



REVIEW ARTICLE

Micronutrient enrichment of leguminous crops through agronomic biofortification: Strategies, challenges and future directions

R Vijayapathipa¹, T Parthipan^{2*}, T Ramesh³, M Senthilkumar¹, P Boominathan¹ & A Gulshan¹

¹Agricultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

²Agricultural Research Station, Tamil Nadu Agricultural University, Thanjavur 613 501, Tamil Nadu, India

³Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Tiruchirapalli 620 009, Tamil Nadu, India

*Correspondence email - parthipan.t@tnau.ac.in

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Abstract

Hidden hunger refers to micronutrient deficiencies affecting nearly two billion people globally, especially in regions dependent on calorie-rich but nutrient-poor staple diets. Legumes, termed as the "poor man's meat" for their high protein content and low cost, are critical for enhancing nutritional security in resource-limited communities. This review emphasises agronomic biofortification as a rapid, promising and versatile strategy for enhancing essential micronutrients, particularly iron (Fe), zinc (Zn) and selenium (Se), in legume grains. It discusses different agronomic strategies such as soil and foliar fertilisation, seed priming and biological interventions. Unlike conventional breeding and genetic methods, which require longer to develop, these agronomic techniques can increase nutrient density within a single cropping cycle. It also focuses on the scope of agronomic biofortification and addresses its challenges related to nutritional bioavailability, notably the inhibitory effect of anti-nutritional factors such as phytates and discusses strategies to enhance nutrient absorption through promoter compounds. Furthermore, emerging technologies such as nanotechnology and precision agriculture are recognised as promising innovations to enhance nutrient use efficiency (NUE) and ensure environmental sustainability. Overall, agronomic biofortification provides a sustainable pathway to combat micronutrient malnutrition and this approach requires integration with genetic advancements and supportive agricultural policies for its long-term success.

Keywords: agronomic biofortification; bioavailability; hidden hunger; iron; micronutrients; selenium; zinc

Introduction

Hidden hunger, a chronic form of micronutrient malnutrition, affects two billion people worldwide (1, 2). It arises from insufficient intake and absorption of essential vitamins and minerals necessary for health and development (3). The term "hidden" refers to the fact that micronutrient deficiencies often lack immediate clinical manifestations, even though they exert significant and frequently irreversible effects on immune function, physical and cognitive development, as well as overall morbidity and mortality (2). The burden of hidden hunger is particularly prevalent in low and middle income nations, especially across sub-Saharan Africa and South Asia, where daily diets frequently consist of low-cost, calorie-rich staple crops that naturally contain limited amounts of essential micronutrients (4, 5). The economic consequences of hidden hunger are severe, with gross domestic product (GDP) losses reaching 11 % in several affected countries across Asia and Africa (6).

Among the various micronutrients, insufficient intake of iron (Fe), zinc (Zn), selenium (Se) and iodine (I) represents a critical public health concern (7, 8).

Iron deficiency is the most widespread nutritional disorder worldwide and results in iron deficiency anaemia (IDA), which

accounts for approximately 20 % of maternal deaths globally and is linked to negative pregnancy outcomes (4, 9, 10). As a catalytic and structural element of over 300 enzymes and numerous transcription factors, Zn plays a critical role in gene expression, cell division and immune system function (11). Zinc deficiency, with prevalence rates approaching 30 % in South Asia, causes childhood stunting and increases susceptibility to infectious diseases such as pneumonia and malaria (11, 12). Approximately one billion people are affected by Se deficiency worldwide, mainly due to the low Se levels in soils that produce nutrient-poor foods (13). Severe deficiency leads to endemic diseases such as Keshan disease (a cardiomyopathy) and Kashin-Beck disease (an osteoarthropathy) (14). Iodine is essential to produce thyroid hormones, which govern metabolism, growth and neurological development and its deficiency causes disorders like goitre, hypothyroidism and cretinism (3, 14, 15).

Legumes constitute the second most important food crops worldwide, following cereals and serve as a dietary staple across many low- and middle-income countries (16, 17). Often termed "poor man's meat", they provide an affordable, protein-rich alternative to animal-based foods for resource-constrained populations (7, 18). Legumes contain 20–45 % protein and rich in lysine, even though they are deficient in sulfur-containing amino

acids (methionine, cysteine) (17, 19, 20). Carbohydrates constitute 60–65 % of seed weight, predominantly as complex carbohydrates, resistant starch and oligosaccharides (17, 21). Legumes are an excellent source of dietary fibre (5–37 %), linked to reduced risks of cardiovascular disease, obesity and gastrointestinal disorders (21). Legumes contain two to three times more protein and Zn and four to ten times more Fe than cereals (22). Several limitations restrict the potential of legumes, including the dilution effect from high-yielding varieties and the presence of anti-nutritional factors (phytic acid) that suppress the bioavailability of minerals (23, 24).

Under these conditions, biofortification offers a promising and long-term strategy to increase micronutrient concentrations during crop cultivation and enhance mineral bioavailability (6). Biofortification is the process of improving the nutritional value of food crops by boosting their concentration of essential vitamins, minerals and bioactive compounds during their growth cycle (5). Among various biofortification methods, agronomic biofortification is preferred for its rapid implementation, ability to address soil micronutrient shortages and broad crop applicability (25–27). This review highlights agronomic biofortification as a simple, quick and practical tool to alleviate hidden hunger and ensure food and nutritional security.

Methodology of literature collection

Relevant literature was retrieved from Scopus, ScienceDirect and Google Scholar using a systematic search strategy. The collected literature comprised English-language articles published between 2010 and 2025, with most articles originating from studies published during the last five years. The literature search was conducted using keywords and Boolean operators such as “agronomic biofortification”, “micronutrient enrichment”, “iron enhancement in legumes”, “zinc biofortification”, “foliar application”, “seed priming”, “hidden hunger”, “nano-biofortification” and “leguminous crops”. The search strings employed included Boolean operators such as AND and OR: (“leguminous crops” AND “biofortification”), (“iron” OR “zinc” OR “iodine”) and (“foliar spray” OR “soil application” OR “seed priming”).

A total of 214 records were identified through database searching. After the removal of 42 duplicate records, 172 articles were screened based on their titles and abstracts. During this stage, 68 records were omitted because they did not align with the scope of the review. Subsequently, 104 reports were sought for retrieval, of which 98 full-text articles were assessed for eligibility. Studies unrelated to leguminous crops, case reports, conference abstracts, conference papers, non-comparative studies and non-peer-reviewed publications were excluded. Finally, 71 studies were included for qualitative synthesis and comparative evaluation.

Although the present article is narrative in nature, the PRISMA framework was adapted to organise the literature search, screening and eligibility assessment of studies relevant to the present review. The overall process of literature identification,

screening, exclusion and final inclusion of studies is illustrated in the PRISMA flow diagram (Fig. 1).

Nutritional significance of legumes

Legumes are cultivated extensively worldwide, with Asia and Africa representing the dominant regions in terms of cultivated area and production volume (24). In 2020, pulses were cultivated worldwide across 93.2 million hectares (Mha), generating 89.8 million tonnes (Mt) at an average yield of 963.9 kg/ha (21). India ranks as the largest global producer (accounting for 26 % of world production), consumer (27 %) and importer (14 %) of pulses (28). During 2023–24, India's pulse cultivation area stood at 27.51 Mha, with overall production of 24.25 Mt (29). The nutritional composition of different legume crops is listed in Table 1.

Concept of biofortification

Biofortification offers a sustainable strategy to enhance essential micronutrients such as Fe, Zn, I and provitamin A in crops during the crop cycle, thereby addressing hidden hunger among resource-deprived populations (26). The primary approaches include agronomic, genetic (comprising both conventional breeding and transgenic methods) and microbial biofortification, each with distinct advantages and limitations (26, 33).

Genetic biofortification (conventional breeding) offers a durable, long-term solution by developing nutrient-enriched varieties. It is cost-effective and socially accepted but it is time-consuming (typically 5–10 years) and is restricted by the availability of genetic diversity within crop gene pools (1). Transgenic approaches and genome editing allow precise gene insertion or modification to elevate nutrient content, even for traits absent in native gene pools, thereby enabling multi-nutrient and targeted enhancements; however, they face high research expenditures, strict regulations and public concern regarding genetically modified crops (24, 26). Beneficial microbes (e.g., plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF)) are utilised in microbial biofortification to enhance nutrient acquisition. It is eco-friendly, enhances soil health and reduces chemical inputs. However, real-world applications are often inconsistent and highly dependent on environmental conditions and the availability of compatible microbial isolates (33, 34).

In contrast, agronomic biofortification or “ferti-fortification”, involves the deliberate application of mineral fertilisers to soil, foliage or seeds (Fig. 2) to enhance the micronutrient density of food crops (26, 35). It does not alter the plant's genetic makeup and serves as an immediate solution to address immediate nutrient deficits (24, 36). Although agronomic biofortification differs operationally from genetic and transgenic approaches, all share the common objective of increasing micronutrient content. While this method bypasses the lengthy timelines required for genetic variety development, its efficacy remains bounded by soil-plant interactions and recurring application demands (26).

Table 1. Nutritional composition of major legumes

Legume	Protein (%)	Fat (%)	Iron (mg)	Zinc (mg)	Folate (µg)	Source
Chickpea	18.77–24	4.1–6.04	4.0–12.3	2.76–4.1	206–290	(30)
Lentil	22–31	1.06–2.17	6.51–7.39	3.27–3.6	204–479	(31)
Common bean	20.9–27.8	0.9–2.4	3.4–8.4	1.9–5.0	165–232	(14, 28, 32)
Mung bean	24–28	1–1.5	3.4–4.4	1.2–2.1	615	(28)
Cowpea	23.5–24.5	1.3–2.2	6.8	4.1	159 (cooked)	(28)

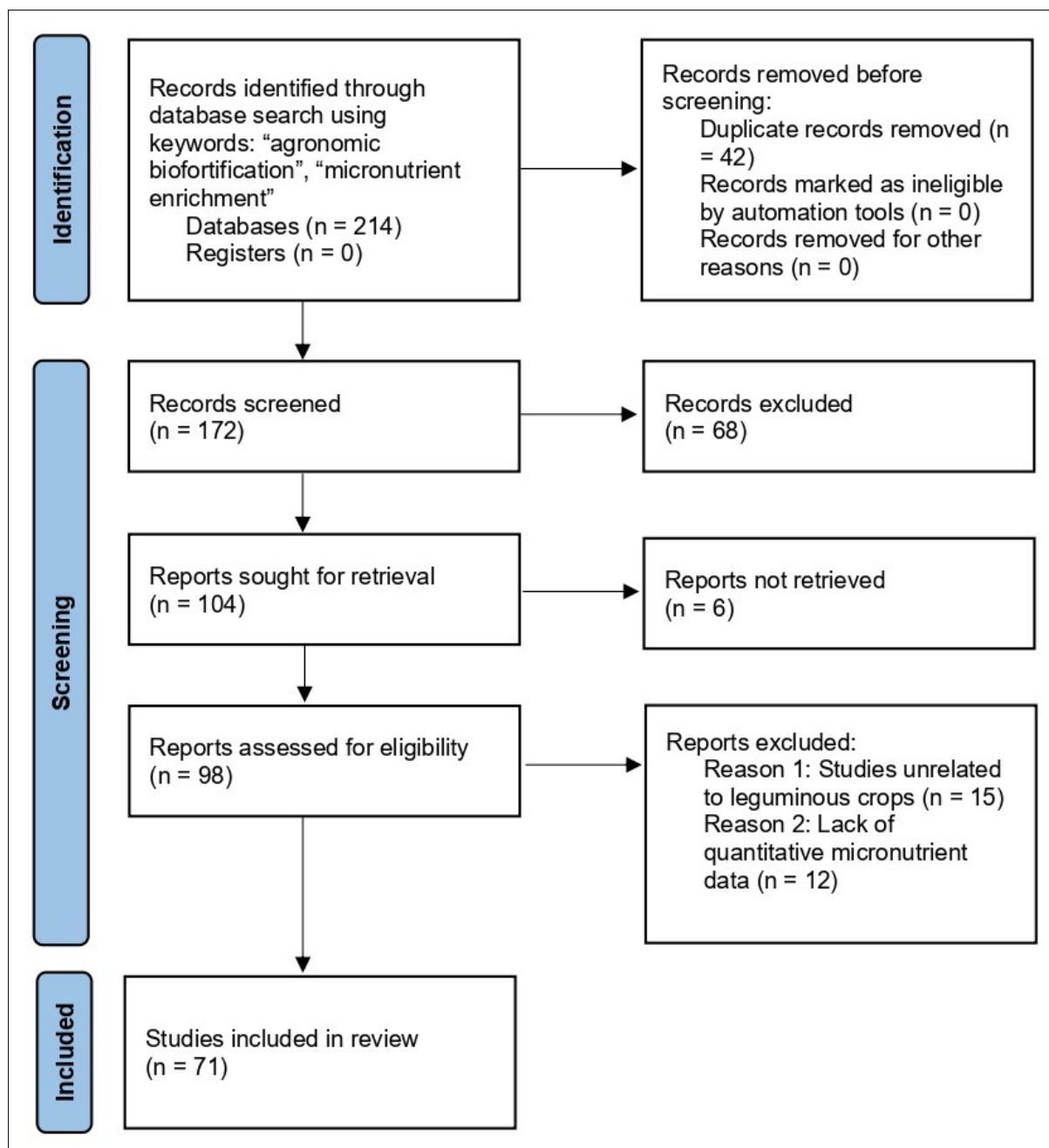


Fig. 1. PRISMA 2020 flow diagram for a narrative review which included searches of databases and registers only.

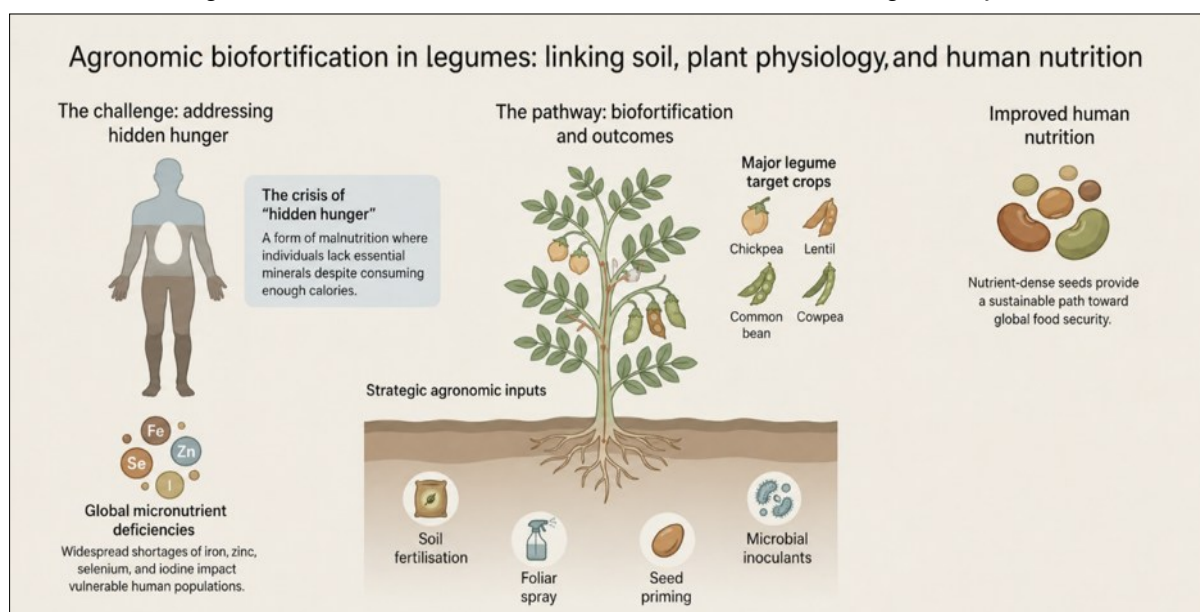


Fig. 2. A framework of agronomic biofortification in legumes integrating soil, plant physiology and human nutrition to mitigate hidden hunger.

Physiological mechanisms of nutrient uptake and translocation in legumes

Rhizosphere processes governing soil-to-plant nutrient transfer

Mineral nutrient acquisition by plants starts within the rhizosphere, where interactions among roots, soil constituents and microorganisms govern nutrient transformation and mobilisation (36, 37). Nutrient bioavailability is determined by the transport of minerals from the surrounding bulk soil toward the root surface, a process driven chiefly by diffusion and mass flow, both of which are heavily influenced by key soil physicochemical characteristics including soil texture, pH levels, organic matter content, cation exchange capacity (CEC), water availability and oxidation-reduction potential (23, 33).

Iron and Zinc uptake strategies in legumes

Legumes and other dicot plants utilise a reduction-dependent mechanism termed Strategy I for acquiring Fe and, partially Zn (38). A key characteristic of Strategy I is acidification of the rhizosphere. When Fe becomes limited, legume roots release protons (H^+) through plasma membrane H^+ -ATPase enzymes of the HA2, H^+ -ATPase family, lowering the pH around the roots and enhancing the solubility of ferric iron (Fe^{3+}) (22, 24, 36). After solubilisation, membrane-bound ferric chelate reductases, especially FRO2, convert Fe^{3+} to the ferrous form (Fe^{2+}). This reduction step often limits Fe acquisition, particularly in alkaline soils (6, 39, 40). The reduced Fe^{2+} then moves across the root plasma membrane through high-affinity transporters, primarily Iron-Regulated Transporter 1 (IRT1) (22, 24, 36). Iron-Regulated Transporter 1 has broad substrate specificity and enables uptake of other divalent cations, including Zn^{2+} , thereby connecting Fe and Zn homeostasis in legumes (22, 24, 39). Strategy I plants also secrete root exudates such as phenolic compounds (e.g., coumarins) and organic acids (e.g., citrate, malate), which chelate and mobilise insoluble Fe pools, especially under stress conditions like elevated soil pH (23, 33, 36).

Translocation of micronutrients to seeds

After root uptake, minerals must move to shoots and then from vegetative tissues (sources) to developing seeds (sinks)—a process that determines seed micronutrient content. Translocation involves xylem loading, long-distance transport, phloem redistribution and regulated seed unloading via specialised transporters and chelation mechanisms that maintain solubility and prevent toxicity (27). Following entry into the root symplast, nutrients are loaded into the xylem for transpiration-driven

transport to shoots (33) (Fig. 3). During reproductive growth, mature leaves shift from sinks to sources, exporting minerals to seeds via the phloem (27). This remobilisation efficiency largely determines final seed micronutrient concentration (41).

The alkaline environment of phloem sap encourages the formation of stable chelated metal complexes. Iron and Zn usually move through the phloem bound to nicotianamine (NA) or occasionally to small metal-binding proteins like iron transport proteins (ITPs) (22, 27). Remobilisation is closely linked to leaf senescence, regulated by transcription factors such as the NAC family (e.g., NAM-B1 in wheat, OsNAC5 in rice), which accelerate senescence and enhance nutrient redistribution to grains (3, 23).

Transporter gene families involved in seed loading

The accumulation of micronutrients in legume seeds is a tightly regulated process involving multiple membrane transporter families that control nutrient movement across cellular and subcellular membranes (Table 2). In legumes, four transporter families regulate Zn and Fe movement. The ZRT/IRT-Like Protein (ZIP) family (PvZIP12, PvZIP13, PvZIP18 in common bean) controls uptake, internal redistribution and seed loading of divalent cations (6, 22, 24). The Yellow Stripe-Like (YSL) family facilitates long-distance transport of metal-NA complexes (Fe -NA, Zn -NA) from xylem to phloem and into seed embryos; quantitative trait locus (QTL) and expression studies in chickpea and navy bean identify YSL transporters as key for Fe and Zn seed loading (6, 22). The Natural Resistance-Associated Macrophage Protein (NRAMP) family releases divalent cations from vacuolar stores for redistribution to developing seeds with specific NRAMP genes such as GmNRAMP1a and GmNRAMP3a in soybean and MtNRAMP1 in *Medicago truncatula* supporting Fe, Mn and Zn transport (6, 22, 24). The Vacuolar Iron Transporter (VIT) and VIT-Like (VTL) families mediate final Fe transport from the cytosol into vacuoles for storage with phytate or ferritin, preventing oxidative damage and securing germination reserves (27).

Agronomic strategies for micronutrient biofortification

Agronomic biofortification refers to the precise application of mineral fertilisers to crops to enhance the micronutrient content of harvestable plant parts (26). This targeted fertilisation strategy provides a fast, adaptable and comparatively inexpensive intervention for addressing micronutrient malnutrition, especially in areas requiring immediate dietary improvements (10, 42). The different agronomic biofortification approaches are illustrated in Fig. 4.

Table 2. Key transporter gene families and uptake mechanisms involved in essential micronutrient acquisition and translocation (24, 33)

Target nutrient	Transporter gene families	Specific mechanism
Iron (Fe)	IRT1, NRAMP, YSL, VIT1, VTL	“Strategy I” (acidification and Fe^{3+} reduction) in dicots and “Strategy II” (phytosiderophore chelation) in monocots.
Zinc (Zn)	ZIP (ZRT/IRT), HMA, MTP, CDF	Transported either in its divalent cationic form (Zn^{2+}) or as complexes bound to nicotianamine (NA) or histidine.
Manganese (Mn)	MTP8.1, NRAMP1, ZIP1, VIT	Essential for photosynthesis; transporters often accept other divalent cations.
Copper (Cu)	CTR (COPT1–4), HMA5–8, ZIP2/4	Uptake occurs primarily as Cu^{2+} via high-affinity transporters or as Cu^{2+} through certain ZIP family members.
Magnesium (Mg)	MRS2 (MGT1/10), MHX	Mg^{2+} enters root cells via permeable cation channels and is typically sequestered within vacuoles.
Selenium (Se)	HAST (High-Affinity Sulfate Transporters), Pht1	Selenate is absorbed via sulfate transport pathways, whereas selenite is taken up through phosphate transporters.
Iodine (I)	CLC (Chloride Channel), ABC Proteins	Transport typically occurs through chloride pathways, utilising H^+ /anion symporters and associated channels

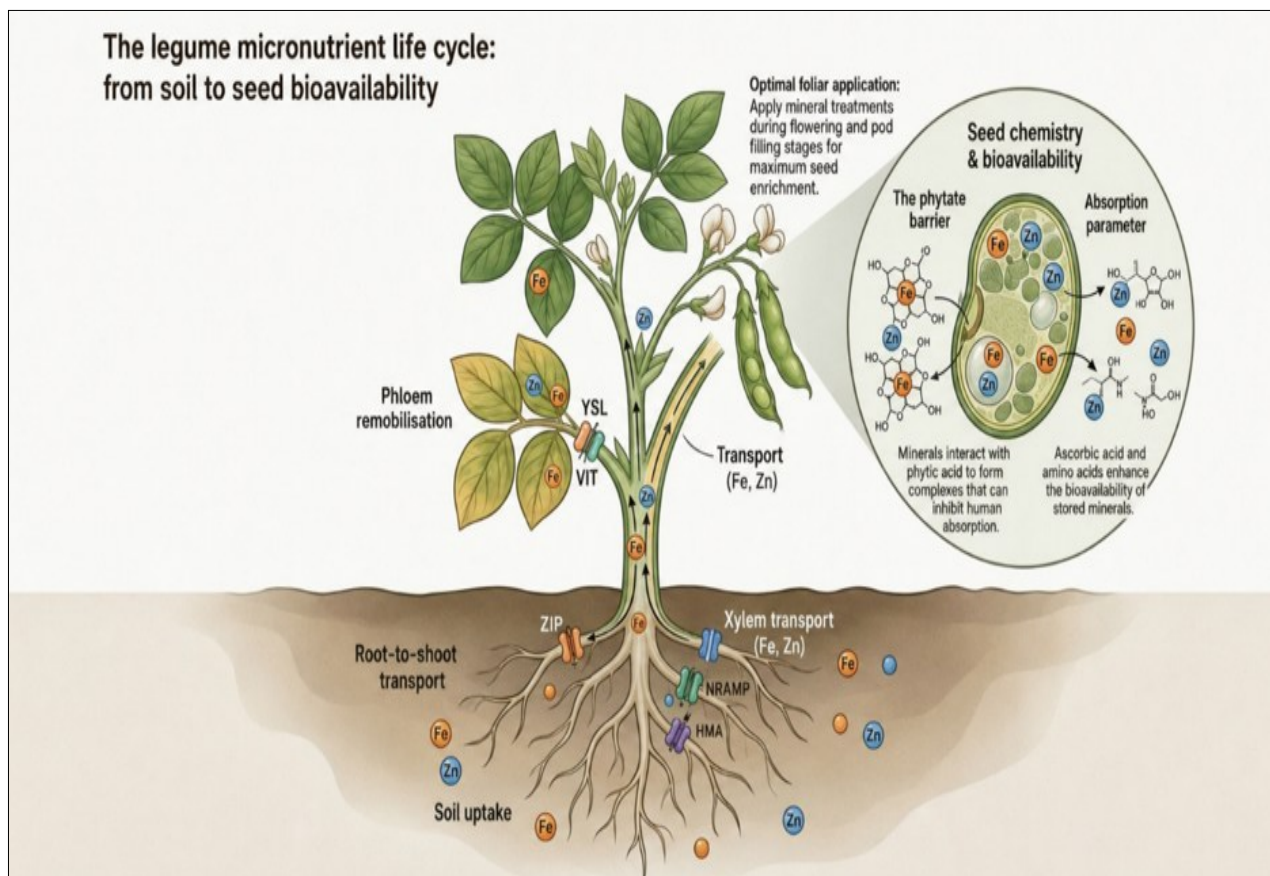


Fig. 3. Micronutrient dynamics in legumes: uptake from soil, root-to-shoot translocation, phloem remobilisation and seed bioavailability determinants.

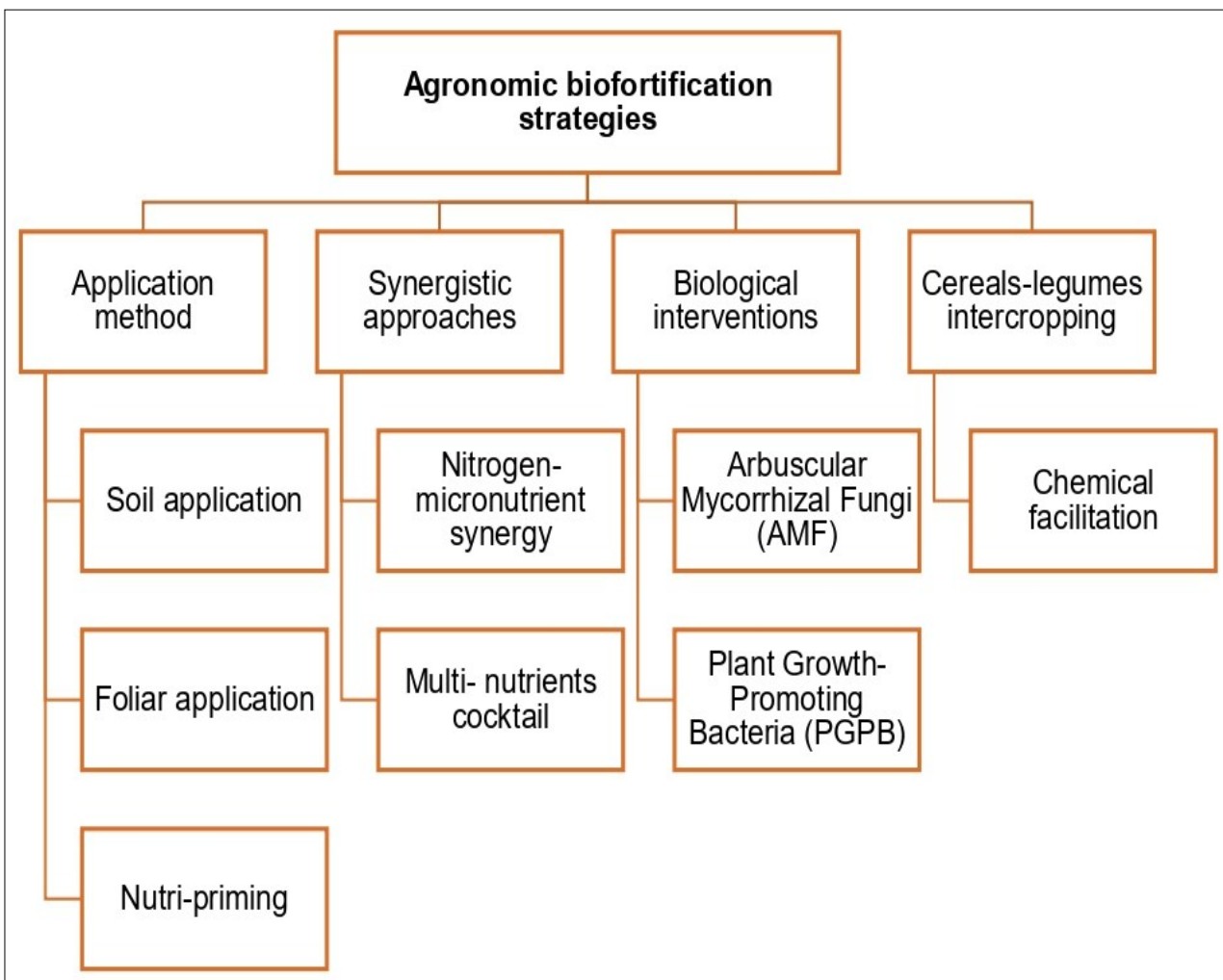


Fig. 4. Types of agronomic biofortification strategies.

Based on application method

Soil-based biofortification involves adding inorganic fertilisers like zinc sulphate (ZnSO_4), ferrous sulphate (FeSO_4) and manganese sulphate (MnSO_4) directly to the soil to increase the reservoir of nutrients available for root absorption (9). However, a major constraint is the rapid fixation and immobilisation of these micronutrients (26, 43). These fixation issues, along with losses from leaching and runoff, lead to poor nutrient use efficiency (NUE), create environmental risks and demand high fertiliser doses to achieve substantial grain enrichment (27). These high requirements place financial strain on smallholder farmers, restricting the widespread adoption of soil-based biofortification.

Foliar fertilisation involves spraying soluble nutrient solutions directly onto the crop canopy and is widely considered the most efficient agronomic method for micronutrient biofortification, especially for Fe, Zn and Se under soil conditions that restrict root uptake (44, 45). The efficiency of foliar spray depends on its interaction with leaf surface characteristics, which vary among plant species (46). The key benefit is avoiding soil-based fixation and immobilisation, thus maintaining nutrients in a soluble and easily absorbable state (7). For instance, foliar ZnSO_4 and FeSO_4 raised lentil grain Zn by roughly 10.9 % and Fe by about 20.4 % (9).

Nutri-priming and seed coating support early seedling nutrition and subsequent crop performance. Nutri-priming requires soaking seeds in dilute nutrient solutions (e.g., Zn, boron (B)) prior to sowing, followed by re-drying (32). Seed coating uses adhesives to apply finely ground nutrients onto the seed surface (7). A study indicates that chickpea seeds coated with 5 mg Zn kg^{-1} seed increased grain Zn concentration by 17.2–22.0 % compared to the control (37). These techniques target the early growth phase when seedlings are most vulnerable to nutrient shortages.

Based on synergistic approaches

The first approach is nitrogen–micronutrient synergy. Sufficient nitrogen (N) supply stimulates the production of nitrogenous molecules like NA and amino acids (e.g., tryptophan), which act as chelating agents that bind Fe and Zn, consequently facilitating their phloem-mediated transport from vegetative tissues to developing seeds (32, 41). Additionally, N nutrition can delay the onset of leaf senescence, prolong the grain-filling stage and offer an extended window for micronutrient mobilisation into seeds (47).

The second approach involves multi-nutrient ‘cocktail’ fertilisation. These multi-nutrient ‘cocktail’ sprays are capable of simultaneously enriching crops with multiple essential elements without harming yield. This method entails the combined foliar application of Zn, I, Fe and Se within a single liquid formulation (41). Evidence from field pea shows that a combined foliar spray of Se and Zn raised seed levels of both elements, confirming the feasibility of dual biofortification in pulses (6).

Based on biological interventions

Biological interventions refer to the use of beneficial soil microorganisms to improve the uptake, transport and accumulation of essential micronutrients in the edible portions of crops (24, 33). This approach is often known as microbe-mediated biofortification (33). As field-level crop management practices, they are frequently classified under agronomic biofortification (1, 27). The primary microbial agents include plant growth-promoting bacteria (PGPB) and AMF. By colonising the rhizosphere, these microbes release organic acids, produce siderophores and participate in symbiotic nutrient transfer.

This leads to the mobilisation of nutrients, enhances their uptake and increases micronutrient accumulation in maturing seeds (39, 48).

Bacillus, *Pseudomonas*, *Rhizobium*, *Enterobacter*, *Acinetobacter* and *Azotobacter* are microbial species that enhance the bioavailability of Zn and phosphorus (P) from insoluble soil fractions (49). These bacteria function primarily by secreting organic acids such as gluconic acid and 2-ketogluconic acid into the root zone, which reduce soil pH and promote the breakdown of poorly soluble Zn minerals (33, 48). Inoculation with *Enterobacter ludwigii* SRI-229 improved the uptake of Fe, Zn, copper (Cu), manganese (Mn) and calcium (Ca) in both chickpea and pigeon pea, an effect attributed to siderophore synthesis and enhanced root development (18, 39). When *Rhizobium* is co-inoculated with *Pseudomonas* or *Bacillus*, synergistic effects often occur, leading to improved nodulation, enhanced N fixation and greater uptake of Fe and Zn through mutually reinforcing mechanisms (18, 29).

Through symbiotic associations with AMF, most legume crops achieve extended root systems and enhanced nutrient acquisition (25, 36). The hyphae of AMF extend beyond the rhizosphere depletion zone, allowing them to access slowly diffusing, immobile nutrients like P, Zn and Cu in the soil solution (34).

Cereal-legume intercropping as an ecological biofortification approach

Cereal-legume intercropping derives its nutritional benefits from two key ecological principles, namely resource complementarity and facilitation (36). When intercropped species draw from different nutrient pools or employ dissimilar acquisition pathways, chemical complementarity emerges. This reduces direct competition and enhances total system nutrient capture. Legumes obtain much of their N through biological N fixation, leaving soil inorganic N available for the accompanying cereal. Concurrently, legumes release soil P fractions that remain largely inaccessible to cereals, thereby creating chemically complementary conditions (36, 50). Positive interactions known as facilitation occur when one species modifies the rhizosphere environment to increase nutrient availability for neighbouring plants. Such modifications involve secreting organic acids (carboxylates), H^+ and enzymes that alter soil pH, redox status and microbial activity, leading to the solubilisation of P, Fe and Zn. As a result, nutrients mobilised by one plant are available to both the exuding species and its intercropped partner (51, 52). Intercropping systems such as maize + peanut and wheat + chickpea have been reported to enhance Fe and Zn uptake and accumulation through improved nutrient availability and rhizosphere interactions (53).

Case studies: Micronutrient biofortification in major legumes

Zinc and Iron

Chickpea is highly responsive among grain legumes to agronomic biofortification targeting Zn and Fe. Strong synergistic effects are exhibited by tank-mix sprays composed of 0.5 % ZnSO_4 , 0.5 % FeSO_4 and 2 % urea applied at flowering and pod formation. This mixture enhances grain Zn by approximately 9–11 % and grain Fe by around 4–5 % compared to separate nutrient applications, while avoiding phytotoxic effects or yield penalties (24, 41).

In calcareous soils where Fe deficiency chlorosis hampers productivity and grain quality, lentil is a primary crop for dual Zn and Fe biofortification (54). A foliar mixture of ZnSO_4 and FeSO_4 applied at pre-flowering and pod formation stages boosted grain Zn and Fe by 10.9 % and 20.4 % respectively (9). For populations in East Africa and Latin America, common bean is both the most widely

consumed grain legume globally and a principal dietary source of Fe and Zn (22). Iron and zinc sulphates applied to foliage at rates of 0.025–0.100 $\mu\text{mol dm}^{-3}$ led to significant increases in mineral content within leaves and pods, showing effective absorption and transport to reproductive structures (55).

In arid and semi-arid regions, cowpea is an important nutritious crop that responds favourably to both soil-based and foliar micronutrient fertilisation. Foliar Zn fertilisation raises grain Zn by over 20 % and, for certain genotypes, enhances grain yield by more than 40 % (53). Integrating foliar Zn with *Azospirillum brasilense* inoculation produces synergistic benefits: inoculated plants attain higher grain Zn concentrations (up to 78.8 mg kg^{-1}) and greater protein content (albumin and globulin fractions) than uninoculated plants given the same Zn fertiliser rate (56). The effects of various agronomic biofortification approaches for improving micronutrient content in legumes are presented in Table 3.

Selenium

Selenium biofortification in legumes is strongly influenced by the chemical form of applied fertiliser and the species' inherent capacity for Se uptake and metabolism. Selenate (SeO_4^{2-}) is markedly more effective than selenite (SeO_3^{2-}) for increasing Se concentrations in edible legume tissues. In field pea, each gram of foliar-applied sodium selenate increased grain Se by approximately 148 $\mu\text{g kg}^{-1}$, whereas sodium selenite increased it by only about 19 $\mu\text{g kg}^{-1}$, representing a four- to sixfold difference in efficiency due to the differences in transport and metabolism (59). Also, the superior performance of selenate over selenite has been demonstrated in several legumes including chickpea, where grain Se concentration reached 2721 $\mu\text{g kg}^{-1}$ with selenate compared to 714 $\mu\text{g kg}^{-1}$ with selenite (44).

Calcium and Magnesium

Agronomic fertilisation has shown encouraging outcomes, particularly for Mg. In snap bean (*Phaseolus vulgaris*), soil application of magnesium sulphate (MgSO_4) and magnesium chloride (MgCl_2)

increased Mg accumulation and enhanced antioxidant capacity and concentrations of bioactive compounds such as flavonoids and anthocyanins in edible pods (60, 61). Magnesium sulphate was consistently more effective than MgCl_2 in stimulating total anthocyanin content (61). In chickpea and pigeon pea, inoculation with *E. ludwigii* and *Acinetobacter tandoii* significantly enhanced nutrient acquisition, increasing Ca by 22 % and 11 % and magnesium (Mg) by 2 % and 39 % respectively (18, 39, 53). Co-inoculation of soybean with *Bradyrhizobium japonicum* and *Streptomyces griseoflavus* similarly enhanced Ca and Mg uptake (39). Agronomic studies on Ca and Mg biofortification in legumes remain limited compared to Fe and Zn with only a few reports available from fertilisation, microbial, nanotechnology and genetic approaches (24).

Iodine

Iodine biofortification poses distinct challenges because I is not essential for plants and exhibits limited phloem mobility, constraining translocation to seeds (27). Despite these limitations, successful I enrichment has been reported. In cowpea, foliar application of potassium iodide (KI) significantly increased I concentration in edible tissues (42). In green bean and garden pea, irrigation with I-enriched water (0.1–0.5 mg L^{-1}) enhanced pod I content, though higher concentrations (0.5 mg L^{-1}) caused substantial biomass reductions (up to 51 % in beans), revealing a narrow margin between effective biofortification and phytotoxicity (15).

Anti-nutritional factors

A major obstacle to the nutritional success of biofortification initiatives is the so-called "phytate barrier". The inhibitory action of phytic acid stems from its highly electronegative molecular configuration under physiological conditions (43). The presence of six phosphate groups imparts a robust negative charge, facilitating high-affinity binding with positively charged mineral cations ($\text{Fe}^{2+}/\text{Fe}^{3+}$, Zn^{2+} , Ca^{2+} , Mg^{2+}). This binding forms stable, insoluble phytate-mineral complexes, frequently referred to as a "chelation cage", that sequester minerals and prevent their solubilisation in the

Table 3. Agronomic biofortification techniques and their outcomes for micronutrient enhancement in legumes

Biofortification approach	Target nutrient	Crop	Treatment details	Result	References
Soil and foliar application	Zn	Pea	Soil/foliar Zn; seed priming	Seed Zn up to 34 mg/kg	(7)
Soil application and seed priming	Zn	Chickpea	ZnSO_4 (25 kg/ha) or 0.05 % $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ priming	29–36 % increase in seed Zn	(7, 24)
Agronomic (irrigation)	I	Common bean	0.5 mg/L iodine in irrigation water	Fruits of beans reached upto 1.6 mg/kg iodine concentration	(15)
Microbial inoculation	Fe, Zn, Cu, Mn, Ca	Chickpea	<i>E. ludwigii</i> (SRI-229)	Yield increase up to 19 %; Fe- 18 %; Zn- 23 %	(18)
Foliar application	Fe and Zn	Common bean	ZnO nanoparticles (10–40 mg/L)	Increased seed Fe and Zn content	(24)
Sprout fortification	Zn	Soybean	Sprout biofortification with ZnSO_4	Enhanced Zn bio-accessibility	(28)
Foliar and microbial application	Zn and Fe	Chickpea	0.5 % ZnSO_4 + 0.5 % FeSO_4 + 2 % urea / AMF / PGP actinobacteria	Improved Zn and Fe content in seed; Zn 44.98 mg/kg ; Fe 71.08 mg/kg	(30, 35)
Foliar application	Se	Lentil	Potassium selenate (40 g/ha)	Seed Se concentration significantly increased from 201 to 2772 $\mu\text{g/kg}$.	(42)
Soil / foliar / microbial application	Fe and Zn	Lentil	ZnO-NP; ZnSO_4 + FeSO_4 ; <i>Trichoderma</i>	Yield increase up to 39.6 %	(47)
Foliar and soil application	Fe	Mung bean	Foliar Fe; Fe-enriched poultry manure	46 % increase in grain Fe	(57)
Soil + foliar application	Zn	Pigeon pea	RDF + ZnSO_4 + 0.5 % Zn-EDTA foliar	Seed yield -1897 kg/ha	(58)
Foliar application	Se	Pea	Sodium selenate (10 g Se/ha)	100g peas provides 179 $\mu\text{g Se}$, which is ~90 % of RDA of Se.	(59)
Foliar-nano spray	Mg	Green beans	Mg foliar spray of nano fertiliser (50 mg/L)	Increase bioactive compounds and antioxidant capacity in seeds	(60)

RDA- recommended dietary allowance; RDF- recommended dose of fertiliser

gastrointestinal tract (48). Humans and other monogastric animals are unable to hydrolyse phytate-mineral bonds during digestion (3, 48). The suppressive effect is highly dose-dependent and even small quantities of phytic acid (2–10 mg per meal) markedly reduces Fe absorption (4).

In biofortified common bean, increases in seed Fe concentration typically occur alongside comparable rises in phytic acid content, resulting in relatively unchanged phytate-to-Fe molar ratios that negate the benefits of enhanced mineral density (62). Predicting phytate-mediated inhibition relies more accurately on the molar ratio of phytic acid to minerals rather than on absolute mineral levels alone (12, 43). Regarding Fe, appreciable improvements in absorption from legume-based meals are generally observed when the phytate-to-Fe molar ratio is below 1 : 1. For Zn, a phytate-to-Zn molar ratio above 15 is associated with critically poor absorption, while ratios below 5 indicate high Zn bioavailability (4). These thresholds emphasise the necessity of combining phytate-mitigation approaches with mineral enrichment in biofortification programmes to guarantee that elevated grain mineral content yields measurable nutritional improvements.

Apart from phytic acid, other anti-nutritional factors such as tannins, oxalates, saponins, protease inhibitors, lectins and lathrogens can also inhibit nutrient availability in legumes (21, 63). Tannins, predominantly present in the seed coat, reduce protein digestibility and mineral absorption (64). Oxalates decrease Ca and Mg availability, while protease inhibitors and lectins impair digestion and nutrient uptake (31, 63). Saponins may interfere with fat-soluble nutrient absorption, whereas lathrogens such as β -ODAP found in grass pea may cause neurological disorders when consumed excessively (31, 65).

Achieving the full nutritional potential of biofortified legumes requires strategies that reduce anti-nutritional compounds through appropriate processing methods and enhance promoters of mineral bioavailability (24, 36). Various processing methods and their mechanisms for improving mineral bioavailability have been elaborated in Table 4.

The key promoters are ascorbic acid (vitamin C), β -carotene and specific amino acids, all of which can partially neutralise the interference caused by phytates and other anti-nutritional substances (23, 24). Ascorbic acid is one of the most potent promoters of Fe bioavailability. It facilitates absorption by converting ferric iron (Fe^{3+}) into the more readily absorbed ferrous form (Fe^{2+}). Furthermore, ascorbic acid creates soluble Fe-ascorbate complexes

that stop Fe from interacting with inhibitors like phytates and polyphenols, thus overcoming the so-called "phytate barrier" (4, 23). β -Carotene, recognised as a provitamin A compound, also acts synergistically to enhance Fe and Zn absorption (24). Certain agronomic practices such as optimised N application and adjustment of environmental conditions like light intensity and temperature, especially within controlled growing systems, can boost carotenoid synthesis in leaves and pods, thereby indirectly improving mineral bioavailability (68).

Natural chelators such as sulfur-containing amino acids (methionine, cysteine), lysine and histidine enhance the uptake of Fe and Zn (6). Through its influence on protein synthesis and amino acid composition in legumes, N management offers an indirect strategy to raise these promoter levels and boost the nutritional performance of biofortified crops (27).

Breeding and molecular approaches have been employed to develop low-phytate (lpa) legume varieties with enhanced mineral bioavailability (6, 16). In peas and common bean, lpa mutants have been reported to show up to a 90 % reduction in phytic acid content (14). Using advanced technologies such as CRISPR/Cas9, target genes (MIPS, IPK1 and PvMRP1) involved in phytate biosynthesis and transport have been modified (24, 48). Despite these advantages, many lpa genotypes exhibit reduced yield and seed vigour (6, 14).

Limitations

Although agronomic biofortification provides a swift and adaptable approach to tackling micronutrient shortages, its enduring viability and widespread implementation are hindered by economic, logistical and environmental obstacles.

In contrast to plant breeding, where a single investment produces nutrient-rich varieties that farmers can reuse, agronomic biofortification demands continual procurement and application of mineral fertilisers (1). Because it relies on repeated fertiliser application, it results in substantial recurrent costs for fertilisers, labour and management, which can hinder widespread adoption by smallholder farmers (24, 26). Beyond financial considerations, fertiliser application is often laborious and logistically complex. Farmers in isolated rural regions frequently encounter limited market access and unreliable distribution networks for micronutrient fertilisers such as Zn and Fe formulations, which are not as widely available as macronutrient fertilisers (69). Policy frameworks heavily favour macronutrients, making micronutrient fertilisers comparatively expensive and less obtainable (53).

Table 4. Mechanisms and impacts of different processing methods for reducing anti-nutritional factors

Processing method	Target anti-nutrient(s)	Mechanism	Impacts	Source
Soaking	Phytic acid and tannins	Hydration initiates endogenous enzymes and reducing phytates and tannins through leaching into the soaking water	It can reduce phytic acid up to 50 %, but some soluble minerals may also be lost if the soaking water is discarded	22
Germination (sprouting)	Phytic acid and lectins	Imbibition triggers endogenous phytase enzymes that hydrolyse phytic acid into lower inositol phosphates and inorganic phosphorus	Most effective methods; sprouting mung bean seeds for 96 hr decreased phytic acid from 1.88 % to 0.33 %.	21, 66
Fermentation	Phytic acid and trypsin inhibitors	Microbial activity lowers pH and accelerating phytate degradation through activating both endogenous and microbial phytases	30–38 % reduction in phytic acid has been reported in fermented mung bean	43, 66
Cooking	Lectins, tannins and enzyme inhibitors	Thermal processing denatures heat-sensitive inhibitors and disrupts its cellular structures, making nutrients release	It can increase Zn bioavailability up to 60 % in biofortified cowpea and has limited effect on phytic acid due to its heat stability	21, 67

The success of agronomic biofortification is also influenced by NUE, which can be adversely affected by soil fixation, nutrient losses to the environment and physiological barriers that restrict the transport and deposition of micronutrients in grains, seeds or other edible tissues (26, 49). There are also significant environmental safety concerns. Excessive or poorly regulated fertiliser application may result in the buildup of minerals within soils and aquatic systems, leading to contamination and potential toxicity (1, 34). Specific ecological hazards include the leaching of mobile nutrients into groundwater, which endangers drinking water quality and downstream ecosystems (27, 43). Global climate change further complicates biofortification efforts by influencing crop physiology and nutrient cycling. Rising atmospheric CO₂ levels are linked to a "dilution effect", where enhanced carbohydrate synthesis and higher yields coincide with marked declines in grain protein and essential mineral concentrations, including Fe and Zn (46, 70).

Future directions and innovations

The limitations of conventional fertiliser-based approaches and the lengthy timelines associated with breeding programmes are driving agronomic biofortification towards advanced technological solutions and ecologically sustainable innovations.

Nanotechnology in micronutrient delivery

Nanotechnology has revolutionised fertiliser development with materials ranging between 1 and 100 nm in size, thereby enhancing nutrient delivery, uptake efficiency and bioavailability (46, 60). When applied to soil or foliage, zinc oxide nanoparticles (ZnO-NPs) boost Zn accumulation in the harvestable tissues of cowpea, mung bean and common bean (24). Nano-priming, an emerging seed treatment approach, uses nutrient nanoparticles like zinc oxide (ZnO) and ferric oxide (Fe₃O₄) (46). Nano-priming triggers controlled reactive oxygen species (ROS) generation, which in turn boosts alpha-amylase activity, speeds up starch breakdown and upregulates aquaporin genes (e.g., *BnPIP1-1*). Enhanced water uptake and metabolic activation facilitate rapid seedling establishment (27). Nano-fertilisers offer significant environmental and agronomic advantages by reducing nutrient fixation in soil, improving NUE and enabling controlled nutrient release (29). Metal-based nanoparticles (Fe, Zn, Se) typically demonstrate higher uptake and translocation efficiencies due to their enhanced ability to cross leaf cuticles and stomata (71, 72). However, large-scale deployment demands rigorous evaluation of risks associated with nanoparticle persistence, accumulation through the food chain and effects on soil microbial communities (29, 73). Against this backdrop, "green synthesis" of nanoparticles via plant extracts or biological routes is gaining traction as a potentially safer and more environmentally benign alternative to traditional chemical synthesis (46).

Agro-ecological integration for sustainable biofortification

Organic amendments: Soil structure, CEC and microbial activity improve when organic residues like poultry manure and biochar are applied, resulting in greater Fe and Zn accumulation in mung bean grains (57). These products enable micronutrients sourced from local organic waste to be delivered through soil application, supporting grain nutrient enrichment while lowering production expenses and reducing reliance on imported synthetic fertilisers (53).

Crop diversification and intercropping: The principles of agro-ecological biofortification are reinforced through crop diversification and intercropping, which leverage functional complementarity across species. In cereal-legume intercropping systems (e.g., maize-

peanut, wheat-chickpea), interspecific root interactions are exploited to enhance the mobilisation and uptake of nutrients (36).

Microbial biofortification: Another pillar of agro-ecological integration is the incorporation of PGPB and AMF. This approach provides a biologically driven, resource-efficient strategy for improving micronutrient availability (26).

Omics and precision agriculture-enabled biofortification

In omics technologies, two complementary approaches, transcriptomics and ionomics, provide valuable insights into plant nutrient dynamics (31). Transcriptomics identifies gene expression patterns associated with nutrient transport and homeostasis pathways, including ZIP, NRAMP and YSL transporter families, under different fertilisation regimes (26). Ionomics, through high-throughput profiling of elemental composition across plant tissues, offers a holistic view of the plant ionome and uncovers nutrient interactions and trade-offs (6, 26). This approach is especially useful for identifying physiological bottlenecks in nutrient movement from vegetative tissues to seeds, helping to design fertiliser formulations and application strategies that better support nutrient enrichment in sink tissues (6, 74).

Biofortification effectiveness is amplified by precision nutrient management, which optimises when and where inputs are delivered. Site-specific nutrient management (SSNM) integrates geospatial tools, soil fertility maps, remote sensing data and decision-support systems to customise micronutrient application based on field-level spatial variability (29). Early detection of micronutrient deficiencies before visible symptoms appear is made possible by advanced sensing technologies such as spectral sensors and unmanned aerial vehicles (UAVs). A further refinement comes from variable rate technology (VRT), which couples spatial soil and crop data with precision application tools. This data-driven approach strengthens the economic sustainability of agronomic biofortification and keeps it consistent with environmental stewardship objectives (29, 75).

Conclusion

Addressing the global burden of hidden hunger requires a comprehensive and sustainable strategy that effectively links agricultural production systems with human nutritional outcomes. Agronomic biofortification has emerged as a critical, quick and adaptable intervention that enhances micronutrient densities in food crops. Among the various agronomic approaches, foliar application is currently the most effective method for grain micronutrient enrichment across legume species, particularly for Fe, Zn and Se, due to its high NUE and direct delivery to plant tissues. Combining the genetic capacity of nutrient-dense varieties with sound agronomic management ensures that nutrients are both available in the soil, efficiently absorbed and allocated to edible plant tissues. Successful implementation of integrated biofortification frameworks is contingent upon enabling policy-making, particularly in developing regions dominated by smallholder farming systems. Current fertiliser subsidy structures in many countries remain heavily skewed towards macronutrients, rendering micronutrient fertilisers comparatively expensive and limiting adoption. Future policy initiatives should prioritise support for micronutrient fertilisers, promote dissemination and adoption of biofortified cultivars and strengthen agricultural extension services to improve farmers' awareness of balanced and SSNM. By harmonising short-term agronomic interventions with long-term genetic improvement, this

integrated approach offers a pathway for mitigating micronutrient malnutrition, enhancing dietary quality and advancing nutritional security for vulnerable populations worldwide.

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