



Advances and Prospects in Fruit Biofortification for Nutritional Security

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Abstract

Micronutrient malnutrition commonly referred to as “hidden hunger” which continues to affect more than two billion people worldwide, particularly in low and middle-income countries. Traditional interventions such as supplementation and industrial food fortification have had limited reach and sustainability. Biofortification, the process of increasing the nutrient content of crops through agronomy, conventional breeding, or modern biotechnology, offers a cost-effective and sustainable solution. While staple crops have been the primary focus, fruit biofortification is emerging as a powerful strategy due to fruits’ inherent richness in vitamins, antioxidants, and phytochemicals, and their widespread raw consumption. This review synthesizes the latest advances in biofortification including agronomic practices, marker-assisted selection, genomic tools, and genome editing (e.g., CRISPR/Cas9) of different fruit crops. Successful case studies involving provitamin A-enriched bananas in Uganda, vitamin C-rich apples in China, carotenoid-rich citrus fruits in Brazil and Spain, anthocyanin-enhanced berries in the USA and Chile, and iron-fortified mangoes in India demonstrate the potential of biofortified fruits to improve human nutrition and food security. Challenges related to regulation, public acceptance, and technical capacity are critically analyzed. The paper concludes that fruit biofortification, if mainstreamed into agriculture and nutrition policies, could play a transformative role in global food and nutrition security. With evolving biotechnology and supportive policies, fruit biofortification is poised to bridge the gap between agricultural innovation and public health nutrition.

Keywords: Agronomic practices, Conventional breeding, CRISPR/Cas9, Genetic engineering, Micronutrient deficiency

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Introduction

Micronutrient malnutrition commonly known as “hidden hunger” is a persistent global health challenge, affecting over two billion people worldwide, particularly in low- and middle-income countries (Rai et al., 2024; WHO, 2021). This condition arises from insufficient intake of essential micronutrients such as iron, vitamin A, zinc, and iodine, which are required in minute quantities yet play crucial roles in human growth, immune defense, cognitive function, and general well-being (Bailey et al., 2015; Avnee et al., 2023). The burden is especially heavy among vulnerable populations, especially children and pregnant women, are disproportionately affected, with the highest burden observed in regions such as Southeast Asia and sub-Saharan Africa (Harika et al., 2017; Chitekwe et al., 2021). Although interventions such as micronutrient supplementation, food fortification, and dietary diversification, micronutrient deficiencies remain widespread due to infrastructural, economic, and behavioral barriers (Rawat et al., 2013). While industrial-scale food fortification programs have shown success in high-income countries but often fall short in developing contexts due to limited processing capabilities and distribution challenges (Bois & Saltzman, 2017). This has prompted the search for more sustainable and context-appropriate solutions.

Biofortification has emerged as a promising intervention for addressing micronutrient deficiencies in resource-poor settings (Blancquaert et al., 2016). While significant attention has been given to staple crops-such as vitamin A-rich golden rice, zinc-enhanced wheat, and orange-fleshed sweet potatoes-there is growing recognition of the untapped potential of fruit biofortification (Jha & Warkentin, 2020; Sen et al., 2024). Fruits are inherently rich in vitamins, antioxidants, and phytochemicals, making them ideal candidates for nutrient enhancement. Moreover, their frequent consumption in raw form reduces nutrient losses associated with cooking or processing, thereby increasing the effectiveness of biofortification (Garg et al., 2018). Beyond enhancing nutritional quality, biofortified fruits contribute to dietary diversity, promote healthier eating habits, and align with sustainable agricultural practices.

In light of these benefits, integrating fruit biofortification into national nutrition and agricultural strategies offers a holistic pathway to combat hidden hunger. This review explores the global burden of micronutrient malnutrition, evaluates the mechanisms and outcomes of fruit biofortification strategies-including agronomic approaches, breeding, and genetic modification and assesses case studies, challenges, and future prospects. By doing so, it highlights the potential of fruit biofortification as a scalable, nutrition-sensitive innovation in addressing micronutrient deficiencies and strengthening food systems worldwide.

Global Burden of Micronutrient Malnutrition

Micronutrient malnutrition remains a persistent public health challenge, especially in low- and middle-income countries. Deficiencies of essential nutrients such as iron, vitamin A, zinc, and folate adversely affect growth, cognitive development, immune function, and overall health, especially among children and pregnant women (WHO, 2021).

Iron deficiency anemia is the most common nutritional disorder worldwide, affecting nearly 30% of the global population and reducing cognitive performance, productivity, and educational outcomes (Pasricha et al., 2021). Vitamin A deficiency, which affects over 190 million preschool-aged children worldwide, is a leading cause of preventable childhood blindness and significantly increases the risk of infectious diseases (UNICEF, 2020; Stevens et al., 2015). Zinc deficiency is another widespread concern, contributing to compromised immune function, increased morbidity, and heightened child mortality rates (Wessells & Brown, 2012). Folate deficiency, especially during early pregnancy, is strongly associated with neural tube defects in newborns, highlighting its importance in maternal health (Crider et al., 2014).

Beyond its health impacts, micronutrient malnutrition imposes significant economic costs through lost productivity and increased healthcare expenditures (FAO, 2019). Although supplementation and food fortification programs have improved nutritional status in many regions, challenges related to coverage and sustainability persist. Consequently, biofortification has emerged as a promising long-term strategy, enhancing the micronutrient content of staple crops to provide sustainable and accessible nutrition for vulnerable populations.

Fruit Biofortification: A Sustainable Strategy to Combat Micronutrient Deficiencies

Fruit biofortification is an emerging strategy that employs scientific approaches to enrich the micronutrient content of fruits, aiming to improve nutritional intake without requiring changes in dietary habits. By boosting essential nutrients, biofortified fruits can serve as effective tools for addressing micronutrient malnutrition. Unlike cereals and legumes, fruit biofortification has received less attention despite its nutritional importance. Nevertheless, the favorable perception of fruits and their widespread consumption make them promising targets for long-term, sustainable nutritional improvement.

Approaches to Fruit Biofortification

Three principal strategies are used in fruit biofortification: agronomic practices, conventional breeding, and genetic engineering. Each method varies in terms of cost, time requirements, societal acceptance, and types of nutrients enhanced (Table 1).

Table 1. Comparative Analysis of Biofortification Strategies

Strategy	Timeframe	Cost	Acceptance	Nutrients Enhanced
Agronomic	1–2 seasons	Low-Medium	High	Zn, Fe, Se, I
Conventional Breeding	5–15 years	Medium	High	Provitamin A, Fe, Zn
Genetic Engineering	3–8 years	High	Low-Medium*	All (customizable)

*Varies by region; higher acceptance in North America, lower in Europe.

Agronomic Biofortification

Agronomic biofortification improves the nutritional quality of fruits through the application of micronutrient fertilizers to soil or foliage, enhancing the uptake of nutrients such as zinc, iron, and selenium. Successful examples include zinc fertilization in banana and iron foliar sprays in apple and grape, which significantly increased fruit micronutrient concentrations (Aciksoz et al., 2011). Prasad et al. (2014) reported enhanced zinc uptake in citrus and banana using zinc sulfate. Zinc sulfate application has also enhanced zinc accumulation in citrus and banana crops (Prasad et al., 2014). Additionally, nutrient-enriched culture media, targeted root-zone fertilization, and the use of plant growth regulators can further improve nutrient assimilation (Sharma et al., 2022). Agronomic biofortification is a cost-effective, non-GMO, and farmer-friendly approach with minimal regulatory barriers. However, its effectiveness depends on soil characteristics, often requires repeated applications, and may have limited impact on some micronutrients.

Conventional Breeding

Conventional breeding is a widely used strategy for fruit biofortification that exploits natural genetic variation to enhance micronutrient content. By selecting and crossing nutrient-rich parental lines, breeders have developed fruit varieties with increased levels of vitamin C, carotenoids, and flavonoids in crops such as banana, apple, citrus, and papaya (Bouis & Saltzman, 2017; Lobato-Gómez et al., 2021). This approach is compatible with organic agriculture and contributes to the conservation of genetic diversity through the use of landraces and wild relatives (Perić *et al.*, 2024).

Despite its advantages, conventional breeding is a slow process, often requiring 5–15 years to develop improved varieties, and is constrained by limited genetic diversity and trait trade-offs (Biselli et al., 2022). To enhance efficiency, marker-assisted selection (MAS) has been incorporated into breeding programs, enabling rapid identification of desirable genes and quantitative trait loci (QTLs) (Collard et al., 2008). MAS has successfully improved fruit quality, disease resistance, and micronutrient content in crops such as apple (Kumar et al., 2024). The integration of conventional breeding with modern genomic tools offers significant potential for accelerating the development of nutrient-rich fruit varieties and addressing global micronutrient deficiencies sustainably (Sen et al., 2024).

Genetic Engineering and Biotechnology

Genetic engineering and biotechnology are powerful tools for biofortification, enabling the identification and manipulation of genes controlling micronutrient accumulation in edible plant tissues. Molecular techniques such as QTL mapping and marker-assisted selection (MAS) accelerate the development of nutrient-rich fruit varieties by facilitating the selection of desirable traits (Yu *et al.*, 2021). Advanced approaches, including intragenesis and cisgenesis, enhance nutritional quality and stress tolerance while addressing some biosafety concerns associated with conventional transgenic methods (Schaart *et al.*, 2016).

The transport of nutrients from source to sink organs like fruits is mediated by the phloem and xylem systems, which are regulated by specific genes and transport proteins (Reid *et al.*, 2011). Biological agents like plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal (AM) fungi enhance micronutrient uptake in fruits. PGPR improve nutrient availability by solubilizing minerals, fixing nitrogen, and releasing siderophores and phytohormones (Compant *et al.*, 2019). AM fungi form root symbioses, extending hyphal networks that boost uptake of phosphorus, zinc, and copper while improving soil structure and stress resistance (Schweiger *et al.*, 2020). These agents offer eco-friendly, cost-effective solutions suitable for organic farming. Although their success depends on plant and soil factors, they remain a promising strategy for sustainable fruit biofortification and improved nutritional quality.

Modern biotechnological interventions have successfully increased micronutrient levels in fruits, including provitamin A-enriched bananas and folate-rich strawberries and tomatoes (Dale *et al.*, 2017; Paul *et al.*, 2017; Blancquaert *et al.*, 2017). Genome-editing tools such as CRISPR-Cas9 provide precise and efficient modification of nutrient biosynthesis pathways, enabling rapid development of biofortified crops.

Biological approaches also contribute to fruit biofortification. Plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal (AM) fungi enhance nutrient uptake, improve soil health, and increase the availability of essential minerals such as phosphorus, zinc, and copper (Compant *et al.*, 2019; Schweiger *et al.*, 2020). These eco-friendly technologies are particularly suitable for sustainable and organic production systems.

Despite their advantages, including targeted nutrient enhancement and faster breeding cycles, biotechnological approaches face challenges related to regulatory restrictions, public acceptance of genetically modified organisms (GMOs), high development costs, and intellectual property concerns, which may limit their widespread adoption.

Success Stories of Fruit Biofortification

Fruit biofortification has demonstrated significant potential in addressing micronutrient malnutrition through various approaches. Some significant case studies implementing fruit biofortification successfully are highlighted below.

Golden Banana Initiative in Africa

A notable success in fruit biofortification is the development of provitamin A-enriched bananas in Uganda by the National Agricultural Research Organization (NARO) and Queensland University of Technology (Fig. 1). The project aims to combat vitamin A deficiency through bananas with enhanced β -carotene content. Study has shown that early activation of carotenoid biosynthesis enzymes and prolonged fruit maturation are key factors in increasing provitamin-A accumulation (Paul et al., 2017). To enhance β -carotene content, genetic engineering techniques were employed, incorporating the phytoene synthase gene from maize (Dale et al., 2017).

Cultivars such as ‘Nakitembe’ can provide up to 50% of the daily vitamin A requirement for children (Mbabazi et al., 2019). However, adoption has been limited by stringent GMO regulations in several African countries. To address this challenge, public awareness campaigns have been launched to improve understanding and acceptance of biofortified crops, highlighting the importance of supportive regulations and community engagement for successful implementation.



Fig. 1. Characteristic phenotypes observed transgenic Cavendish banana lines (g-h) compared to wild-types (a-f)

Apple Biofortification in China

China has made notable advancements in apple biofortification by combining conventional breeding with molecular tools such as genomics and marker-assisted selection (MAS). Key genes involved in vitamin C biosynthesis, including MdGGP and MdDHAR, have been identified to develop high-ascorbate apple cultivars (Wang *et al.*, 2019). Agronomic practices, such as foliar application of zinc and selenium and optimized fertilization, have further enhanced the mineral content and antioxidant capacity of apples (Zhang *et al.*, 2021). These integrated strategies have improved the nutritional quality of apples and hold promise for enhancing food security and public health.

Citrus Biofortification in Spain and Brazil

Spain and Brazil have achieved significant progress in citrus biofortification through breeding, genetic, and metabolic engineering approaches (Table 2). In Spain, a high-vitamin C mandarin hybrid was developed through conventional breeding (Rodríguez *et al.*, 2020), while CRISPR-Cas9 technology has been used to enhance vitamin C biosynthesis in lemons (Perez *et al.*, 2022). In Brazil, high-carotenoid orange cultivars such as ‘Pera Rio’ and ‘Valencia’ have been selected (Silva *et al.*, 2021), and QTLs associated with elevated folate content have been identified (Oliveira *et al.*, 2021). Metabolic engineering has increased folate levels in citrus fruits up to tenfold, supporting public health initiatives aimed at improving maternal nutrition (Strobbe & Van Der Straeten, 2018)

Table 2. Biofortified varieties of citrus fruits

Citrus cultivar	Biofortification traits	Reference
Ruby blood red citrus	Deep red colour due to anthocyanins	Butelli <i>et al.</i> (2012).
Malta (Maltase) citrus	Sweet taste and high vitamin C content	Medina-Remon <i>et al.</i> (2011)
Star ruby grapefruit	Pink-red flesh rich in lycopene	Strother and Lila (2016)
Rio red grapefruit	Red-fleshed with high lycopene content	Dorado <i>et al.</i> (2021)

Despite existing challenges, sustained innovation and supportive policy frameworks have the potential to significantly improve the nutritional quality of citrus fruits, thereby advancing global health and contributing to food security.

Berries Biofortification in USA/Chile

The USA and Chile have made notable advances in blueberry biofortification to enhance antioxidant intake and reduce oxidative stress-related diseases. Conventional breeding combined with marker-assisted selection (MAS) has produced high-

anthocyanin cultivars containing 30–50% more anthocyanins than conventional varieties (Bassil et al., 2022). These 'superberries' have gained popularity in the functional food market due to their proven cardiovascular and cognitive health benefits (Kalt *et al.*, 2020). Growing consumer awareness of the role of nutrition in disease prevention has further increased demand for these nutrient-enriched berries (Granato et al., 2023)

Mangoes Biofortification in India

In India, mango biofortification has emerged as a promising strategy to address iron-deficiency anemia, particularly among women. Agronomic biofortification using iron-EDTA fertilizers has increased iron content in mango pulp from 0.5 to 2.8 mg/100 g (Singh et al., 2020). Combined with mango's naturally high vitamin C content, which enhances non-heme iron absorption, this approach provides significant nutritional benefits (Saunders et al., 2022). Field trials have demonstrated that biofortified mangoes maintain improved nutrient levels and acceptable fruit quality after harvest (Patil et al., 2021), making them a practical and scalable solution for combating micronutrient malnutrition in South Asia.

Challenges and Limitations

Despite its potential, fruit biofortification faces several challenges. Stringent and evolving GMO regulations often delay commercialization and adoption of biofortified fruits. Limited genomic resources and breeding tools for many fruit species also constrain research and development. In addition, high investment costs and long breeding cycles make biofortification a resource-intensive process. Consumer skepticism and misinformation regarding biotechnology and genetically modified crops further hinder public acceptance and market penetration

Future Prospects of Fruit Biofortification

Fruit biofortification presents a promising frontier in the global effort to reduce micronutrient deficiencies through sustainable agricultural practices. Future progress will rely on integrating conventional breeding with advanced technologies such as marker-assisted selection (MAS), genomic selection, and genome editing. MAS and whole-genome sequencing will accelerate the identification and incorporation of nutrient-enhancing traits, while CRISPR/Cas9 will enable precise genetic modifications for improving nutrient content, shelf life, flavor, and stress tolerance (Mathiazhagan et al., 2021; Roy & Sandhu, 2024). Recent successes in β -carotene-enriched bananas and nutritionally enhanced tomatoes highlight the potential of these approaches (Tripathi et al., 2024). As research advances and regulatory frameworks become more supportive, biofortified fruits are expected to contribute significantly to reducing hidden hunger and strengthening global food and nutritional security (Chen et al., 2024; Sen et al., 2024).

Expected Impacts on Human Nutrition

Fruit biofortification can substantially improve human health by reducing deficiencies of iron, vitamin A, folate, and zinc. Vulnerable groups, including children, pregnant women, and low-income populations, are likely to benefit through enhanced immunity, cognitive development, and maternal health. Biofortified fruits also promote dietary diversity and overall nutritional quality while providing a sustainable, food-based alternative to supplementation programs. In the long term, improved nutrition can increase productivity, reduce healthcare costs, enhance educational outcomes, and strengthen food system resilience, making fruit biofortification an important strategy for achieving global nutrition goals.

Conclusions and way forward

Fruit biofortification represents a transformative frontier in addressing global micronutrient malnutrition through sustainable agriculture. With the integration of agronomic practices, conventional breeding, and cutting-edge biotechnological tools such as marker-assisted selection, genomic prediction, and CRISPR/Cas9 gene editing, significant strides have been made in enhancing the nutritional profile of fruits. Successful implementation across diverse geographies for instance, β -carotene-rich bananas in Uganda, iron-fortified mangoes in India, and high-vitamin C apples in China demonstrates both the feasibility and global relevance of fruit biofortification initiatives.

Despite progress, challenges related to regulatory constraints, high development costs, and limited consumer awareness continue to hinder large-scale adoption. Addressing these barriers through supportive policies, transparent regulatory frameworks, public engagement, and international collaboration will be essential. Fruit biofortification not only addresses nutrient gaps in vulnerable populations but also aligns with global efforts toward sustainable food systems, climate resilience, and the United Nations Sustainable Development Goals.

Future efforts should focus on integrating fruit biofortification into national nutrition and agricultural policies, strengthening research and breeding programs, promoting consumer awareness, ensuring equitable access to planting materials, and fostering partnerships among governments, research institutions, and the private sector. With continued innovation and coordinated action, fruit biofortification can evolve into a widely accepted strategy for improving diets, enhancing public health, and strengthening resilient and sustainable food systems. By pursuing these actions, fruit biofortification can transition from a scientific innovation to a scalable, socially accepted solution that enriches diets, improves health outcomes, and enhances the resilience of food systems.

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