africa (Pakistan, India, Kenya, Tanzania, Nigeria, and Bangladesh) based on their malnutrition status. Approximately 2 million people have incorporated biofortified products into their daily diets[26]. The orange-fleshed sweet potatoes, which can synthesize several times higher amounts of Vitamin A, have been introduced to overcome malnutrition deficiencies in Africa [27,28]. Similarly, Golden Rice, which contains high levels of β-carotene, has been developed through genetic engineering, and the Philippines is the first country to initiate the commercial cultivation of Golden Rice. High-iron beans have been designed to combat anemia, due to their high iron content, which aims to lower the incidence of iron deficiency in various parts of the world [29,30]. The biofortified pearl millet had a positive outcome in children in India. CIMMYT has been assisting in developing maize with higher vitamin A and iron content, which may help alleviate iron deficiencies in African countries such as Zambia and Nigeria. As progress is made in conventional plant breeding with improved selection

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tools, such as marker-assisted selection for predicting breeding value and resolving linkage drag, more precise information about the genetic basis of biofortification target traits will enable more crops to be designated as biofortified. Cultivars with improved novel micronutrients will be released.

**Modeling the potato crop as space food**

Several items, including tomato, microgreens, lettuce, and potatoes, have been considered in various investigations as food for astronauts during space journeys. The crops are selected based on the occupied space, lifecycle, and large harvestable fractions. The astronaut's nutrition must be rationalized based on the demineralization of bones, immune system dysfunction (in a microgravity environment), and carcinogenesis (due to the high magnitude of cosmic radiation). Specific space-related issues, such as demineralization and immune system dysfunction, may necessitate a highly nutritious diet, which can also help maintain optimal levels of micronutrients. Biofortification has been proposed to enhance nutritional levels in various crops during long-term space missions, including tomatoes [31], lettuce [32], microgreens [33], and potatoes[34]. The microgreens (basil, coriander, tatsoi) have been considered for biofortification by applying potassium iodide [33]. The concept of "superplant", combining the characteristics of several medicinal plants into a single plant using CRISPR technology, has been proposed [35]. One of the problems with highly nutritious crops is their edibility, as astronauts come from diverse cultural backgrounds and may not be adaptable to many crops. On the other hand, potatoes have a highly edible value among all nations of the world.

Potatoes are an ideal crop for space research and could serve as a food source for astronauts. The successful cultivation of this crop in various systems, such as hydroponics and aeroponics, makes it a strong candidate for studying its response in future space exploration programs [34]. A preliminary study in a potato hydroponic system revealed that hydroponically grown potatoes had 200% greater yield potential (in terms of both tuber mass and a higher number of large tubers) than field-grown potatoes. At the same time, factors such as fertigation cycles need optimization to prevent cracking and other issues in potatoes [34]. However, there was also a decrease in quality, such as the availability of dry matter. In addition to the higher yield, the growth cycle was shortened by 24%, measured in terms of growing degree days. A NASA space shuttle experiment showed that tubers were well-formed in space and on the ground. This may be attributed to effective control of light and temperature in a controlled environment. Nevertheless, the crop requires engineering before becoming an ideal source of space food. Several breeding objectives must be addressed; for instance, shortening the growth cycle by achieving a higher growth rate and an increased rate of tuber formation could help enhance its production potential. Some cultivars, such as 'Norland', 'Denali' and 'Russet Burbank', have been identified as having the ability to form tubers under continuous light [36,37]. The varietal yield potential under controlled environment was about 19.7 kg FM $m^{-2}$, equivalent to nearly 200 t $ha^{-1,}$ and harvest index 0.7 [36,37]. One of the significant impediments to space food is the rapid loss of nutrients from the food due to its low shelf life, and the rate of loss of nutrients, such as vitamins B and C, is higher than that of other nutrients. The vegetables maintain their quality for about 1–4 years as opposed to fruits (1.5 years) and meat products (2 years) [38].

Golden potatoes (GP) have been enriched with β-carotene, which is a precursor of vitamin A. The shelf life of the GP was studied, which showed that potatoes enriched with β-carotene, $\alpha$-carotene ($\alpha$C), lutein, phytoene, and $\alpha$TC retained 80% of the nutrients after boiling, and a 150 g serving of potato fulfilled 17- 42% of the retinal activity equivalent in various human population groups [39]. Biofortification has been recommended to address nutrient loss. Moreover, astronauts may also experience rapid loss and deficiency of minerals from their bodies in a gravity-free environment, along with a limited variety of food available to scientists.

**Oil-Rich Potatoes: A Low-Cost Frying Solution with Carotenoids and Long-Chain Fatty Acids for Mental Well-being**

Potatoes are commonly fried in vegetable oils and fats to create crispy fries and chips. The deep-frying process often has high oil consumption, which poses a health risk due to the deterioration of oil during the frying process. The deteriorated oil produces free radicals, which may cause cellular

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damage. One potential solution is to increase the oil content within potatoes themselves, which can reduce the use of excessive edible oil during frying. The increased oil content could enable potatoes to be cooked in air fryer appliances, potentially lowering cooking costs and reducing health risks associated with deep-frying. Advanced technologies, such as genetic modification, offer a promising approach to enhancing oil content within tubers. Several genes from oilseed crops have been identified that could be used to genetically transform potato cultivars. Three genes—namely, *wrinkled 1* (*WRI1*), *Diacylglycerol Acyltransferase 1* (*DGAT1*), and *Oleosin*—were simultaneously used to improve oil content through a tuber-specific promoter (patatin) in potatoes [40]. *WRI1* is a transcription factor that regulates lipid synthesis. At the same time, *DGAT1* encodes an enzyme that catalyzes the final step in triacylglycerol formation and is widely used in field crops to increase oil content. The oleosin gene stabilizes oil bodies by anchoring the phospholipid membrane in the oil bodies. This metabolic engineering of the genes resulted in a 100-fold increase in oil content, with potatoes containing about 3.3% oil at the expense of starch [40].

Although potato cultivars have a very low oil content; their fatty acid profile is healthier than that of popular field crops like canola, olive, sunflower, and soybean, due to their high proportion of α-linolenic acid (ALA), which accounts for approximately 20%. Omega-3 fatty acids are essential for human health. It serves as a substrate for producing long-chain fatty acids (LCPUFA), such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), in the human body [41,42]. LCPUFAs are vital for neuron cell receptor function, neuroprotection, mood regulation, heart rhythm, anti-inflammatory cytokine production, and eyesight, and can be obtained directly through diet to improve health. EPA and DHA have initially been sourced from microalgae and protists, such as thraustochytrids, which enter the human food chain by consuming marine fish. Increasing oil content in potatoes could also lead to higher levels of α-linolenic acid. Furthermore, crops such as *Camelina sativa* or canola have been genetically engineered to produce long-chain fatty acids like EPA and DHA, and it is possible that potatoes could also be modified for this purpose [41,42]. The canola line "LBFLFK" was genetically modified with 10 genes (various elongase and desaturase) to produce long-chain omega-3 fatty acid DHA in the seeds [43].

One of the challenges of modern life is the increased prevalence of depression, insomnia, or mood swings driven by rigid routine, poor lifestyle choices, and high mental stress. The potatoes, with their vibrant colors — yellow, red, and purple skin/flesh — are rich in anthocyanins, carotenoids, and antioxidants, which can help combat these issues by promoting mental wellbeing and other health benefits (Table 1). The purple and red fleshed potato contains cyanidin-3-O-glucoside and peonidin-3-O-glucoside, in concentrations ranging from 62 to 574 mg, which have been known to act as an antidepressant and reduce anxiety by acting as an antioxidant, anti-inflammatory, and neuroprotectant, while also interacting with dopamine D2 receptors to improve mood [44]. Moreover, red and purple-fleshed cultivars contain higher antioxidant activity than white and yellow-fleshed potatoes. Genetic variability was also observed among the potato cultivars, with cultivar 'British Columbia' having the highest cyanadin content [45]. There was a positive relationship between the anthocyanin contents and antioxidant properties of the potato cultivar.

**Table 1.** Potato skin and flesh diversity with salient features.

| Trait | Skin Colour | Significance | Reference |
|---|---|---|---|
| Provitamin A carotenoids (α- and β-carotene) and xanthophylls |  | 91 μg provitamin A carotenes (PAC)/g D, | [46] |

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| | | | |
|---|---|---|---|
| Anthocyanin, Zn |  | Cyanidin-3-O-glucoside and peonidin-3-O-glucoside, 61.5 to 573.5 mg. High antioxidant activity and total anthocyanin contents in blue-fleshed cultivars. Zn contents in "Provita" cultivar 15 mg 100 $g^{-1}$ | [44,47] |
| Anthocyanin, Fe, Zn contents |  | "Herbie 26" had Fe contents averaging 78 mg 100 $g^{-1}$, while also having very high Zn contents of 16 mg 100$g^{-1}$. Individual anthocyanin in cultivar "Highland Burgundy Red"contained pelargonidin (98 .7%) | [45,47] |
| Protein, Vitamin C |  | Potato cultivars with high protein and vitamin C, and lower Zn (25 vs 28 μg $g^{-1}$ ) and Fe (19 vs 28 μg $g^{-1}$ dry mass) contents than red and yellow accessions | [48,49] |
| Carotenioids |  | Zeaxanthin 2055 μ g 100 $g^{-1}$ | [50] |
| Oil contents |  | (*WRI1*), Diacylglycerol Acyltransferase 1 (*DGAT1*), and Oleosin, oil content 3.3% | [40] |

**Improved efficiency for micronutrient uptake in potato germplasm**

A deficiency of micronutrients causes abnormal growth and significant yield losses in potato tubers. Potato plants absorb micronutrients at three levels: from the soil to the root hairs, from the roots to vascular tissues, and then translocate them to the tubers. Metal transporters form transmembrane helices that act as channels for micronutrient transport (Figure 2). These transporters contain 12 transmembrane domains arranged to create a pore or channel. The iron-regulated transporter protein (*IRT1*) has 12 transmembrane domains that form a channel allowing iron to be absorbed from the soil into the root hairs [51]. Additionally, multidomain oligopeptide transporters specialize in moving peptide proteins that bind micronutrients in their peptides or linked amino acids. The gene *StOPT3* encodes an oligopeptide transporter in the potato. The gene *StNAS4* encodes an enzyme called nicotianamine synthase, which is involved in the biosynthesis of nicotianamine (NA), a metal-binding ligand. Nicotianamine is crucial for transporting and storing metals, including iron, in plants. The gene *StFRO3* encodes a ferric chelate reductase enzyme that reduces $Fe^{3+}$ to $Fe^{2+}$, facilitating iron absorption from the soil. Iron homeostasis is negatively regulated by the gene *StbHLH47*. CRISPR-edited potato lines targeting *StbHLH47* exhibited higher iron content compared to the wild type, accompanied by increased activity of transporters [52]. Table 2 presents examples of various genes encoding enzymes involved in the absorption and transport of zinc (Zn) and iron (Fe).

The proteomic analysis of potato breeding lines subjected to a deficient supply of Fe, Mn, and Zn induces the differential expression of proteins identified through MALDI-TOF. There were 42 proteins involved in signaling, transport, cellular structure, and transcription-related processes, and their expression was increased under micronutrient stress [53]. These proteins function in metabolic pathways, photosynthesis, defense, and redox homeostasis under conditions of micronutrient deficiency. The deficiency of micronutrients induces lower photosynthesis efficiency, but the effects are more pronounced during iron deficiency in the growth medium.

**Table 2.** Function of putative genes related to metal movement under various environmental conditions.

| Metal | Gene | Function | Environment | Reference |
|---|---|---|---|---|
| Zn | *NtZIP11-like*, *NtNRAMP3*, *NtMTP2*, and *MRP/ABCC* genes | Increased expression for sequestration (storing Zn in vacuoles) | High Zn | [53] |
| Zn | *NtZIP1-like* and *NtZIP4* | Downregulation to reduce the accumulation in the cell | High Zn | [53] |
| Zn | *NtZIP1-like* | Upregulation increases the accumulation in the cell | Low Zn | [53] |
| Fe | *StMIT* | Transport iron into mitochondria | Drought and salinity | [54] |
| Fe | PGSC0003DMG400024976 | A metal transporter across the cell membrane acquires Fe from the soil and moves it to the plant. | Iron-rich soil | Xiao[43] |
| Fe | PGSC0003DMG400013297 | Oligopeptide transporter, transports Fe from roots to plant after binding with proteins | Vascular tissues | [51] |
| Fe | PGSC0003DMG400021155 (IRT1) | Absorb iron from soil | Root hairs, low iron availability | [51] |
| Fe | *StbHLH47* | Negative regulator, the CRISPR-edited lines had higher activity of genes, StNAS4, StOPT3, and StFRO3, resulting in higher iron contents | Edited lines | [52] |
| Ca | *CAX2B* | 65% more $Ca^{++}$ in engineered potatoes, transport Ca across the vacuole with magnee | Salinity stress | [21] |

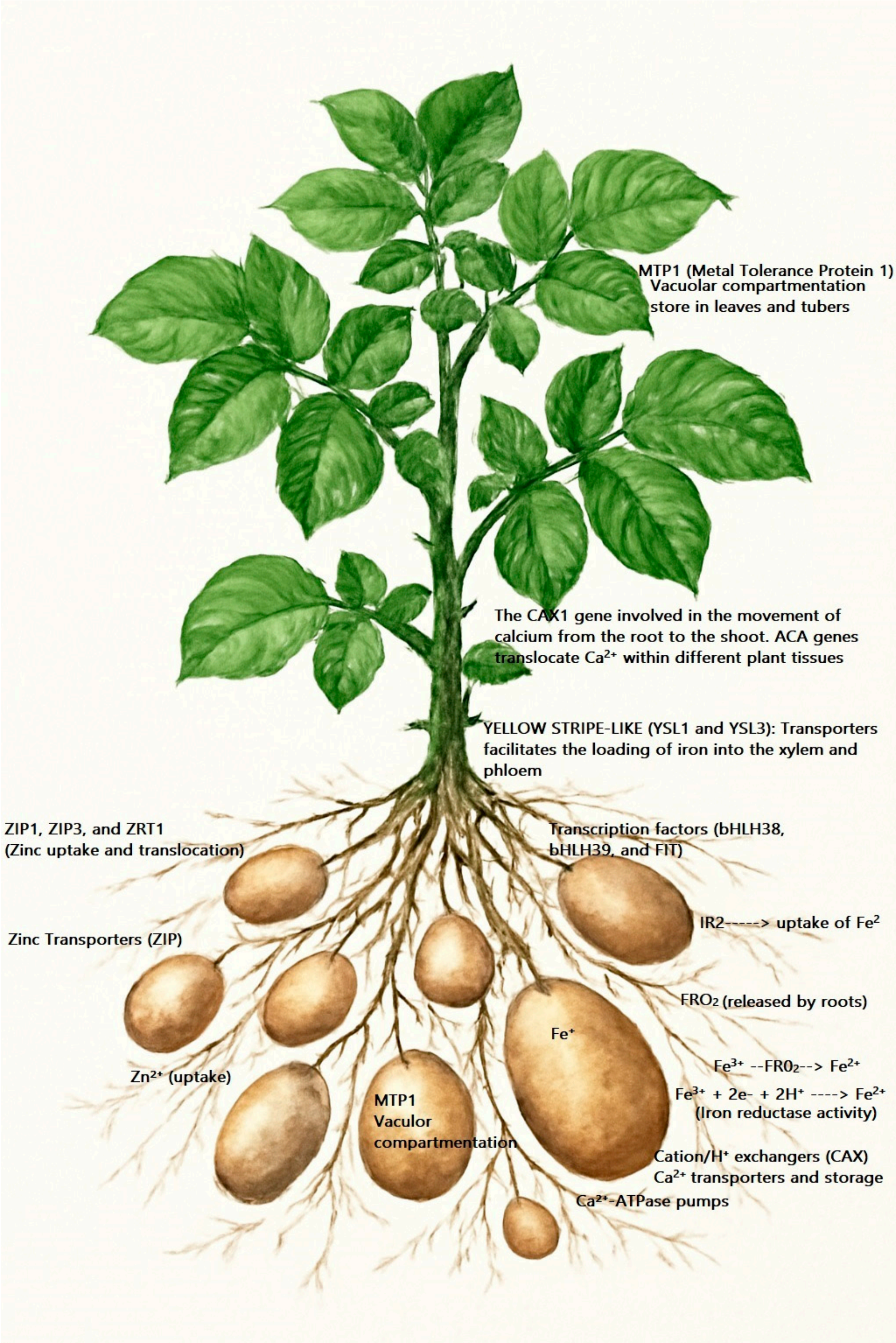


**Figure 2.** Micronutrient uptake and translocation mechanisms within plants.

**In vitro screening and identification of putative genes**

The potato germplasm can be screened in a micronutrient-deficient environment to select accessions that demonstrate a higher growth rate and exhibit fewer deficiency symptoms than other accessions. The selected accessions may be more efficient at taking up micronutrients and could be better accumulators under non-stress conditions.

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In vitro screening may be more effective in developing cell lines with enhanced micronutrient uptake efficiency. The cell lines were screened using media that were deficient in micronutrients. A comparison of iron deficient (1 mg $L^{-1}$ FeNaEDTA) and iron optimum (100 mg $L^{-1}$ FeNaEDTA) concentration in the media showed the switching between the iron deficient genes and reduced expression of ferritin (the protein which oxidized the useable form of $Fe^{2+}$ to $Fe^{3+}$ for storing large amount of iron in their cavity) as ferric hydroxide ($Fe(OH)_3$) [55]. The ferritin molecule stores excess $Fe^{3+}$ and protects the cell from iron toxicity, while also preventing the production of reactive oxygen species during stress. The ferritin genes *FR1* and *FR2* regulate the synthesis of ferritin protein in response to iron deficiency or stress signals, which contribute to iron storage and management. The plant grown in high-iron concentration media accumulated more iron in its roots. In a study, cell lines were screened with low $Fe^{++}$ (0–5 μM $Fe^{++}$) supply. Twenty-three percent of the callus–derived regenerants were considered $Fe^{++}$ efficient based on reduced leaf chlorosis [56]. The regenerated $Fe^{++}$ efficient plants were compared with the inefficient group, revealing that the $Fe^{++}$ efficient plants had an extensive root system with more lateral roots and root hairs [56]. The mechanism of resistance was also studied, showing higher expression of ferritin (*fer3*) in the leaves and iron-regulated transporter (*irt1*) in the roots [56].

In vitro screening can identify cell variants within calli clumps that may have a better ability to survive in a micronutrient environment. The origin of these soma clone variants is generally attributed to point mutations or epigenomic changes that occur during the continuous selection of cells under a deficient environment. In a study, a two-step selection pressure was applied on calli in potato by growing the calli on half-strength MS media supplemented with the (0–5 μM FeNaEDTA). The calli, having the ability to proliferate under iron-deficient media, were continuously selected under pressure and subsequently shifted to regenerate shoots from these calli [57]. There were also differences between the two types of calli (compact and friable) regarding their response to iron deficiency. The compact calli exhibit greater resilience against stressful environments due to higher levels of ferric chelate reductase and improved phenolic compounds [58].

**Agronomic treatments for biofortification of potato crops**

Micronutrient fertilization increased the micronutrient status of Fe2+ by 70% and Zn by 27% for both the raw and processed forms of the potato [59]. The mild processing resulted in the loss of $Fe^{2+}$ (-29%) and $Ca^{++}$ (-17%) due to removal of skin, while storage for 12 days did not alter the micronutrient profile of the potatoes. Fertilization of soil with potassium iodide (KI) and foliar application of $KIO_3$ of 2 kg $ha^{-1}$ could improve the iodine availability in potato, and 100g intake of the biofortified potato could supplement about 25% of the daily dietary recommendation of iodine [60]. The biofortification of $KIO_3$ (as an iodine positive control) and two iodoquinolines [8-hydroxy-7-iodo-5-quinolinic acid (8-OH-7-I-5QSA) and 5-chloro-7-iodo-8-quinoline (5-Cl-7-I-8-Q)] had tuber iodine contents of 1400, 694, and 503 μ g kg-1 of dry weight, respectively [61]. The 8-hydroxy-7-iodo-5-quinolinic acid source of iodine also decreased the toxic elemental uptake of chromium, lead, and nickel, indicating that the potato plant prioritizes the uptake of iodine over heavy metals. The polyphenolic concentration increased, while carotenoids were decreased due to the application of 8-hydroxy-7-iodo-5-quinolinic acid [61]. The foliar fertilizer, with a concentration of 3.6 g Zn plot−1 (0.92 × 2 m), has also been recommended to improve the Zinc content in potato tubers. Zinc sulphate and zinc oxide yielded better results than zinc nitrate, and lower concentrations were preferred over higher doses, which had an adverse effect on the potato yield [62]. The biofortification value due to foliar spray was 2.4 – 3.6 mg Kg-1 after cooking [62]. The calcium biofortification was achieved using CaCl2 and Ca-EDTA at 12 and 24 kg $ha^{-1}$. Both applications resulted in a significant accumulation of Ca content in tubers for potato cultivars 'Picasso' and 'Agria'. The percentage of increase ranged from 6 to 96% depending on potato cultivar and fertilizer dose [63].

The strategies for biofortification through fertilizers are complicated, and the overuse of fertilizers may have toxic effects on plants, also increasing the production cost of the crop. The uptake of fertilizer and accumulation in the tubers will also depend on the physiological efficiency (uptake rate and translocation efficiency) of the plants. On the other hand, the exploitation of natural genetic

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variation within potato germplasm and the selection of accessions through marker-assisted selection or the development of overexpression lines may increase the nutrient value of potato tubers. In comparison between the potato and carrot, it was observed that the potato was a better accumulator of iodine under controlled conditions, with iodine contents ranging between 0.15 and 0.2 mg $kg^{-1}$ in various soils, including sand, silt, and sandy silt. The accumulation was highest in the silt soil under the control condition. The carrot showed a several-fold higher accumulation of iodine when crops were treated with 0.5 mg $L^{-1}$ of iodine. Thus, it shows that the potato did not respond better than the carrot in terms of biofortification but may give a better response under natural conditions [64].

The mycogenic ZnO nanoparticles were obtained from *Aspergillus flavus* and sprayed over tomatoes and potatoes. The spectrophotometric analyses revealed that both species were able to accumulate Zn in their leaves; however, the potato failed to translocate it into the tubers [65]. These results also showed that the accumulation of biofortified Zn was complicated by the poor translocation of resources to the developing tubers. This brings a challenge for plant physiologists and soil nutritionists to devise new strategies to make biofortification effective in potatoes. In comparison between the potato cultivars 'Cara' and 'Lady Rosetta'), the latter showed higher translocation and accumulation of Zn contents in the tubers, accumulating about 77% of the total Zinc contents in the biomass. At the same time, 'Cara' was able to take 68% of the total Zn contents in the tubers [66]. The foliar application of ZnSO4 mixed in plasma-activated water increased yield by 40%, zinc content by 2-fold, and iron content by 3-fold [67].

Plant breeders may select new accessions with a better capacity for translocation from above-ground biomass to the leaves. It has been concluded that Zn contents are translocated and remobilized from aerial plant parts through xylem-phloem vessels during tuber bulking [66]. Among the micronutrients, $K^{+}$ had the highest mobility, while $Ca^{++}$ had the least mobility within the potato plant, indicating a preferential site for the accumulation of these micronutrients. The Fe was preferentially stored in leaves, and new enzymatic machinery may be identified that can translocate micronutrients from leaves to tubers, enhancing the nutritive value of the tubers[68]. CRISPR/Cas9 may be utilized to modify the genes that hinder the translocation of photosynthates and stem reserves to the tubers. Research also showed that micronutrient accumulation was a rate-limiting process, where one micronutrient is prioritized over the other. There is a need to understand the mechanism of micronutrient transport within the plant. There are membrane transporters within the cell that absorb micronutrients and transport them to their target sites. At the same time, the plant also removes excessive micronutrients to mitigate the toxic effects of these micronutrients [69]. The metal tolerance protein functions as an efflux metal transporter throughout plants, regulating the metal level in various biological processes. *The Fe/Zn-MTP, Zn-MTP, and Mn-MTP are genes that regulate the levels of various micronutrients within a cell [70]. There is a need to identify the metal transporter that regulates micronutrients in plants and translocates them to the tubers.*

**Status of the potato germplasm for the micronutrients**

The genetic variation among potato germplasm has shown significant main effects and interactions with micronutrients across accessions [71]. The manganese and zinc contents exhibited very high heritability (0.80). In contrast, Fe demonstrated medium heritability (0.49), indicating that these nutrients could be selected to enhance trait value [71]. In a study conducted in Ethiopia, potato germplasm selected from the biofortified core set showed ranges of 15–26 mg kg $^{1}$ and 10–21 mg kg $^{1}$ for iron and zinc contents, respectively [72]. The clone CIP312725.052 displayed the highest iron content, while clone CIP312621.069 had the highest zinc content [72]. The clone also had significant values for starch, specific gravity, and dry mass [72]. There were also accessions obtained from the INTA Balcarce. For example, 'CL836' had the Mg, Ca, and Zn contents of 190, 112, AND 1.29 mg/100 g dw, respectively. Another accession 'CL 790' was noted for its Mn content (2.09 mg/100 g dw), while "CL 516" and "CCS 1349' had high Zn and Ca (2.23 and 123 mg/100 g dw) respectively [73]. The specific examples for the research on the potato germplasm are given in Tables 1 and 3.

The heritability estimates for both traits (Zn and Fe) were lower in the tetraploid accession compared to the diploid clones, suggesting that epigenetic factors may influence the expression of micronutrients in potatoes. These epigenetic factors may inactivate the loci through differential packaging, forming a complex DNA bond with packaging protein molecules that results in transient heterochromatin. The genetic variability among accessions, estimated through the genotypic coefficient of variation (single environment), was only 10%, indicating a low variability estimate in the study [72]. There were negative relationships between the micronutrients and yield-related traits, suggesting that selecting for higher micronutrients may come at the expense of yield and related traits. Additionally, enhancing one micronutrient may not facilitate the increase of another micronutrient. To identify the genetic basis of linkage or pleiotropic effects, populations may require targeted analysis, and new genetic recombinants may need to be developed to subsequently select for multiple micronutrients in a high-yielding potato background using markers. The type of gene action may influence the selection process for iron and zinc contents. Several diploid potato populations underwent selection for Zn and Fe contents through three cycles of recurrent selection, with significant effects observed for cycle and cycle × location interactions, indicating that both traits were improved due to selection [74]. The additive gene effects and high heritability (0.81) for both traits were estimated, showing that the traits were highly selectable through recurrent selection [74]. The genetic gain from selection was about 29% and 26% for iron and zinc, respectively. There was a negative impact of selection on dry matter contents, which decreased by 2–5% in each selection cycle. The iron content had a positive effect on the number of tubes per plant, whereas the zinc content had a negative impact on tuber weight. This may pose challenges for breeders, as such accessions may not gain popularity among farmers due to their low yield potential unless a premium is offered for these cultivars, which may be less common in developing countries. Wild germplasm has also been a source of novel genetic variation, as well as related species such as *Solanum tuberosum* subsp. *andigenum*, *Solanum vernei*, and *Solanum boliviense* have the potential to produce 2 times more folate than the standard check "Russet Burbank"[74].

Association mapping has revolutionized our knowledge for further use in crossbreeding and selection. The technique helps to map directly the region that may affect the traits of interest in a core set of germplasm. It has been utilized to identify quantitative trait loci (QTL) for biofortification traits, including β-carotene, iron, zinc, and essential amino acids, in various field crops [75,76]. These crops have developed with higher biofortified contents and retain their nutritional value after processing, cooking, and absorption in the intestine. A core set of germplasm is formulated from a large gene pool through different programs. In potatoes, a panel of 214 core sets was used to phenotype the mineral contents at three locations[77]. The same set was also genotyped using the Infinium Illumina 22K V3 single-nucleotide polymorphism (SNP) array, which identified two QTL on chromosome 7 associated with zinc content. In contrast, three QTL were associated with potassium and manganese content at chromosome 5[77].

**Table 3.** Genetic variation in potato breeding lines for various functional compounds and minerals.

| Genotype | Minerals | Heritability | Results | Reference |
|---|---|---|---|---|
| 36 breeding lines | Zinc 2 to 18 μg $g^{-1}$ | 0.61 | Genotypes provided only 4% of the total zinc required | [78] |
| 214 accession | 12 micronutrients | 2 major Zn quantitative trait loci at chromosome 5 | Red-skinned potato had the highest minerals like P, K, S, and Zn | [77] |

| | | | | |
|---|---|---|---|---|
| 33 clones | Fe | 0.63 – 0.71 | 17–62 µg per gram. Red-skinned potatoes had 3x higher iron contents | [78] |
| 'Freedom', 'Yukon Gold', and particularly the very stable mineral source 'Russet Burbank' | Iron, Zinc, and Copper | | One serving per day of these cultivars provides a significant contribution. | [79] |
| 71 Indian accessions | Zinc | | 10.62–27.58 ppm iron (30.49–56.29 ppm). Low genetic variation. Negative relationships between yield and micronutrient traits | [80] |
| Golden potato | Vitamin A | High expression of transformed genes | 91 µg provitamin A carotenes, increased levels of xanthophylls, phytoene and phytofluene, 78 µg vitamin E/g DW | [81] |
| 77 accessions and 10 *Solanum* species | Folate (B9) | - | 2-fold difference | [82] |
| Andean Landrace | Fe and Zn | Additive genetic variance. Heritability (0.36) and (0.57) | Negative relationship between the minerals when estimated on a dry basis | [83] |

**Engineered fortification in potato**

The genes that may promote the translocation of micronutrients were identified. The *Arabidopsis thaliana NICOTIANAMINE SYNTHASE 1* (*AtNAS 1*) gene, driven by a constitutive promoter, and the *Phaseolus vulgaris FERRITIN* (*PvFERRITIN*) gene, governed by a tuber-specific promoter, were used to transform the potato cultivar 'FN 4'. The transgenic lines exhibited 2.2 and 1.2 times more accumulation of iron and zinc, respectively. This cultivar meets 33% of the daily iron and 20% of the daily zinc needs of women in the reproductive stage[84]. In another study, the overexpression lines for the *AtNAS 1* gene with the strong 35S promoter achieved Fe contents of 52.7 µg/g dry weight, which is 2.4 times the amount found in wild-type tubers, without any adverse effect on the transformation of plant phenotype and yield between the wild type and transgenic lines[85]. The primary function of the gene is to promote the translocation of $Fe^{+}$ from the leaves to the tubers, potentially enhancing the plant's response to fertilization. However, there is also a need to identify genes that would facilitate a higher rate of soil micronutrient absorption and improve translocation from the stems and leaves to the tubers. The *StZIP 2* gene in roots enhances Zn pumping from the soil and its translocation to the leaves. Overexpression lines exhibited a significantly higher ratio of above-ground Zn content to root content compared to non-transgenic lines [86]. Transcriptome analysis has been utilized to identify genes associated with biofortification by comparing high- and low-accession genotypes [87]. These analyses indicated that γ- γ-γ-γ-γ-glutamyl hydrolase 1 (GGH 1) is related to the high folate contents in the potato accession “Solanum boliviense”[87]. The genes *GTPCHI* and *ADCS* had sufficiently produced folate in rice and tomatoes, but inefficiently produced folate in potato, which was supported by the transformation of the additional gene *HPPK/DHPS* and/or *FPGS* for the biosynthesis of folate in the mitochondrial genome. There was a 12-fold increase in folate production, and the postharvest folate contents did not degrade over time [88].

Vitamin A deficiency is a significant concern among nutrition specialists and dietitians. It is a leading cause of blindness, and its deficiency can cause morbidity and mortality in children due to the increased susceptibility to infectious diseases. All major food crops, including rice, wheat, maize, and potato, are deficient in vitamin A. There is a lack of natural variability within potato germplasm; thus, it may not be improved by conventional selection methods and requires genetic engineering to increase the potato vitamin A content. There were three genes encoding phytoene synthase (*CrtB*), phytoene desaturase (*CrtI*), and lycopene beta-cyclase (*CrtY*) from *Erwinia*, under tuber-specific promoters, which were used for the transformation of potato [89]. The expression of these three genes resulted in the development of a golden yellow color in potatoes, with a 20-fold increase in carotenoids to 114 mcg/g dry weight and a 3,600-fold increase in β-carotene to 47 mcg/g dry weight. In another study, it was demonstrated that golden potatoes contain provitamin A (up to 91 µg/[90]g dry weight), vitamin E (up to 78 µg/g), and other carotenoids, such as lutein and phytoene. Approximately 80% of key nutrients, including β-carotene and vitamin E, were retained after boiling. In comparison, 14–20% for provitamin A and xanthophylls, 43–45% for phytoene, 23–27% for phytofluene, 53% for α-tocopherol (vitamin E) were absorbed in the simulated intestinal cells. A 150g serving may provide up to 42% of children's and 23% of women's daily vitamin A needs, as well as a significant amount of vitamin E [90].

**Conclusion**

Potatoes are a staple food and a favorite vegetable in many nations. Biofortification of potatoes holds great promise in addressing malnutrition, particularly in sub-Saharan Africa, South Asia, and Latin America. There has been some progress in developing biofortified potatoes, such as golden potatoes. The potato germplasm was screened for various minerals, including Zn, Fe, Cu, and Mn, which showed moderate to low genetic variation among the germplasm accessions. This indicates that wild germplasm accessions of potato may be screened to introgress diversified sources of genetic variation within elite accessions. However, the consequences of linkage drag from wide crosses may need to be addressed through marker-assisted selection. Field trials revealed negative relationships among the key micronutrients, which may complicate the simultaneous improvement of these micronutrients.

Association mapping may be used to elucidate the genetic basis of micronutrients and subsequently identify the locus linked with the trait of interest. Moreover, SNP markers can be applied to establish the breeding value of the selected materials, which can then be crossed to develop transgressive segregating populations for selection. To break the undesirable negative linkages between micronutrients, gene editing may be used to modify the genome and disrupt these associations. The fertilizers have also been recommended when growing biofortified crops. However, the overuse and additional cost of these fertilizers may not be beneficial for biofortified crop production.

The biofortification of tubers is also dependent on the translocation efficiency and absorption potential from the roots, which are influenced by the complex actions of metal transporters in the roots. To enhance the absorption and translocation potential of micronutrients, understanding the role of various metal transporters may be necessary.

In vitro screening methods using micronutrient-deficient media have successfully retrieved calli with high potential for survival in a micronutrient-deficient environment. The regenerated plantlet from micro-nutrient deficiency-resistant calli has higher potential and, consequently, a higher potential for metal absorption. A highly robust root system could also make the climate-resilient potato accessions more resilient and may also be helpful in the absorption of micronutrients. There is a strong need to develop biofortified potato cultivars with high yield potential and better resilience against stress. Otherwise, biofortified crops will command higher premiums, and farmers will be reluctant to adopt these cultivars in the field in the absence of a premium system.

The integration of biofortified crops, including the potato, into national food policies and international research organizations should include the development of cultivars suitable for biofortification and support for farmers adopting them. Partnerships with organizations such as the Global Alliance for Improved Nutrition (GAIN) and CGIAR HarvestPlus could also accelerate the distribution and consumption of biofortified crops.

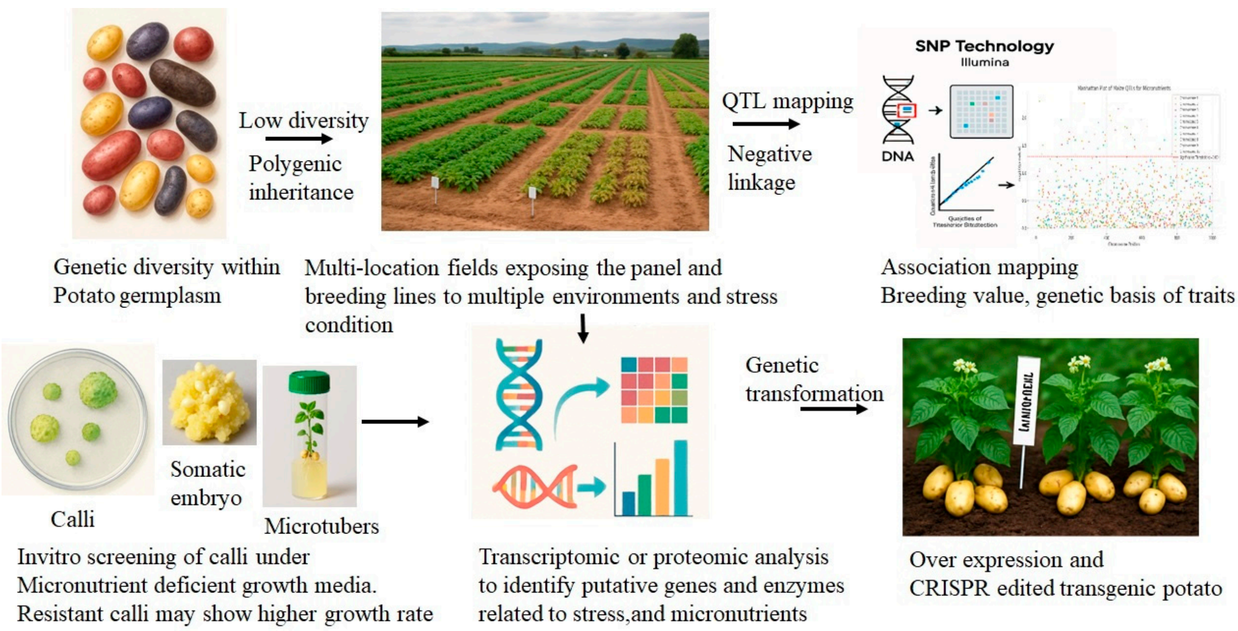


**Figure 3.** Illustration showing the strategies for the development of breeding lines with higher micronutrients.

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