



REVIEW ARTICLE

# Advances in vegetable biofortification: Strategies, impacts and future perspectives

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## Abstract

Vegetables are a great source of vitamins and minerals, including sodium, iodine and phosphorus, as well as carbohydrates, proteins and fibre. Micronutrients such as iron, zinc, selenium, magnesium, calcium and iodine, along with vitamins like provitamin A and folate, are crucial components of the biofortification program. Biofortification addresses the hidden hunger of widespread deficiency of essential vitamins and minerals in human diets. It directly enhances the nutritional value of vegetables to combat malnutrition and improve public health, offering a sustainable and cost-effective solution compared to other interventions. In this review, we discussed three main methods employed for biofortification of staple crops, including genetic engineering, agronomic approach (using mineral fertilizer) and conventional breeding. These methods offer a great deal of promise to alleviate the deficiency of vitamins and micronutrients. Overall, this review highlights the importance of biofortifying vegetable crops for human nutrition.

**Keywords:** genetic biofortification; malnutrition; micronutrients; nutritional security

## Introduction

Biofortification is the process of cultivating crops that are rich in micronutrients produced using current biotechnology, agronomical techniques and conventional plant breeding techniques. Biofortification aids in reducing malnutrition among people. Biofortified vegetables are more resistant to biotic and abiotic stresses and generally provide higher yields compared to unfortified varieties. The objectives of biofortifying vegetables are to improve nutritional status and the quality of the produce. 800 million people worldwide suffer from malnutrition and almost 98 % people live in developing countries. Globally, approximately 30 % of people suffer from micronutrient deficiencies in iodine (30 %), zinc (60 %), iron (60 %) and selenium (15 %). Micronutrients are essential for human nutrition, disease prevention and treatment and the enhancement of both physical and mental well-being (1). Furthermore, an additional 2 billion individuals worldwide suffer from a different kind of hunger called hidden hunger, which is brought on by inadequate daily dietary intake of vital micronutrients. Nutritional supplementation, dietary diversification and the inclusion of nutraceutical vegetables through biofortification are viable options.

Vegetables, which are either annual or perennial horticulture crops, are consumed raw or cooked. They are rich in nutrients, vitamins, fibre and antioxidants and play a key role in preventing diseases such as stroke, cardiovascular disorder and certain cancers. They also aid, digestion, weight management, blood pressure regulation and bone health. Biofortified vegetables contain many essential vitamins and micronutrients, which help minimise hidden hunger by enhancing the supply of vitamins and

minerals (2). The fight against malnutrition and hunger is a major issue faced by emerging nations (3). Consumption of fruits and vegetables has been reducing the risk of cancer and cardiovascular disease (4). Biofortification of vegetables will improve human health and reduce the risk of diseases. This review gives detailed information about new techniques for biofortification of vegetables.

## Importance of Different Nutrients on Human Health

Nutrients are fundamental for sustaining human life and health, with each playing a unique and critical role, macronutrients such as proteins build and repair tissues, carbohydrates provide essential energy and fats support cell function and vitamin absorption (5), while micronutrients such as vitamins and minerals act as cofactors in biochemical processes improving bone strength (calcium, vitamin D) and oxygen transport (iron) to immune defence (zinc, vitamin C), vision (vitamin A) and DNA synthesis (folate) (6). Deficiencies in these essential nutrients remain a leading cause of global morbidity, contributing to conditions like anaemia, stunting and neural tube defects. It underscores the critical need for nutritious diets and interventions like biofortification to address hidden hunger. The importance and role of micro and macronutrients are discussed further.

Protein is composed of amino acids, required for tissue growth and its deficiency causes. Mental development, abnormal bodily functions and can lead to death. Due to a deficiency of protein, humans suffer from disorders called kwashiorkor and marasmus. Lysine is a building block in the production of proteins and is necessary for health and growth. Lysine is also a key component in the synthesis of carnitine, a nutrient that helps

decrease cholesterol and converts fatty acids into energy. Tryptophan is a precursor of serotonin and melatonin, which regulate appetite, sleep, mood and pain. Niacin, or vitamin B3, is another substance synthesised from tryptophan and is essential for DNA synthesis and energy metabolism. Iron is an essential for the brain and muscular tissues to function properly. Red blood cell haemoglobin transports oxygen from the lungs to other tissues. Anaemia is one of the most prevalent signs of iron deficiency in humans. Iron deficiency slows human growth and development. Zinc functions as a cofactor for more than 300 enzymes in human metabolism. It is required for controlling the synthesis and breakdown of proteins, lipids, carbohydrates and nucleic acids. A zinc deficiency causes growth retardation, appetite loss, weakened immunity and heightened infection susceptibility. Calcium is a crucial component needed to create strong, healthy teeth and bones and it is essential for both cardiovascular and muscle function. Osteoporosis, which results from a calcium deficiency, makes bones fragile (7). Vitamin C is necessary for metabolism and tissue regeneration, including cartilage, teeth, skin and bones. It facilitates the gastrointestinal tracts' absorption of iron. Deficiency of vitamin C in the human body leads to scurvy, which is characterised by bleeding gums, bruises and poor wound healing in the teeth, as well as joint and muscular pain (8). Both micro and macro nutrients play a major role in the human body's metabolism and a small deficiency in any nutrient leads to cause a disorder. So, there is scope to improve the nutrient content of the vegetable by biofortification. Biofortified vegetables are detailed in Table 1.

### Biofortification Strategies for Vegetables

#### Agronomic practices for improving nutrient uptake and bioavailability

Agronomic biofortification is an efficient and practical method to improve a crops' nutritional quality (22). Agronomic biofortification generally employs techniques for mobilising nutrients from source to sink (consumable portions of a plant), solubilising mineral elements and applying fertiliser. As microminerals, potassium (K), phosphorus (P) and nitrogen (N) help achieve greater yield targets. The successful implementation of mineral fertilisers in agronomic biofortification has been demonstrated using zinc (Zn) in Turkey (23) and selenium (Se) in Finland (24). Agronomic biofortification differs from genetic biofortification in that it uses crop-neutral fertiliser formulations and application methods. A major advantage of agronomic biofortification over genetic biofortification is that it

relies on crop-neutral fertiliser formulations and application methods. For example, field peas can be supplemented with Zn through foliar application, either by themselves or in conjunction with soil application (25). Applying foliar fertiliser to beans increased the content of Zn (26). In common beans, Cu, Mn and Zn can be increased by using both synthetic and organic fertilisers (27). Moreover, foliar application of Zn increased Zn concentration in potato flesh and skin. Based on the results of the trials, it was determined that zinc oxide (ZnO) and zinc sulphate (ZnSO<sub>4</sub>) were more effective than zinc nitrate (ZnNO<sub>3</sub>) at increasing zinc concentration while preserving yields (28). Application of selenite and seleniate improved selenium in potatoes (29). Tomato crops have demonstrated the biofortification of iron and iodine when fed with their corresponding fertilisers (30). Foliar and soil incorporation of Zn to biofortify broccoli (31). The application of fertiliser improves the nutrient content of the vegetable crops.

#### Conventional breeding techniques for nutrient enhancement

Conventional breeding is the most widely recognised approach to biofortification. It provides an affordable, long-term substitute for agronomic and transgenic approaches. For conventional breeding to be practical, there must be adequate genotypic variation in the desired characteristic. The mutation can be used in breeding programs to increase the amounts of vitamins and minerals in crops. To create plants with desired nutrient and agronomic qualities, conventional plant breeding crosses recipient lines with desirable agronomic traits with parent lines with high levels of nutrients over several generations. Natural variety is the foundation of conventional breeding, which may be a better option than genetic engineering experiments. Several reports suggested that new breeding lines have a two-fold rise in the folate content of crops, including potatoes and tomatoes (32). The inheritance of the genes causing the specific phenotype and advantageous quantitative trait loci (QTL) from sexually compatible paternal lines is the foundation of conventional breeding for increased nutrition. Therefore, the limitations of biofortification through breeding include the need to locate a natural variety of desired features and the time-consuming procedure of collecting vegetable germplasm (33). Marker-assisted breeding and genome-wide association are important techniques for biofortification in recent advancements. Breeders were able to determine the QTLs that contributed to the 3.22 and 5.76-fold increases in  $\beta$ -carotene and  $\alpha$ -tocopherol,

**Table 1.** List of biofortified vegetable crop varieties

Vegetable crop	Biofortified variety	Biofortification method	References
Tomato	Pusa Rohini	Conventional breeding for higher lycopene content.	(9)
Potato	Kufri Neelkanth	Conventional breeding for high anthocyanins and iron content.	(10)
Cowpea	Pant Lobia-1, Pant Lobia-2	Conventional breeding for high iron and zinc content.	(11)
Brinjal	Punjab Sadabahar	Conventional breeding for high antioxidants and iron content.	(12)
Radish	Kashi Lohith	Conventional breeding for high anthocyanins and iron.	(13)
Carrot	Ooty-1, Kashi Arun	Conventional breeding for high beta-carotene (vitamin A precursor) content.	(14, 15)
Cauliflower	Pusa Beta Kesari 1	Conventional breeding for high beta-carotene (Vitamin A precursor) in the curd.	(16)
Bitter gourd	Pusa Hybrid 4	Conventional breeding for high iron and beta-carotene content.	(17)
Sweet potato	Bhu Krishna, Bhu Sona	Conventional breeding for high beta-carotene (Vitamin A precursor) content.	(18)
Okra	Kashi Lalima	Conventional breeding for high anthocyanins and iron.	(19)
Watermelon	Arka Jyoti, Durgapur Lal	Conventional breeding for high lycopene content.	(20)
Pumpkin	Arka Chandan	Conventional breeding for high beta-carotene (Vitamin A precursor) content.	(21)

respectively (34).

Biofortification initiatives are replacing the low-provitamin sweet potato cultivars with orange-coloured, high-provitamin cultivars. Potato varieties have 32  $\mu\text{g/g}$  provitamin, but biofortified varieties have 100  $\mu\text{g/g}$  of provitamin content (35). Beans are termed as poor mans' meat because they are a rich source of protein and contain a wealth of vitamins and minerals, including zinc and iron. Common bean mineral biofortification has several advantages and requirements that span from trait breeding phases like inheritance, germplasm screening, physiological, or bioavailability studies to the development of new biofortified varieties as a result (36). In addition, iron and zinc are only found in trace amounts in cassava and improved the beta-carotene through biofortification programs (37). Among 632 accessions from the 5500 accessions in the CIAT germplasm collection were analysed, for higher  $\beta$ -carotene concentration, germplasm with 20  $\mu\text{g/g}$ , indicating a greater genetic variability that could enable the successful biofortification of cassava and satisfy adults' daily retinol requirements (38). The iron (Fe) content of ordinary beans is approximately 50 parts per million (ppm), while the aim for biofortification of beans by traditional breeding is 94 ppm. Around 60 % of the estimated average requirement (EAR) is met by biofortified beans. Conventional breeding techniques are a better approach for the selection of biofortification germplasms. The process of biofortification through conventional breeding techniques is represented in Fig. 1.

#### Genetic engineering approaches to fortify vegetables with essential micronutrients

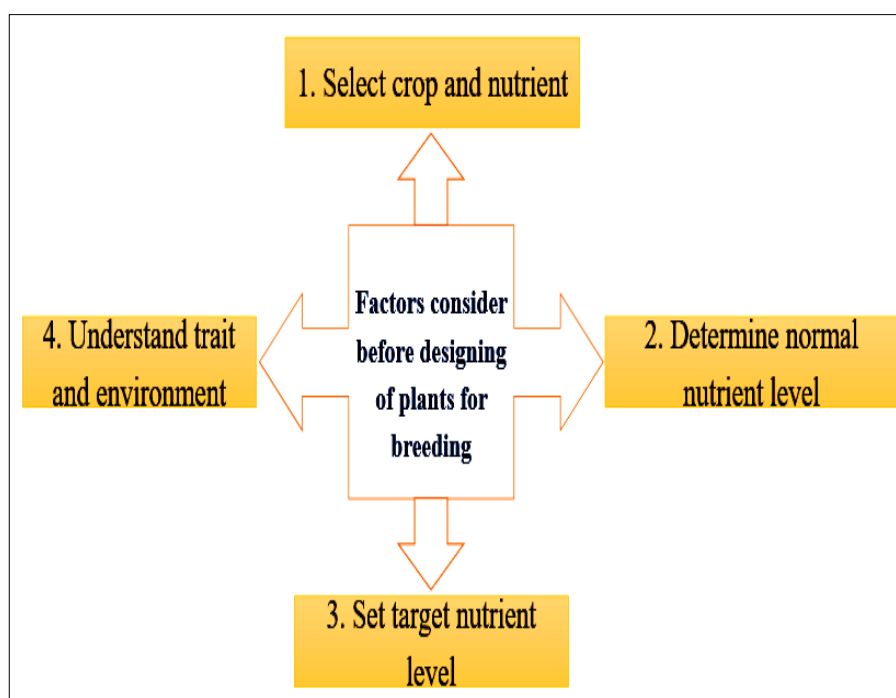
Around the world, biotechnology is being utilised as an efficient tool for biofortification over the conventional breeding method (39). Genetic engineering (GE) is a technology for producing future food and energy crops. The release of the 'FlavrSav' tomato in 1996 marked a breakthrough in genetic engineering. Transgenic crops, also known as genetically modified (GM) crops, give plant breeders the ability to add advantageous genes to cultivars that were previously unattainable, increasing their worth and offering unique

chances to fight infections, insects and other pathogens, as well as improving nutritional quality. Genetic engineering is a feasible method for boosting micronutrient bio-accessibility and enrichment in edible crop tissues when the crop is unsuitable for traditional plant breeding (because it lacks sexuality) or when there is not enough variation across genotypes for the required character or trait within the species. Breeders of vegetables are urged to apply genetic engineering to introduce desirable transgenes into new cultivars, boosting their market value.

Use of a fruit-specific promoter will improve the conversion of  $\beta$ -carotene from lycopene, which is typically present in high concentrations in tomato fruit, by altering the  $\beta$ -lyc gene from *Arabidopsis* (40). Additionally, *BIO101*, *Macia* and *NERICA* are bean lines that are rich in iron and zinc developed through conventional breeding and marker-assisted selection. Moreover, potato, which produces provitamin A ( $\beta$ -carotene) from geranylgeranyl diphosphate via the MEP pathway, has integrated the bacterial origin pathway (41). Using a tuber-specific or constitutive promoter, three genes from *Erwinia* encoding phytoene synthase (CrtB), phytoene desaturase (CrtI) and lycopene beta-cyclase (CrtY) were expressed in potatoes. Transgenic potatoes were shown to have increased levels of  $\beta$ -carotene by 20-fold and carotenoid content by 3600-fold (42).

#### Transgenic breeding in staple vegetable crops

**Tomato:** Strong antioxidant lycopene may protect against epithelial malignancies and enhance human health. Thus, there is a great deal of interest in genetically modifying tomato fruit to increase its carotene content and enhance the crops' nutritional value. The Psy-1 enzyme catalyses the first committed step of the carotenoid biosynthesis pathway, which is the conversion of GGPP (geranylgeranyl diphosphate) into phytoene. The Psy-1 gene was constitutively expressed in tomatoes to increase the fruits' carotenoid content (43). The research indicates that to increase the anthocyanin content of fruits grown commercially, specifically Arka Vikas, by expressing two transcription factors, Ros1 and Del, specifically in the fruit by *Agrobacterium*-mediated transformation.



**Fig. 1.** Important characteristics and factors before designing breeding plans.

With an average anthocyanin level of 0.1 mg g<sup>-1</sup> fresh weight, the transgenic fruit outperformed the control fruits by a factor of 70–100 (44). Tomato transformed with *epetunia chi-a* gene, which codes for chalcone isomerase. Fruit peel flavanols in the resulting transgenic tomato lines increased up to 78 times, primarily because of rutin buildup (45). Chalcone isomerase, a single biosynthetic enzyme, was expressed ectopically to increase fruit flavanol content by 78-fold (46). Utilising a yeast *S*-adenosylmethionine decarboxylase gene (*ySAMdc*; *Spe2*) coupled with a ripening-inducible E8 promoter, researchers were able to raise the amounts of the polyamines spermine and spermidine in tomato fruit during development. Longer vine life, improved fruit juice consistency and more lycopene were the results of this (47).

**Potato:** Approximately 70 % of the dry matter in potato tubers is made up of starch, which is the main carbohydrate storage component. When the bacterial *ADP-glucose pyrophosphorylase* gene (*glgC16*) was introduced into a potato, the resultant transgenic plant had a high tuber starch content (48). Protein-rich potatoes that express the seed protein gene *AmAl* (Amaranth Albumin 1) from *Amaranthus hypochondriacus* can express a non-allergenic seed albumin gene, increasing the nutritional value of the potato. Biochemically speaking, *AmAl* expression in both transgenic groups results in a significant rise in every important amino acid, especially tyrosine, lysine and sulfur-based amino acids, in addition to a commensurate increase in total protein content (49).

**Cole crops:** The successful cloning of the *Or* gene in cauliflower demonstrates that carotenoid accumulation is significantly impacted by the modulation of chromoplast production, offering an efficient metabolic sink for carotenoid sequestration and deposition. The use of the *Or* gene to increase the carotenoid content in transgenic potatoes provides an alternative, unique method to supplement effects based on the expression of a carotenogenic gene for enhancing carotenoid levels in food crops (36). Due to its high antioxidant content and abundance of anthocyanins, red cabbage may reduce the incidence of cancer, cognitive disorders and cardiovascular diseases (50).

**Root crops:** Increased calcium levels in genetically modified carrots may improve calcium absorption and lower the prevalence of calcium shortages like osteoporosis. Carrots that underwent genetic modification displayed elevated expression of the plant Ca transporter *SCAX1* (51). High-level fructan accumulation was achieved in sugar beet for improving carbohydrate storage quality (52). Black carrots (*Daucus carota* subsp. *sativus*) are becoming more popular among consumers due to their high antioxidant, anthocyanin and phytochemical content (53).

### Genome Editing for Bio-fortification in Vegetable Crops

Endonuclease is the basis of genome editing technologies, which

cleave DNA sequences at precise, recognized sites (54). One of the most innovative, effective, widely used and efficient methods for biofortification of vegetable crops is the use of genome editing technologies like Zinc Finger Nuclease (ZFN-1, ZFN-2 and ZFN-3), Transcriptional Activator Like Effector Nuclease (TALEN) and Clustered Regularly Interspersed Short Palindromic Repeats (CRISPR/Cas-9). The CRISPR/Cas-9 system, which includes the Cas-9 nuclease and single guide RNA to direct Cas-9 at a specific recognition site and create a double-strand break to cleave DNA sequence, is widely used in many vegetable crops for biofortification. This system also creates a rapid repair mechanism to ligate DNA. In 2014, the "AGRONAUTE-7" (*SIAGO-7*) gene, which is crucial for the growth of leaves, was the target of the first vegetable genome editing technique using CRISPR/Cas-9 (55). Tomatoes are the most fascinating crop when it comes to biofortification. For example, genome editing has been used to create anthocyanin-enriched tomatoes by specifically modifying the anthocyanin 1 (*ANT1*) gene (56). Genome editing has been used to create carotenoid bio-fortification by mutating genes involved in carotenoid biosynthesis, such as phytoene desaturase (*SIPDS*), phytochrome interacting factor (*SIPIF4*) and phytoene synthase (*PSY1*) (57). Granule-bound starch synthase (*GBSS*) gene mutations are made using CRISPR/Cas9 editing technology to make starch-free potato tubers (58). The transgenomic vegetable, targeted genes and method are detailed in Table 2.

### Health Impacts of Biofortified Vegetable Crops

Biofortification is an important strategy to combat the global issue of vitamin deficiency. People across the world can eat more vital nutrients by including biofortified crops in their daily diets, which will improve their general health. To address hidden hunger brought on by micronutrient deficiencies, biofortification is recognized as a viable and economical strategy. Increasing the intake of biofortified crops can lead to better health outcomes, especially for susceptible groups like expectant mothers and children. Biofortified crops rich in vitamin A help to prevent blindness and maintain good vision, especially in populations where deficiency of vitamin A is common. The prevention and treatment of micronutrient deficiencies through bio enrichment can help lower the expense of healthcare connected to the treatment of nutritional deficiencies and related illnesses. By preventing diseases linked to insufficient nutrient intake, biofortification addresses nutritional inadequacies and promotes health security. Global human health may be greatly impacted by biofortification, particularly in developing nations. Eating a varied diet is simpler and more reasonably priced in industrialized nations, where vitamin supplements are also available. Another generally accepted component of the strategy to combat hidden hunger is

**Table 2.** Status of genome editing for biofortification in vegetable crops

Crops	Traits	Targeted genes	Method	References
Tomato	Anthocyanin	ANT-1	CRISPR/Cas-9	(59)
Tomato	Carotenoid	SIPDS	CRISPR/Cas-9	(60)
Tomato	Carotenoid	SIPIF4	CRISPR/Cas-9	(61)
Tomato	Fruit colour	PSY	CRISPR/Cas-9	(62)
Tomato	Pink tomato fruit colour	SIMYB12	CRISPR/Cas-9	(63)
Tomato	Fruit ripening	Rin	CRISPR/Cas-9	(64)
Watermelon	Carotenoid		CRISPR/Cas-9	(65)
Tomato	Parthenocarpy	SIIAA9, SIAGL6	CRISPR/Cas-9	(66)
Potato	Starch quality	GBSS	-	(67)
Potato	Starch biosynthesis	StALSI, StALS2	-	(68)
Watermelon	Carotenoid biosynthesis	Phytoene desaturase (CIPDS)	CRISPR/Cas-9	(69)
Carrot	Anthocyanin biosynthesis	F3H		(70)

biofortification. When populations have enough food in general but not enough nutrients in it for people to stay healthy, hidden hunger arises (71). The amount and quality of the food supply must rise in tandem with global population growth. In the future, biofortification will play a bigger role in helping people stick to healthier diets. The real effectiveness of biofortification will still be determined by consumer opinions, though.

### Future Directions and Research Priorities

The focus of current research is on maintaining a healthy lifestyle through the consumption of nutraceutical supplements and a diet richer in fruits and vegetables. Thus, by putting in place a biofortification program, there is potential to enhance vitamins and micronutrients in vegetables on a large scale. This will assist poor nations in overcoming the problem of malnutrition, called hidden hunger. On the other hand, a lot of breeding initiatives concentrate on increasing productivity and production, as well as abiotic stress tolerance and biotic stress resistance. However, improving the quality of vegetables will assist those poor nations in saving money that could be used to combat the condition, which is brought on by a lack of vitamins and micronutrients. The cooperation of plant breeders, plant physiologists, biochemists, molecular biologists and other nutrition specialists is needed to achieve the biofortification of vegetables. However, before being released, the genetically modified crop might need regulatory permission from several organisations. Advances in genome editing and genetics, such as CRISPR/Cas9 and TALENS, will enable this biofortification initiative to proceed more quickly.

### Conclusion

Biofortification can help people get access to micronutrients by complementing other interventions, but it cannot totally prevent or control deficiencies of certain mineral elements. To be successful, a biofortification program must be carefully thought out. This involves studying nutrition and dietary habits, developing and validating a sustainable biofortification process and assessing health impacts. The production of vegetable crops rich in minerals deserves attention in the present and the future. Given the high rate of genetic turnover in the horticultural industry and the length of time needed for genetic improvement initiatives, agronomic biofortification, even though it involves expensive experimental measures, is a productive way to enhance leafy and fruiting vegetables.

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### Authors' contributions

TAS conceptualised the topic, collected the literature and wrote the manuscript. HS supervised and edited the manuscript. TKV collected the literature and wrote the manuscript. All authors read and approved the final version.

### Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interest to declare.

**Ethical issues:** None

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