



Biofortifying the Common Bean-Interplay of Iron, Zinc and Phytic Acid: A Review

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ABSTRACT

Common bean is a vital basic food and vegetable legume crop cultivated worldwide. Despite its nutritional importance, more than a third of humanity is affected by deficiencies in important micronutrients like iron (Fe) and zinc (Zn). A primary barrier to improving the nutritional content of common bean is the presence of phytic acid (PA), the principal phosphorus reservoir in legumes, which significantly reduces the bioavailability of these essential minerals. However, the interaction among Fe, Zn and PA in common bean remains poorly understood. This review focuses on the complex interplay among Fe, Zn and PA in common bean and this interaction's combined implications for sustainable agriculture and human nutrition. Recent advances in phenotyping approaches have transformed more precise quantification of Fe, Zn and PA content across diverse bean genotypes, paving the way for effective selection and breeding strategies. Building on these phenotyping tools, this review explores the substantial genetic variation in mineral and PA content, as well as the molecular mechanisms regulating their accumulation and transport. PA significantly impedes mineral absorption, underscoring the importance of breeding efforts that aim to enhance Fe and Zn concentrations while simultaneously reducing PA levels. Molecular biology developments, such as genome-wide association studies (GWAS) and transcriptomic analysis, have enabled researchers to pinpoint crucial genes and quantitative trait loci (QTL) linked to these characteristics. Furthermore, the review addresses current challenges and future directions for developing biofortified common bean varieties, considering both genetic and environmental influences.

Key words: Biofortification, Common bean, Genetic variation, Iron, Phytic acid, Zinc.

Common bean (*Phaseolus vulgaris* L.) is one of the most important dietary staples among food legumes. It plays a crucial role in sustainable agricultural growth and is the most widely cultivated edible legume worldwide (Wu *et al.*, 2020). Beyond its agronomic significance, the common bean is rich in protein, micronutrients and bioactive compounds, making it an excellent plant-based protein source (Weller *et al.*, 2019).

Currently, more than 2 billion people worldwide are affected by Fe and Zn deficiencies (Kassebaum *et al.*, 2014), the most prevalent forms of micronutrient malnutrition (Welch and Graham, 1999). There are substantial variations in mineral content among crops, with common bean grains containing significantly higher levels of Fe and Zn compared to major cereal staples (Welch and Graham, 2004; Blair, 2013; Rana and Dahiya, 2019). Therefore, enhancing these mineral concentrations in common bean is of critical importance for alleviating global hidden hunger.

Myo-inositol hexakisphosphate (IP₆), widely referred to as PA, is the hexaphosphate of cyclohexane. PA serves as the primary phosphorus reserve in plants, is found naturally in legumes (Vats and Banerjee, 2004) and is widely recognized as a key limiting factor in mineral absorption from plant-based foods, including legumes (Ahmed *et al.*, 2014).

Research using both *in vivo* and *in vitro* models has confirmed that PA forms insoluble complexes with divalent cations such as Fe and Zn, significantly reducing the

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bioavailability of these trace elements and thereby increasing the risk of their deficiency (Green and Rogers, 2004). Previous literature reviews have predominantly focused on the interactions within food matrices (Cheryan, 1980; Chen and Xu, 2023) and substantial evidence suggests that reducing PA content can enhance mineral bioavailability in plant-based foods (Chondrou *et al.*, 2024). However, there remains a lack of systematic synthesis specifically regarding *Phaseolus* species (Gregory *et al.*, 2017). The review aims to systematically elucidate the interaction mechanisms among Fe, Zn and PA in common bean, integrate advances in phenomics and molecular biology, comprehensively evaluate current strategies for reducing PA and enhancing mineral bioavailability and identify future research directions for developing high-nutrition common bean varieties.

Evaluation of analytical methods for Fe, Zn and PA in common bean

Quantitative methods for Fe and Zn in common bean

Currently, mineral content in common bean is typically determined by inductively coupled plasma atomic emission spectrometry (ICP-AES), inductively coupled plasma-mass spectrometry (ICP-MS), X-ray fluorescence spectroscopy (XRF) and atomic absorption spectroscopy (AAS). Flame atomic absorption spectroscopy (FAAS) offers excellent short-term precision (0.1-1%), but it requires time-consuming wet digestion and dilution (Rasool *et al.*, 2019; Mogwasi *et al.*, 2022). ICP-MS considered the gold standard in biofortification research for validating Fe, Zn and Se data obtained via XRF or AAS. Authors who used ICP-MS to establish reference values for common bean reported that portable energy-dispersive X-ray fluorescence spectroscopy (EDXRF) delivers Fe (35-95 mg kg⁻¹) and Zn (20-55 mg kg⁻¹) within 1-2 minutes with $r \geq 0.93$ compared to ICP-MS, thus meeting the throughput demanded by breeding programmes (Guild *et al.*, 2017). Likewise, 20min microwave digestion ICP-AES yielded Fe (34-97 mg kg⁻¹) and Zn (21-55 mg kg⁻¹), correlating with EDXRF at $r \geq 0.94$, confirming that XRF is suited for high-throughput pre-screening while ICP-AES/MS provides definitive values (Stangoulis and Knez, 2022). For a detailed overview of the detection principles and key characteristics of these analytical techniques, please refer to Table 1.

Quantitative methods for PA in common bean

Six of PA's twelve ionizable hydrogen atoms have significant acidity (pKa 1.1-2.1) (Lönnerdal, 2002). Therefore, under physiological pH conditions, PA exhibits substantial ionization and a negative charge, readily binding cationic entities to form phytates (Kulathunga *et al.*, 2024). At pH < 3, this acidic environment promotes the dissociation of PA-metal complexes. However, when

pH>4, insoluble metal phytates tend to form and precipitate (Marolt and Kolar, 2020). This pH-dependent dissolution-precipitation equilibrium directly affects the extraction efficiency of PA. In most studies focusing on PA extraction from legumes, hydrochloric acid at a concentration of approximately 0.6 mol L⁻¹ is commonly employed (Park *et al.*, 2006; Al-Numair *et al.*, 2009). Compared to analytical detection methods, the purification of PA has received comparatively little standalone investigation. Owing to its cost-effectiveness and superior efficiency, ion-exchange chromatography predominates over traditional purification methods like precipitation (Marolt and Kolar, 2020). Currently, a variety of mature methodologies have been developed for the qualitative and quantitative analysis of PA, with a comprehensive summary provided in Table 2. However, the effectiveness of each method varies significantly depending on the sample type. Thus, selecting and optimizing the most suitable analytical strategy based on sample matrix and research objective remains essential for achieving accurate and reproducible phytic acid quantification.

Genetic diversity and varietal differences in Fe and Zn content in common bean

Common bean is among the most thoroughly investigated legumes for micronutrient composition and has been shown to exhibit significant genotypic differences in Fe and Zn content across different varieties. Islam *et al.* (2002) observed that genotypes from the Andean and Mesoamerican gene pools generally differ in seed mineral concentrations. Specifically, common bean from the Mesoamerican gene pool shows higher Zn content but lower Fe content than that from the Andean pool (Islam *et al.*, 2002). Beebe *et al.* (2000) evaluated Fe and Zn content in 1,031 cultivated common bean accessions and 119 wild accessions. The average Fe content in cultivated common beans was 55 mg kg⁻¹, ranging from 34-89 mg kg⁻¹, while

Table 1: Comparative evaluation of analytical methods for Fe and Zn quantification in common bean.

Method	Detection principle	Key characteristics	Reference
EDXRF	Detects characteristic X-ray energies from excited samples	Non-destructive, <10 min/sample, limited sensitivity for light elements (S, P)	(Światły-Błaszczewicz <i>et al.</i> , 2025)
WDXS	Detects characteristic X-ray wavelengths under X-ray excitation	Non-destructive, multi-element, high-throughput, best fit for Ca/Mn/Cu/Zn	(Perring <i>et al.</i> , 2005)
ICP-AES	Element excitation in high-temperature plasma with characteristic emission spectra	Wide linear range, RSD<5%, internal standard for matrix	(Hannaker <i>et al.</i> , 1984)
ICP-MS	Ionization in plasma followed by mass-to-charge ratio separation	Ultra-high sensitivity, lowest LODs, collision cell (e.g., He for ⁴⁰ Ar ¹⁶ O ⁺ interference on ⁵⁶ Fe)	(Meyer <i>et al.</i> , 2018)
FAAS	Absorption of specific wavelength light by atomized elements	Low cost, simple operation, single-element sequential, moderate Fe/Zn sensitivity	(Mohd Fairulnizal <i>et al.</i> , 2019)
GFAAS	Atomization in graphite tube, absorption measurement	Higher sensitivity than FAAS, minimal sample volume (μL), background correction (Zeeman)	(Mohd Fairulnizal <i>et al.</i> , 2019)

WDXS: Wavelength-dispersive X-ray spectroscopy, RSD: Relative standard deviation, LOD: Limit of detection, GFAAS: Graphite furnace atomic absorption spectrophotometry.

the average Zn content was 35 mg kg⁻¹, with a range of 21-54 mg kg⁻¹. In contrast, the average Fe content in wild common beans was 60 mg kg⁻¹, with a peak value of 96 mg kg⁻¹ and the average Zn content was 29 mg kg⁻¹, peaking at 34 mg kg⁻¹. The coefficients of variation for Fe and Zn contents in cultivated common beans were 15% and 14%, respectively, while those in wild common beans were 17% and 15.5%, indicating substantial potential for genetic improvement (Beebe *et al.*, 2000). The Fe and Zn content in common beans is regulated by multiple genetic mechanisms. Subsequently, they utilized two sets of near-isogenic lines derived from crosses between parental materials with differing Fe and Zn concentrations to further dissect the genetic characteristics underlying iron and zinc accumulation in common bean (Blair *et al.*, 2009). However, Astudillo-Reyes *et al.* (2015) crossed the high-Zn cultivar Voyager with the low- Zn cultivar Albin and measured Zn content in the parents, F₁, F₂ and backcross generations. The results indicated that high Zn content in seeds is governed by one dominant gene, with a broad-sense heritability of 0.84 and a narrow-sense heritability of 0.82. These high heritability values suggest that breeding programs aimed at increasing seed Zn content can be effective in selecting for this trait at early generations (Astudillo-Reyes *et al.*, 2015).

Moreover, genetic variations that influence levels of Fe and Zn can be expressed across different environments and seasons. This implies that superior genotypes with high Fe or Zn content selected in one environment can maintain their high concentrations characteristics in other environments. Gelin *et al.* (2007) used 73 recombinant inbred lines (RILs) derived from the Voyager/Albin cross, determined Fe and Zn concentrations in this segregating population and observed transgressive segregation.

Correlation analyses revealed significant positive correlations between Fe and Zn contents and macronutrients such as calcium and phosphorus, as well as yield traits, with correlations of 0.40, 0.23, 0.39 and 0.21. Additionally, Fe content showed a positive correlation with seed weight ($r = 0.61$) (Gelaw *et al.*, 2023).

In summary, significant genetic variation and high heritability exist for Fe and Zn content in common bean and both elements show consistent positive associations with seed weight and macronutrient content. Collectively, this evidence suggests that the uptake, transport and accumulation of Fe and Zn in seeds may be partly regulated by shared genetic factors, thereby providing a genetic basis for the simultaneous selection of common bean varieties with high Fe and Zn content, large seed size and high yield potential.

Distribution and impact of PA in common bean

Studies have shown that PA can be stored in different tissues and organs in crops. In mature leguminous plants, most phosphorus occurs as phytate, which accounts for 60-90% of the total phosphorus in dormant seeds and is primarily formed during the maturation process, with particularly high concentrations in the embryo, cotyledons and seeds (Cui *et al.*, 2023). In these tissues, PA typically chelates mineral cations (Ca²⁺, Fe³⁺, Zn²⁺, Mg²⁺, K⁺) to form insoluble phytate complexes.

PA levels vary markedly across common bean cultivars. Shang *et al.* (2015) analyzed the PA content of 56 common bean varieties and found that the average value was 3.102 mg g⁻¹, with a coefficient of variation less than 41%, indicating significant variation in PA accumulation capacity among different varieties (Shang *et al.*, 2015). When studying the pods of common beans with two different

Table 2: Comparative evaluation of analytical methods for PA quantification in common bean.

Method	Detection principle	Key characteristics	Reference
HPLC-MS/MS	Amide-column separation, triple-quadrupole MS of m/z	LOD:0.012mg/L,no derivatization, enables simultaneous detection of phytic acid and its degradants (IP1-IP5)	(Barbosa-Pereira <i>et al.</i> , 2021)
HPLC	Ultrasound cell disruption,RP-LC with UV detection	Extraction efficiency increased by 41.3%, pretreatment time reduced	(Castro Alba <i>et al.</i> , 2019)
SP	Competition with Felz-sulfosalicylate, absorbance drop at 500 nm	Simple, low cost, yet prone to low-grade inositol phosphate interference	(Fabbri <i>et al.</i> , 2016)
IC	Anion-exchange separation, conductivity detection	Phosphorylated inositol variants separable	(Chen and Li, 2003)
NMR	Chemical shift of phytic acid phosphate group detected by ³¹ P NMR (~4.5 ppm)	Non-destructive, resolves phytic acid isomers, but costly and low-sensitivity	(Hernández-Guerrero <i>et al.</i> , 2021)
Colorimetric assay	Phytase hydrolysis, molybdenum-blue determination	Highly specific, yet enzyme-dependent, pH and temperature must be strictly controlled	(Melini and Melini, 2021)

HPLC-MS/MS: High performance liquid chromatography-tandem mass spectrometry, HPLC: High performance liquid chromatography, RP-LC: Reversed-phase liquid chromatography, UV: Ultraviolet, SP: Spectrophotometry, IC: Ion chromatography, NMR: Nuclear magnetic resonance.

growth habits, namely dwarf and climbing types, it was found that the PA content decreased during pod development in both types. In dwarf common beans, the PA content decreased from 15.07 mg g⁻¹ to 14.33 mg g⁻¹, while in climbing common beans, the PA content decreased from 14.57 mg g⁻¹ to 12.18 mg g⁻¹. These results indicate that, despite differences in the absolute levels of phytate accumulation between the two bean types, they exhibit similar dynamic patterns of phytate accumulation during pod development.

Metabolism and interaction mechanisms of Fe, Zn and PA in common bean

Molecular mechanisms of Fe and Zn uptake and transport

In leguminous plants, the proteins H⁺-ATPase (the enzyme of HA2, H⁺-ATPase family), ferric reduction oxidase (*FRO2*) and the iron-regulated transporter 1 (*IRT1*) mainly facilitate iron acquisition and translocation to root systems (Fig 1a) (Roorkiwal *et al.*, 2021). The plasma membrane transporter yellow stripe-like protein (*YSL*) facilitates Fe acquisition via Fe³⁺-phytosiderophore uptake (Curie *et al.*, 2001; Zhang *et al.*, 2024). *IRT1* transporter is responsible for initial Fe uptake (Palmer and Guerinot, 2009). Other transporters including zinc-induced protein (*ZIP*) and *YSL* facilitate metal transfer in the xylem (Fig 1a) (Gupta *et al.*, 2021).

When it comes to Fe regulation in plants, the *NRAMP* gene family, which covers *NRAMP3* and *NRAMP4*, holds a crucial part in maintaining iron balance, whereas *YSL* and Oligopeptide transporters (*OPTs*) are responsible for the movement of iron-nicotianamine (NA) complexes within and beyond the phloem (Palmer and Guerinot, 2009). The Fe reductase defective 3 (*FRD3*) protein governs Fe distribution in plants (Rogers and Guerinot, 2002). NA is a plant-derived non-protein amino acid that pops up all over the plant kingdom, particularly in stem tissues. This compound has a knack for binding to various metal ions, which makes it absolutely essential for shuttling Fe and Zn around and keeping these vital elements in balance within the plant (Pich *et al.*, 1994). *YSL* genes additionally facilitate translocation during seed maturation, reproductive organ development and systemic movement of metal-NA complexes (DiDonato *et al.*, 2004). In summary, the candidate gene families and their encoded transport systems outlined above hold significant potential for improving the uptake efficiency and bioavailability of Fe and Zn in crops.

Zn²⁺ is the primary form in which Zn crosses the plasma membrane of root cells for uptake. Zn translocation from roots to seeds is facilitated by *ZIP* transporters (Palmgren *et al.*, 2008). Primary Zn transport systems include zinc-regulated transporter (*ZRT*), *IRT*-like proteins, heavy metal ATPases (*HMA*), Zinc-induced facilitator (*ZIF*) and metal tolerance proteins (*MTP*) families (Fig 1a) (Gupta *et al.*, 2016). Specific *ZIP* genes contributing to Zn transport have been identified in common bean, including *PvZIP12*, *PvZIP13*, *PvZIP16* and *PvbZIP1* (Astudillo *et al.*, 2013).

The movement of Zn within the stem is shaped by a combination of symplastic and apoplastic pathways. When it comes to apoplastic Zn transport, the element makes its way into the cytoplasm by crossing the plasma membrane that interfaces with the cell wall, which is a process that casts a wider net in terms of selectivity compared to its symplastic counterpart. By contrast, symplastic transport selectively regulates the passage of which nutrients get through and in what quantities, making it a more gatekeeper-like system (Gupta *et al.*, 2016). The transporters *MTP1* and *ZIF1* are involved in the sequestration of Zn into vacuoles, while members of *NRAMP* family participate in the mobilization of Zn out of the vacuole (Haydon and Cobbett, 2007). Zn enters the xylem via *HMA* and is transported within the xylem either as Zn²⁺ or as complexes with histidine or NA (Palmgren *et al.*, 2008). *YSL* proteins are engaged in loading Zn into the phloem and releasing it into the seeds in the form of Zn-NA complexes. *ZIP* transporters mediate the influx of Zn²⁺ into leaf tissues and the phloem (Waters and Grusak, 2008). The expression of the genes *IRT1*, *FRO1* and *Ferritin1* serves a pivotal function in iron and Zn absorption/transport

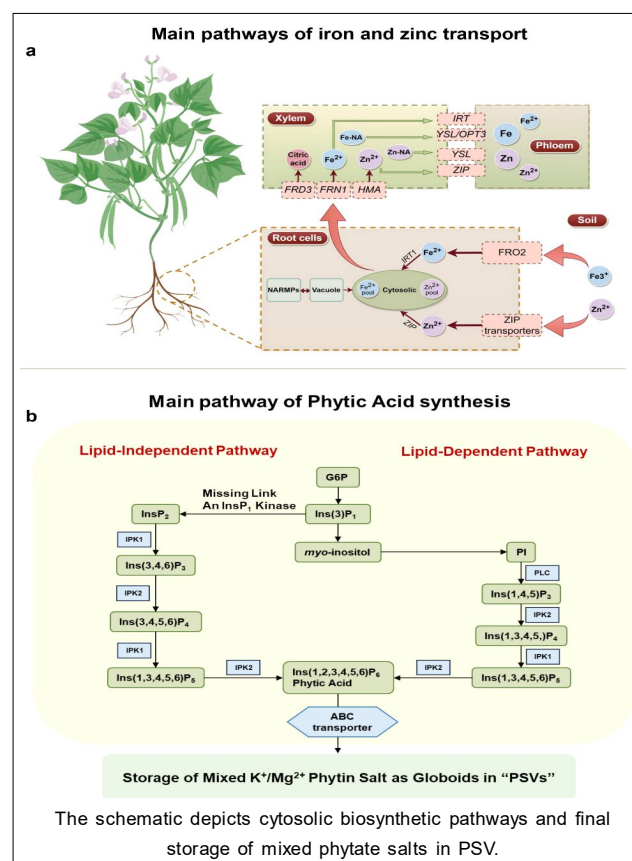


Fig 1: (a) Main pathways of Fe and Zn transport in common bean. Key processes include root uptake and xylem/phloem translocation. Created with Fig draw. (b) Metabolic network of PA biosynthesis.

and signaling under Fe and Zn stress. In contrast, the manifestation of the genes *ZIP2*, *NRAMP1*, *HA2* and *GLP1* is highly sensitive to Zn uptake (Urwat *et al.*, 2021). Furthermore, comprehensive genomic characterization and transcriptomic profiling of *MTP* genes by Yilmaz *et al.* showed that *PvMTP4*, *PvMTP5* and *PvMTP12* are important for Fe and Zn absorption and transport. The concentrations of Fe and Zn in seeds were substantially associated with their expression levels of these aforementioned genes (Yilmaz *et al.*, 2023).

Biosynthesis of PA

The cytoplasm acts as the main site for PA biosynthesis. During its synthesis, a six-carbon ring structure is initially formed, which subsequently yields inositol (cyclohexanehexol). Inositol then undergoes multiple phosphorylation reactions to form PA (Raboy, 2007). During seed germination, PA serves as a phosphorus storage reservoir and is hydrolyzed to release phosphorus for utilization by the developing seedling (Larson and Raboy, 1999). In the initial phase of seed development, inositol is an important component of the endosperm and seed coat. PA synthesized in seeds is stored in the form of mixed salt inclusions (e.g., calcium or magnesium phytates) within the protein storage vacuoles (PSVs) of cells (Madsen and Brinch-Pedersen, 2020).

PA biosynthesis requires *myo*-inositol as the carbon skeleton. In *myo*-inositol synthesis, glucose-6-phosphate (G6P) serves as the primary substrate and is transformed by *myo*-inositol-3-phosphate synthase (MIPS) into *myo*-inositol-3-phosphate (Melini *et al.*, 2021). The expression of *MIPS* genes is closely related to PA synthesis within cells during seed development.

In seeds, PA can be produced from inositol via two distinct pathways: lipid-dependent and lipid-independent, as illustrated in Fig 1b. These pathways differ in whether lipid substances are involved in the conversion of inositol triphosphate (InsP_3). On the one hand, the lipid-dependent pathway is the primary pathway for PA synthesis in most eukaryotic organisms (including the vegetative organs of plants). Other inositol phosphates formed in this process are very important for signal transduction (York *et al.*, 1999; Seeds *et al.*, 2004; Fujii and York, 2005; Stevenson-Paulik *et al.*, 2005). In the lipid-dependent pathway, inositol is initially transformed into phosphatidylinositol (PI). This complex is first cleaved by specific phospholipase C (PLC) to yield IP_3 , which is subsequently converted into PA through phosphorylation at multiple sites catalyzed by three distinct inositol polyphosphate kinases (IPK) (Raboy, 2009). On the other hand, when PA functions as a phosphorus reserve in seeds or other organs, its synthesis is likely to occur primarily via the lipid-independent pathway. In common bean, PA is synthesized stepwise in the cytosol via the lipid-independent pathway, wherein *myo*-inositol is sequentially phosphorylated to soluble inositol phosphates and finally converted to PA. The resulting PA is then sequestered as mixed Ca^{2+} - Mg^{2+} phytate within specialized

storage vacuoles (Stephens and Irvine, 1990; Brearley and Hanke, 1996). Compared with the lipid-dependent pathway, the most significant difference in the lipid-independent pathway is whether the sequence inositol/inositol phosphate/ inositol diphosphate is made possible by *myo*-inositol kinase (MIK) and inositol monophosphate kinase. The lipid-dependent pathway has a relatively smaller impact on the PA content in plant seed organs. The key enzyme-encoding genes in the PA synthesis pathway play an important role in common bean seeds.

Physiological implications of PA interactions with Fe/Zn

In plants, PA uses its six negatively charged phosphate groups to form stable, insoluble complexes with $\text{Fe}^{2+}/\text{Fe}^{3+}$ and Zn^{2+} through multidentate coordination. Due to the lack of endogenous phytase in the digestive tracts of monogastric animals, these complexes cannot be effectively degraded, making it difficult for them to dissociate and be absorbed in the small intestine. This significantly reduces the bioavailability of trace elements such as Fe and Zn, thereby increasing the risk of deficiencies caused by inadequate intake (Zhang *et al.*, 2022). During seed maturation in common bean and other legumes, this complexation occurs largely in the cytosol. The resulting mixed phytate salts are then immediately sequestered as globoid crystals within protein storage vacuoles (PSVs) (Madsen and Brinch-Pedersen, 2020). Under conditions of high-Zn stress, analogous Zn-phytate globular deposits can also be detected in root cortical and endodermal cells.

Phytate formation is tightly coupled to PA synthesis. Therefore, targeted modulation of the expression of key synthesis genes (e.g., *MIPS*, *MIK* and *IPK*) through gene-editing and related technologies can effectively alter PA accumulation (Fileppi *et al.*, 2010; Pelletier *et al.*, 2017), thereby influencing the nutritional availability of essential minerals including Fe and Zn. Furthermore, the synthesis of PA is also closely associated with various physiological processes such as carbohydrate metabolism, signal transduction, hormone regulation, inositol/phosphoinositol metabolism and ROS responses. IP_{1-4} has been shown to have a negligible impact on Zn absorption in animal studies. Similarly, only inositol phosphates below IP_3 had no influence on Fe bioavailability, according to five human investigations utilizing extrinsic labeling (Sandberg *et al.*, 1999). These findings are significant for understanding the relationship between Fe/Zn content and PA accumulation in common bean, elucidating their collective impact on mineral bioavailability.

Genetic network regulating the accumulation of Fe, Zn and biosynthesis of PA

Genetic networks regulating Fe/Zn accumulation in common bean

To date, biofortification efforts have depended on phenotypic selection for advanced breeding lines based on seed mineral concentrations. To identify genomic regions

associated with elevated Zn and Fe in seeds, numerous QTL analyses have been conducted. For example, employed QTL mapping to analyze the molecular genetic characteristics of Fe and Zn content in common bean. Their results revealed that Fe content in common bean is connected to two loci situated on separate chromosomes (QTL1-Fe\QTL2-Fe), while Zn content is associated with one locus (QTL1-Zn) (Guzmán-Maldonado *et al.*, 2003).

QTL analysis helps pinpoint genetic regions influencing Fe and Zn accumulation in wild species and landraces, thus speeding up the formation of varieties with improved Fe and Zn richness. Supporting this, Gelin *et al.* (2007) used a RIL population generated from the Voyager/Albin cross to confirm that the gene controlling Zn content in common beans is located on linkage group 9. Fe and Zn concentrations are subject to multigenic control. Using 87 RILs from the cross of DOR364 × G19833, Blair *et al.* found 26 QTLs linked to Fe and Zn content in common bean, including 13 Fe-related and 13 Zn-related QTLs (Blair *et al.*, 2010). Among these, 11 QTLs (5 for Fe and 6 for Zn) clustered in the upper half of linkage group B11 (currently designated as Pv11) and these 11 loci can account for 47.9% of the phenotypic variation, which may be important loci for marker-assisted selection. In a subsequent study, Izquierdo *et al.* identified two Fe-specific meta-QTLs and two Zn-specific meta-QTLs. Eight meta-QTLs that co-localize with genetic segments linked to Fe and Zn concentration were identified across seven chromosomes. Loci for Zn mapped to linkage groups B3, B6, B7 and B9, while those for iron were found on B4, B6, B7 and B9. Meta-QTLs that are common to both Fe and Zn represent valuable targets for marker-assisted breeding designed to enhance seed levels of these two micronutrients concurrently. Furthermore, the study identified 12 meta-QTLs, five of which harbored candidate genes from six gene families participating in plant Fe and Zn transport (Izquierdo *et al.*, 2018). These results were further corroborated by a diallel cross experiment utilizing six parental lines, which demonstrated narrow-sense heritability values of 71% for Fe and 83% for Zn. Notably, the two elements showed a robust positive correlation, evidenced by a correlation coefficient of $r = 0.75$ (Mukamuhirwa *et al.*, 2025). Cyclic selection and backcrossing based on quantitative genetics is expected to serve as a tool for creating Fe-rich and Zn-rich genotypes.

Gelaw's group estimated SNP markers linked to grain Fe and Zn contents by analyzing 289 common bean genotypes using 11,480 SNP markers (Gelaw *et al.*, 2023). The results indicated that 43 QTLs were associated with grain iron and zinc concentrations. Notably, five quantitative trait nucleotides (QTNs), namely QTN Fe_1.1, QTN Fe_6.3, QTN Fe_6.5, QTN Fe_10.3 and QTN Fe_11.6, were detected at both Haramaya and Melkassa locations. QTN Fe_11.6 showed a large, consistently positive effect in all regions. These five stable QTNs and potential candidate genes can be employed for Fe biofortification through

marker-assisted selection. Complementarily, Maxwell *et al.* identified genetic variability in Fe and Zn content in the common bean crosses CAL96 × RWR2154 and MCR-ISD-672 × RWR2154 and confirmed that the accumulation of high concentrations is significantly influenced by combined and interactive genetic influences (Lampitey *et al.*, 2023). Both crosses exhibited moderate to high broad sense heritability for Fe and Zn, but their narrow sense heritability values fluctuated. Therefore, selection in early segregating generations to improve Fe and Zn contents would be an effective strategy. The results generally showed that common bean F_1 hybrids had superior Fe and Zn contents compared to mid-parents and better-parents, exhibiting significant heterosis. Key QTLs associated with Fe and Zn content are summarized in Table 3 and their corresponding chromosomal distributions and effects are visualized.

Genetic manipulation of PA biosynthesis

In common bean, several QTL associated with PA biosynthesis and accumulation have been identified. Blair *et al.* (2009) detected four QTLs associated with total seed phosphorus content and two QTLs linked to PA content. Mapping in a RIL common bean panel showed that they were located on chromosomes B5 and B7, respectively (Blair *et al.*, 2009). Their subsequent research further revealed that the QTLs controlling phytate accumulation in common bean seeds could be categorized into two types: one determining the PA proportion (key to nutritional quality) and the other determining the net content (associated with seed weight, influencing seed phosphorus reserves and ecological adaptability). Notably, a key co-localized region controlling both seed phosphorus content and seed weight coincided with the known *Phs* locus, providing a critical target for synergistically improving nutritional quality and agronomic traits through genetic breeding (Blair *et al.*, 2012). The major QTLs are summarized in Table 3 and visually integrated in. Beyond common bean, silenced the gene that encodes inositol pentakisphosphate 2-kinase 1 (*IPK1*) in durum wheat using the TILLING method. They found that in the single knockout mutants, PA accumulation in the grains was diminished, while the contents of certain essential micronutrients, like Fe, Zn and manganese, were increased (Frittelli *et al.*, 2023). Therefore, selective silencing of PA biosynthesis-related genes, like *MIPS* and *IPK*, can influence PA content, thus altering the bioavailability of Fe and Zn.

To date, there have been no definitive reports confirming the co-localization of genes related to PA metabolism with Fe and Zn QTLs in common bean.

Challenges and strategies in biofortification breeding

Biofortification must not only increase micronutrient levels in crops but also reduce antinutritional compounds to improve mineral bioavailability (Hummel *et al.*, 2020). The challenge in enhancing the nutritional value of plant-based Fe and Zn lies in their inherently low bioavailability (La Frano *et al.*, 2014). To address this, breeding objectives

Table 3: QTL identification for Fe, Zn and PA levels in common bean using biparental mapping and association mapping.

QTL	MP	Marker	Chr	Trait	Reference
<i>Fe-ICPa4</i>	RIL	BMd16	4	Fe concentration (mg kg ⁻¹)	(Blair <i>et al.</i> , 2009)
<i>Fe-ICPa6</i>	RIL	Bng95	6		
<i>Fe-ICPa7</i>	RIL	Bng60	7		
<i>Fe-ICPa8.1</i>	RIL	M13D	8		
<i>Fe-ICPa8.2</i>	RIL	Bng96	8		
<i>Fe-ICPa11.1</i>	RIL	BMd33	11		
<i>Fe-ICPb8.1</i>	RIL	H203D	8		
<i>Fe-ICPb11.1</i>	RIL	BMd33	11		
<i>Fe-ICPb11.2</i>	RIL	Bng187	11		
<i>Fe-AASb4</i>	RIL	BMd16	4		
<i>Fe-AASb7</i>	RIL	Bng60	7	Zn concentration (mg kg ⁻¹)	
<i>Fe-AASb11.1</i>	RIL	BMd22	11		
<i>Fe-AASb11.2</i>	RIL	BMd27	11		
<i>Zn-ICPa3</i>	RIL	I161G	3		
<i>Zn-ICPa7</i>	RIL	M125D	7		
<i>Zn-ICPa11</i>	RIL	BMd33	11		
<i>Zn-ICPb3</i>	RIL	L064D	3		
<i>Zn-ICPb9</i>	RIL	AK067G	9		
<i>Zn-ICPb11.1</i>	RIL	BMd27	11		
<i>Zn-ICPb11.2</i>	RIL	K126G	11		
<i>Zn-AASb3</i>	RIL	F702G	3		
<i>Zn-AASb6.1</i>	RIL	DA39	6		
<i>Zn-AASb6.2</i>	RIL	AK061D	6		
<i>Zn-AASb11.1</i>	RIL	Bng91	11		
<i>Zn-AASb11.2</i>	RIL	BMd27	11		
<i>Zn-AASb11.3</i>	RIL	K126G	11		
<i>SeedFe-LP2005_1</i>	RIL	Bmd10	1	Fe content (µg seed ⁻¹)	(Cichy <i>et al.</i> , 2009)
<i>SeedFe-LP2005_6</i>	RIL	BM170	6		
<i>SeedFe-LP2005_11</i>	RIL	GGAG02	11		
<i>SeedFe-HP2005_1</i>	RIL	fin	1		
<i>SeedFe-HP2005_5</i>	RIL	GGAT02	5		
<i>SeedFe-HP2005_6</i>	RIL	BM170	6		
<i>SeedFe-HP2005_9</i>	RIL	GCTC02	9		
<i>SeedFe-HP2005_11</i>	RIL	GGAG01	11		
<i>SeedFe-LP2000_6</i>	RIL	AGAC01	6		
<i>SeedFe-LP2000_8</i>	RIL	M12.1600A	8		
<i>SeedFe-LP2000_11</i>	RIL	GGAG02	11	Zn content (µg seed ⁻¹)	
<i>SeedFe-HP2000_6</i>	RIL	AGAT05	6		
<i>SeedZn-LP2005_1</i>	RIL	fin	1		
<i>SeedZn-LP2005_6</i>	RIL	AGAT05	6		
<i>SeedZn-LP2005_11</i>	RIL	CTTA02	11		
<i>SeedZn-HP2005_1</i>	RIL	fin	1		
<i>SeedZn-HP2005_11</i>	RIL	CTAA04	11		
<i>SeedZn-LP2000_1</i>	RIL	BMd10	1		
<i>SeedZn-LP2000_6</i>	RIL	AGAT05	6		
<i>SeedZn-LP2000_11</i>	RIL	CTTA02	11		
<i>SeedZn-HP2000_1</i>	RIL	PV7	1		
<i>SeedZn-LP2000_5</i>	RIL	CGTC01	5		
<i>SeedZn-HP2000_6</i>	RIL	AGAT05	6		

Table 3: Continue..

Table 3: Continue..

QFeDaAA4.1	RIL	BMc127	4	Fe concentration (mg kg ⁻¹)	(Blair <i>et al.</i> , 2010)
QFePaAA6.1	RIL	R0405B	6		
QFePaAA7.1	RIL	BMc248	7		
QFePoAA6.1	RIL	BM158	6		
QFePoICP6.1	RIL	BM158	6		
QZnDaAA6.2	RIL	V1001B	6	Zn concentration (mg kg ⁻¹)	
QZnDaAA8.2	RIL	H1201A	8		
QZnPaAA6.1	RIL	BM158	6		
QZnPaAA8.2	RIL	H1201A	8		
QZnPoAA2.1	RIL	PV15	2		
QZnPoAA3.1	RIL	BMd1	3		
QZnPoAA6.1	RIL	BM158	6		
QZnPoICP6.1	RIL	BM158	6		
QFe_contDaAA6.1	RIL	BM218	6	Fe content (mg seed ⁻¹)	
QFe_contPaAA1.1	RIL	W0901B	1		
QFe_contPaAA7.1	RIL	BM201	7		
QZn_contDaAA1.1	RIL	W0901B	1	Zn content (mg seed ⁻¹)	
Fe-ICP2a	RIL	H1902B	2	Fe concentration (mg kg ⁻¹)	(Blair <i>et al.</i> , 2011)
Fe-ICP7a	RIL	BM185	7		
Fe-ICP9a	RIL	MBc65	9		
Fe-AAS2a	RIL	E0403A	2		
Fe-AAS6b	RIL	BM137	6		
Fe-AAS6c	RIL	N0401B	6		
Zn-AAS2c	RIL	PV11	2	Zn concentration (mg kg ⁻¹)	
Zn-AAS7c	RIL	BM239	7		
Zn-AAS8c	RIL	BM165	8		
SdFe3.1	RIL	Chr03_128924_178169	3	Fe concentration (mg kg ⁻¹)	(Diaz <i>et al.</i> , 2022)
SdFe3.2	RIL	Chr03_32241300_32532209	3		
SdFe6.3	RIL	Chr06_26259338_26444453	6		
SdFe6.4	RIL	Chr06_28871402_28878273	6		
SdZn4.1	RIL	Chr04_22568_55665	4	Zn concentration (mg kg ⁻¹)	
SdZn5.1	RIL	Chr05_3779357_3956110	5		
SdZn5.1	RIL	Chr05_11706425_11785008	5		
SdZn8.2	RIL	Chr08_62309944_62325409	8		

Table 3: Continue..

Table 3: Continue..

<i>SdZn10.1</i>	RIL	Chr10_ 7899489_ 8099574	10		
<i>DArT-3366319</i>	NP	SNP	8	Zn concentration (mg kg ⁻¹)	(Altaf <i>et al.</i> , 2025)
<i>DArT-3372823</i>	NP	SNP	6		
<i>Zn-5388249</i>	NP	SNP	11	Zn concentration (mg kg ⁻¹)	(Mukamuhirwa <i>et al.</i> , 2025)
<i>Zn-5397187</i>	NP	SNP			
<i>Zn-5397233</i>	NP	SNP			
<i>Zn-5456950</i>	NP	SNP			
<i>Zn-5598498</i>	NP	SNP			
<i>Ppa6.1</i>	RIL	V100.16B	6	Total seed phytate (%)	(Blair <i>et al.</i> , 2009)
<i>Pac5.1</i>	RIL	BMd018B	5	Net phytate content (mg seed ⁻¹)	
<i>Pac7.1</i>	RIL	BMd40	7		
<i>Seed phytic acid% _LP2005</i>	RIL	I6.550A	8	Seed phytic acid content (mg seed ⁻¹)	(Cichy <i>et al.</i> , 2009)
<i>Seed phytic acid% _HP2005</i>	RIL	PVctt1	4		

MP: Mapping population, Chr: Chromosome, NP: Natural population.

must shift from merely increasing mineral concentrations toward improving the release of these minerals during digestion and their binding efficiency with intestinal transporter proteins (Petry *et al.*, 2010).

Synergistic enhancement of mineral bioavailability

Iron bean, developed as biofortified varieties with increased Fe and Zn contents through biofortification programs (Saltzman *et al.*, 2017). Iron-bean targets (94 mg kg⁻¹) are derived from population intake, storage and processing losses and human bioavailability, approximately double the 50 mg kg⁻¹ concentration typically found in common bean (Hotz and McClafferty, 2007; Bouis and Saltzman, 2017). Thus far, studies on the Fe bioaccessibility and bioavailability of biofortified beans have employed the Caco-2 cell model (Tako *et al.*, 2016), *in vitro* digestion models (Wiesinger *et al.*, 2016; Glahn *et al.*, 2017; Wiesinger *et al.*, 2018) and others. Zn is also a key target in common bean breeding programs. Zn represents another key target in common bean breeding programs. Research has demonstrated that crosses with *Phaseolus parvifolius* can lead to a significant increase in seed Zn content (Diaz *et al.*, 2022). However, assessing Zn bioavailability remains challenging, as *in vitro* methods are ineffective, necessitating *in vivo* studies (Devarshi *et al.*, 2024). Breeders now need quick, cheap phenotyping tools that fit large-scale programs. Seed-coat color is one such trait that modulates micronutrient accumulation in common bean. Katuuramu *et al.* (2021) demonstrated that red-mottled accessions accumulate the highest Zn and Fe concentrations, whereas yellow/white-seeded genotypes exhibit superior Fe uptake capacity; notably, the Manteca landrace combines both advantageous traits. Despite these insights into the phenotypic correlation between seed-coat color and micronutrient traits, no

commercial varieties with inherently enhanced Fe/Zn uptake efficiency have been officially released to date. Enhancing the bioavailability of Fe and Zn would therefore allow biofortified beans to exert substantial nutritional benefits even at moderate consumption levels.

Reducing PA represents a direct pathway to enhancing mineral bioavailability (Campion *et al.*, 2009; Petry *et al.*, 2013). To date, the low-phytic-acid (*lpa*) mutants identified and profiled in common bean correspond to mutations in genes encoding ABC transporters that are similar to Arabidopsis *AtMRP5* (Nagy *et al.*, 2009; Panzeri *et al.*, 2011). Campion *et al.* (2009) isolated a homozygous mutant line, *lpa-280-10*, from a mutagenized population of common bean. In contrast to the wild type, this line exhibited a 90% reduction in PA and a 25% reduction in raffinose, coupled with substantially elevated levels of uncomplexed or loosely iron ions within the seeds. Moreover, two years of field trials showed no negative impact on yield. The novel *lpa-280-10* mutant may be the first to show no discernible detrimental effects on the plant, pod, or seed. However, potential pleiotropic effects warrant careful consideration (Petry *et al.*, 2016). For instance, reduced PA may lead to alternative binding forms of Zn or increased leaching of Zn into processing water (Hummel *et al.*, 2020). Therefore, systematic comparison of *lpa* mutants is required to clarify whether these effects stem from PA reduction itself or from regulatory roles of PA-pathway components (Sparvoli and Cominelli, 2015; Freed *et al.*, 2020).

Integration of multi-strategy approaches and precision breeding

Currently, achieving a balance between Fe and Zn enrichment and PA reduction has become a top priority in breeding goals. Previous studies have shown that when the PA/Fe

Table 4: Comparison of major biofortification approaches.

Strategy	Core approach	Key advantages	Major limitations	Reference
Genetic improvement	Breeding nutrient enhanced varieties	Sustainable, precise, cost effective, long term	Long cycles, high costs, regulatory barriers	(Varshney <i>et al.</i> , 2021)
Agronomic fortification	Field based nutrient management	Flexible, rapid, targeted	Environment dependent, recurring costs	(White and Broadley, 2009)
Dietary intervention	Post harvest processing, dietary strategies	Consumer directed, culturally adaptable	Acceptance dependent, may alter food properties	(Gibson <i>et al.</i> , 2010)

molar ratio remains <1 , PA hardly inhibits Fe absorption, whereas >1 strongly suppresses it. Likewise, Zn bioavailability stays high as long as $PA/Zn < 15$, but drops sharply once that threshold is exceeded (Grases *et al.*, 2004). This finding provides a key reference for breeding superior common bean varieties rich in Fe and Zn yet low in PA.

Environmental factors exert a profound influence on the interactions among these three components (Bhattacharya *et al.*, 2025). Acidic soils enhance phytate-metal binding, whereas alkaline soils precipitate metals and hydrolyze PA (Nath *et al.*, 2024). Symbiotic microorganisms, such as rhizobia and arbuscular mycorrhizal fungi (AMF), can enhance Fe and Zn uptake while regulating PA metabolism through the secretion of organic acids and siderophores (Zhang *et al.*, 2021). Thus, harnessing plant-microbe interactions has emerged as an effective strategy for iron and zinc biofortification in crops (Nazma *et al.*, 2025). A separate study quantified genotype-environment effects on seed Zn, Fe and Fe iron bioavailability (FeBIO). Genotype explained 28.0% of Zn variation, location 26.2% and location $\times$ season 14.7%. For Fe, genotype accounted for 25.7% and location 17.4% (Katuuramu *et al.*, 2021).

These findings underscore that any effective biofortification strategy must systematically address the complex challenges posed by genotype, environment and their interactions. Given this complexity, relying on a single technological approach is unlikely to reliably produce nutritionally stable, widely adapted and agronomically balanced varieties. Consequently, integrating the strengths of diverse breeding methodologies is essential.

Conventional breeding utilizes naturally occurring genetic variation and is characterized by well-established techniques, although its progress is often constrained by extended selection cycles (Bassi *et al.*, 2016). Mutagenesis breeding, exemplified by *lpa* mutants, effectively reduces antinutritional factors and enhances micronutrient content, yet potential pleiotropic effects require careful assessment (Raboy, 2020). Molecular breeding approaches, such as gene editing, offer precise and efficient genetic improvement but face limitations related to cost intensity and regulatory considerations (McCouch *et al.*, 2013; Bevan *et al.*, 2017). These three approaches exhibit a complementary relationship: molecular techniques enable

the rapid creation of key allelic variations, conventional breeding is responsible for integrating desirable background traits, while mutant resources provide direct sources for target traits. This multi-path synergistic framework establishes a methodological foundation for systematic biofortification.

Collectively, conventional breeding, mutagenesis breeding and molecular breeding constitute the core technical system for crop genetic improvement. Expanding the perspective from genetic improvement to the complete biofortification chain necessitates the inclusion of agronomic fortification and dietary intervention strategies. To systematically compare the core principles and applicable scenarios of these strategies, their key characteristics are summarized as follows (Table 4).

CONCLUSION

Looking ahead, a deeper understanding of the biological characteristics, homeostasis regulation and accumulation mechanisms of Fe and Zn in common beans is crucial for accelerating the genetic improvement of their nutritional content. Identifying the key determinants of micronutrient bioavailability will lay the foundation for related advancements. By selecting germplasm with both low PA and high Fe and Zn content, combined with marker-assisted breeding, this targeted strategy provides a systematic framework for improving the mineral utilization efficiency of bean varieties. These complementary traits can yield synergistic benefits: as our understanding deepens, varieties of common beans with higher nutritional density and bioavailability will provide significant health benefits, even with moderate consumption.

However, the breeding of such superior varieties still faces challenges. Given that crop breeding typically takes 8 to 10 years, researchers must consider the following questions in the process: which populations will become the primary consumers of the new products? How should the products be presented? Only by taking these social and practical considerations into account can we ensure that biofortified beans maximize their potential impact on global nutrition.

Conflict of interest

All authors declared that there is no conflict of interest.

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