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REVIEW

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# Mechanisms underlying cereal/legume intercropping as nature-based biofortification: A review

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**Abstract**

The deficiencies of micronutrients known as hidden hunger are severely affecting more than one-half of the world's population, which is highly related to low bioavailability of micronutrients, poor quality diets, and consumption of cereal-based foods in developing countries. Although numerous experiments proved biofortification as a paramount approach for improving hidden hunger around the world, its effectiveness is highly related to various soil factors, climate conditions, and the adoption rates of biofortified crops. Furthermore, agronomic biofortification may result in the sedimentation of heavy metals in the soil that pose another detrimental effect on plants and human health. In response to these challenges, several studies suggested intercropping as one of the feasible, eco-friendly, low-cost, and short-term approaches for improving the nutritional quality and yield of crops sustainable way. Besides, it is the cornerstone of climate-smart agriculture and the holistic solution for the most vulnerable area to solve malnutrition that disturbs human healthy catastrophically. Nevertheless, there is meager information on mechanisms and processes related to soil-plant interspecific interactions that lead to an increment of nutrients bioavailability to tackle the crisis of micronutrient deficiency in a nature-based solution. In this regard, this review tempted to (1) explore mechanisms and processes that can favor the bioavailability of Zn, Fe, P, etc. in soil and edible parts of crops, (2) synthesize available information on the benefits and synergic role of the intercropping system in food and nutritional security, and (3) outline the bottlenecks influencing the effectiveness of biofortification for promoting sustainable agriculture in sub-Saharan Africa (SSA). Based on this review SSA countries are malnourished due to limited access to diverse diets, supplementation, and commercially fortified food; hence, I suggest integrated research by agronomists, plant nutritionists, and agroecologist to intensify and utilize intercropping systems as biofortification sustainably alleviating micronutrient deficiencies.

**Keywords:** Biofortification, Intercropping, Micronutrients, Hidden hunger, Bioavailability

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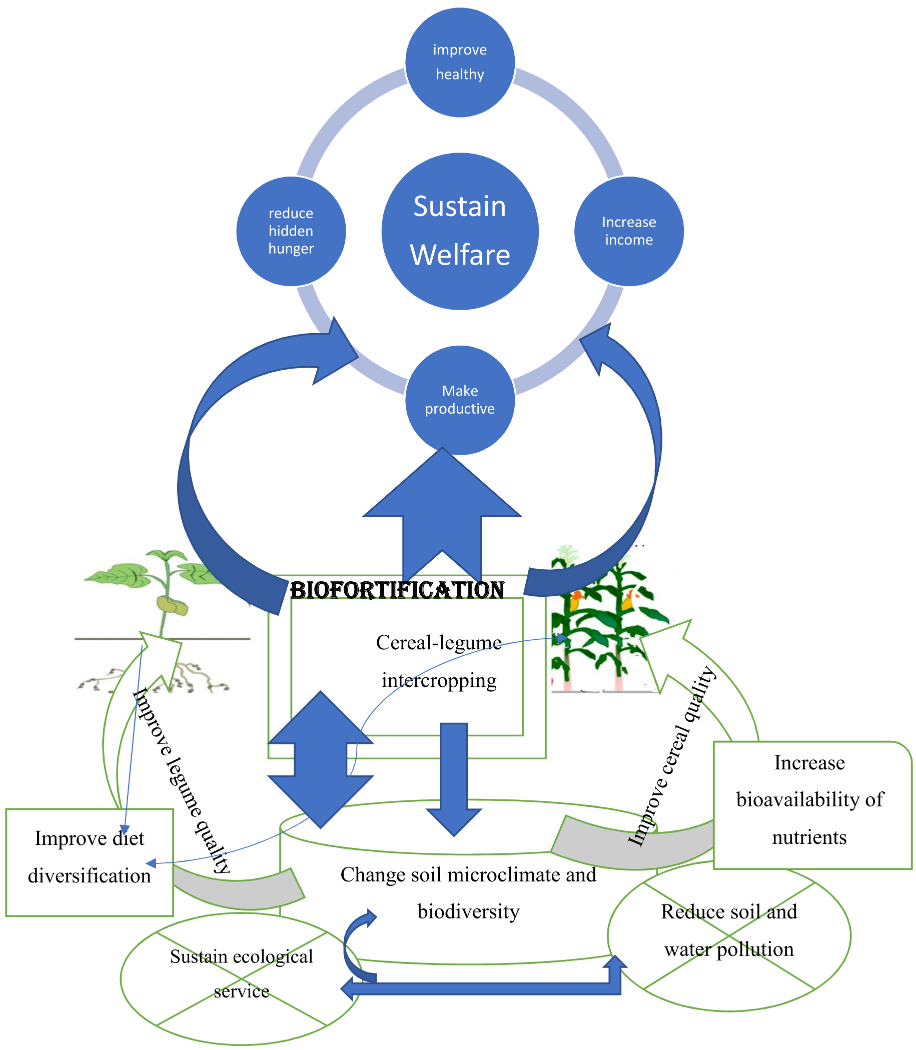
## Graphical Abstract




## Introduction

Achieving food security while promoting sustainable agriculture is becoming the main challenge for most developing countries. Typically, the deficiencies of micronutrients (*hidden hunger*) such as zinc (Zn), iron (Fe), selenium (Se), and cobalt (Co) severely affect public health throughout Sub-Saharan Africa (SSA) (Bouis et al. 2017; Singh et al. 2015). Zn and Fe deficiencies (Kumar et al. 2019; Sharma et al. 2020) is the most catastrophic factor leading to the death of pregnant women and children in SSA (Kumar and Pandey 2020; Singh 2016). This problem is highly related to low solubility and relative immobilization of P, Zn, and Fe in soil (Fageria et al., 2012; Lurthy et al. 2021), which reduces the nutritional quality of foods and leading public health crisis (Maqbool et al. 2020). In addition, poor quality diets (Taylor and Kini 2012; Singh 2016), monotonous consumption of cereal-based foods (Cakmak, 2002; Kifle, 2020; Roorkiwal et al. 2021), and fewer options for soil fertility management (Manzeke et al., 2019; Manzeke-Kangara et al., 2021) are the bottleneck for the fight against hidden hunger and resulted in chronic health consequences (Bouis et al. 2017).

Biofortification, supplementation, and fortification of crops are successful ways to combat hidden hunger worldwide (Bouis and Welch, 2010; Taylor and Kini, 2012). Among those techniques, biofortification offers a rural-based intervention and complements fortification and supplementation programs (Bouis and Welch

2010; Szerement et al. 2021). However, the effectiveness of the biofortification program relies on the farmer's and consumers' acceptance, and future policy interventions (Singh et al. 2016), and its overall success remains limited in developing countries.

The fact that the enrichment of micronutrients and vitamins hurts color, taste, and yield resistance to stresses of the product is the main factor that curbs poor and smallholder farmer from obtaining bio-fortified seed and result in hidden hunger (Hafeez et al. 2013). Likewise, agronomic biofortification may result in adversely affect long-term economic and ecological services that are not a sustainable option for alleviating hidden hunger (Lurthy et al. 2021). It is also results in sedimentation of heavy metals in the soil and leads to contamination and toxicity of soil (Khoshgoftarmanesh et al. 2010; Sharma et al. 2013) and poses another detrimental effect on plants and human health (Kumar and Verma 2018).

In response to those challenges, intercropping is one of the feasible, cost-effective, and sustainable approaches to alleviating micronutrient deficiency of plants in smallholder farmers (Gunes et al. 2007; Singh et al. 2016; Szerement et al. 2021). Sustainable food security not only requires full access to sufficient and nutritious food at all times by all people, but also the produced food should be with minimal environmental impact, sustainable agriculture, and balancing the agroecology (Maitra and Ray 2019). Sustainable food security not only requires full access to sufficient and nutritious food at all times by all people, but also the produced food should be with minimal environmental impact, sustainable agriculture, and balancing the agroecology (Maitra and Ray 2019).

Several studies showed that intercropping improves crop quality, grain yield, protein content, and better utilization of resources in a sustainable way (Akhtar et al., 2013) while improving Fe and Zn grain content (Dissanayaka et al. 2021; Inal et al. 2007; Zuo and Zhang 2009) that disturbing human healthy catastrophically (de Valença et al. 2017; Palmgren et al. 2008; Singh et al. 2016). In addition, Gunes et al. (2007) stated that intercropping of wheat and chickpea improves the concentrations of N, P, K, and Fe in wheat seeds and N, P, K, Fe, Zn, and Mn in chickpea seeds. Correspondingly, multiple cropping systems reduce anthropogenic perturbation levels N and P flows while maintaining soil fertility and $CO_2$ emissions from the cropping system (Soares et al. 2019), which may save money on expenses for mitigation. This strategy is the cornerstone of climate-smart agriculture and a comparatively cost-effective and holistic solution for the most vulnerable area (Bouis et al. 2017; Maqbool et al. 2020). Hence, intercropping is a nature-based solution that can reduce the gaps of malnutrition and achieve twin objectives of sustainable crop production in low-input agriculture that reduce the cost of cultivation and save land for nature while managing ecosystems more holistically (Hu et al. 2018; Kiwia et al. 2019). According to the review of Zuo and Zhang (2009) intercropping of dicot with monocot plants enhance seed contents of Fe and Zn by interspecific root interaction and rhizosphere modification.

There have been several recent reviews on the strategies for the biofortification of crops (Augustine and Kalyanasundaram 2020; Galić et al. 2021; Sharma et al. 2020; Szerement et al. 2021). Understanding the mechanism and processes linking intercropping with the biofortification concept is crucial for creating advanced breeding and agronomic practice for further use of intercropping, yet there were a few studies available in these areas. In this regard, this review explores mechanisms that can favor the nutritional quality of staple crops for solving the malnutrition problem. It is also intended to discuss factors influencing the effectiveness of biofortification for sustainable agriculture while safeguarding household food security.

## Concept of biofortification

Biofortification is a promising crop-based strategy that refers to the process of enhancing mineral levels and bioavailability of essential nutrients in the edible portion of the crops during plant growth through agronomic intervention, breeding practices or genetic modification, and microbiological changes (Bouis and Saltzman 2017; Sharma et al. 2020; Singh et al. 2015). Genetic or breeding techniques enhance mineral levels in the grain and/or the development of new varieties containing required elements (Kumar et al. 2019).

Agronomic biofortification is the physical application of fertilizers and other agronomic practices into agriculture production and has an exceptional potential for the fight against hidden hunger worldwide (Rajan et al., 2020; Jan et al. 2020; Szerement et al. 2021). It is the most promising way to alleviate hidden hunger by increasing the mineral content in the crops and simultaneously enhancing their bioavailability (absorption and utilization) through reducing antinutritional compounds or improving the concentration of mineral absorption promoters (Augustine and Kalyanasundaram 2020; Szerement et al. 2021). Generally, it refers to 'pulling' nutrients from the soil and 'pushing' them to economic parts of plants in their bioavailable forms (Kumar et al. 2019). Thus, agronomic biofortification provides a reliable, short-term, and sustainable approach for increasing yields and nutritional quality of crops (de Valença et al. 2017; Jan et al.2020; Singh et al. 2015).

## Concept and principle of intercropping

Intercropping is growing two or more crops simultaneously on the same piece of land at the same time (Reddy et al., 1976) and is known as polyculture or mixed cropping, which provides a balanced diet while mitigating global climate change (Yang et al. 2021). It is the practical application of basic ecological principles such as diversity, competition, and facilitation, for crop production (Layek et al. 2018). It ensures higher productivity, efficient use of resources, and more income (Maitra et al. 2021). There are several types of intercropping based on the degree of a temporal and spatial mixture such as (i) row intercropping (separated regular rows), (ii) mixed cropping (without using any row and spatial configuration), (ii) strip cropping (several rows of a crop species in separate adjacent rows/strips) and (iv) relay cropping system (planting the component at mind stage major crop life cycle) (Bybee-finley and Ryan 2018; Lithourgidis et al. 2011).

The intercropping system should follow its guidelines and principles to get a bonus from pulse yield without seriously jeopardizing cereal productivity. The principles of the intercropping lie in maximizing the complementary resource use (i.e., canopy and root architecture), facilitation (i.e., $N_2$-fixation, P, and micronutrient acquisition), and resource sharing (mycorrhizal association) between different species traits such as tall and short species, cereal and legume species, or C3 and C4 species (Rob et al. 2015). An intercropping system differs in competitive ability for using available resources such as water, nutrient, and solar radiation; hence the selection of suitable cultivars, seeding ratio, competition ability of component crops, etc. to match efficiently crop demands to the available resources and labor is the paramount factor affecting the success and efficiency of the intercropping system (Lithourgidis et al. 2011). Yield advantages of intercrops can occur if one specific trait of the component crop in the intercropping system is less affected due to the combined effect of interspecific and intraspecific competition (Berghuijs et al., 2020).

#### Factors influencing effectiveness of biofortification

Several critical and interrelated factors determine the success of biofortification in alleviating micronutrient deficiencies (Singh et al. 2016). These factors depend on nutrient bioavailability at different stages from the soil to crop for uptake, the crop to food for remobilization, and the food to humans for assimilation (de Valença et al. 2017), which in turn affected by a different factor (Singh et al. 2016). The total amount of micronutrients in the soil does not indicate the amounts of available nutrients for plant uptake because certain soil factors (pH, organic matter content, soil texture, and interactions with other elements) induce deficiencies of micronutrients (Antunes et al., 2006; Kumar et al., 2016; Maqbool et al. 2020; Lurthy et al. 2021). They are also affected by cultivar differences such as low nutrient mobility and remobilization efficiency to grains showed main differences in correlations between leaves and edible parts (Ray et al., 2020; Fischer 2021) and highly affecting the effectiveness of biofortification. For instance, there is an antagonistic effect between P, Fe, and Zn in roots or shoots depending on the host-plant species (Rakshit et al. 2015). Fe deficiency leads to the accumulation of Zn, while Pi deficiency affects the uptake and transport of Zn and Fe by up-regulating the expression of genes involved in their homeostasis (Xie et al. 2019).

Soil pH is the master soil variable that controls biogeochemical processes such as solubility, mobility, bioavailability, and acquisition of trace elements (Li et al. 2014; Rakshit et al. 2015; Neina 2019). In addition, climate change like extreme temperature and soil moisture may lead to the reduction of nutrient uptake, poor plant growth, and yield losses due to root damage (Moraghan et al., 1991; Maqbool et al. 2020). This dilution effect is responsible for decreased grain nutrient concentration with significantly increased grain yield (Rose and Wissuwa 2012; Xue et al. 2016; Smith et al. 2018; Aliyu et al. 2021). All factors disturbing proper plant growth and development also influence the effectiveness of biofortification micronutrients (Szerement et al. 2021). In the same way, not all micronutrients in foods are bioavailable to humans who eat those foods due to antinutrients (Blair 2013; Bouis and Welch 2010). Khoshgoftarmanesh et al. (2010) suggested that high levels of antinutrients such as phytate, polyphenolics, and tannins in the diet and interaction with other nutrients reduce the bioavailability of micronutrients. The presence of phytate in pulses makes complex compounds with Ca, Mg, Cu, Fe, and Zn to their low bioavailability (Kumar and Pandey 2020). This situation affects the ability of the soil to supply plants to absorb and utilize micronutrients. The adoption level by farmers, the number of food products, the postharvest process, the time taken to release biofortified crops, and additional political and regulatory issues affect the effectiveness of biofortification (Taylor and Kini 2012).

Three primary issues are required to make biofortification successful: (i) a biofortified crop must be high yielding and profitable to the farmer, (ii) the biofortified crop must be shown to be efficacious and effective at reducing micronutrient malnutrition in humans, and (iii) the biofortified crop must be acceptable to both farmers and consumers in target regions where people are affected with micronutrient malnutrition programs (Bouis and Welch 2010). Generally, the introduction of high-yielding varieties, intensive cultivation systems, micronutrient-free fertilizer application, non-addition of organic manures, nutrient interactions, type of plant, and imbalanced plant nutrition have led to multi-micronutrient deficiencies in soils in many parts of the globe (Kumar et al. 2016). Likewise, Fe and Zn are lower in modern wheat lines (Shewry et al. 2016). Thus, maintenance of soil quality and selection best cultivar and agronomic management enhance biofortification and eliminate micronutrient deficiency (Kumar et al. 2016).

## Possible mechanisms and processes in intercropping system for enhancing bioavailability of Zn, Fe, and P.

### Increasing soil enzyme activities and root exudates

Plants have evolved numerous strategies to cope with low inorganic phosphate (Pi), Zn, and Fe availabilities (Xie et al. 2019). Root exudates comprise high and low-molecular-weight solutes released or secreted by the roots. The most important components of the high-molecular-weight solutes (metal chelators fulvic acids, toxins, and ectoenzymes) and those of the low molecular-weight fraction (organic acids, ions, sugars, phenolics, vitamins, amino acids, etc.) released by grasses can play a major role in modifying the chemical composition of the rhizosphere then increase in micronutrient solubility and mobility (Marschner 2012). Plant roots also release enzymes such as phosphatases, phytase, and carboxylates (Li et al. 2013; Rojas-downing et al. 2017), which can help to improve the mobilization and utilization of the nutrients such as P, Fe, Mn, and Zn in mixed cropping (Gaxiola et al., 2011; Gunes et al., 2007; Marschner 2012; Zhang et al. 2004) by decomposition of organic residues and nutrient cycling in the soil (Xiao et al. 2013).

The physiological mechanisms increasing Fe and Zn uptake are summarized by the terms 'Strategy-I' and 'Strategy-II' (Marschner 2012). Strategy-I increases ferric reductase activity and acidification of the rhizosphere by releasing protons from the roots while Strategy-II plant species respond to P, Fe, and Zn deficiency by exuding phytosiderophores (Inal et al. 2007; Palmgren et al. 2008; Xie et al. 2019). Intercropping, Zn, and Fe deficiency lead to enhance production and expression of the Ferric reductase oxidase (FRO) enzymes, iron-regulated transporter (IRT) genes, and genes of Zn transporter (ZIP) genes, which are the primary uptake systems for Fe and Zn in plants (Palmgren et al. 2008; (Xiao et al. 2013; Xie et al. 2019; Xue et al. 2016). FRO-protein used to reduce Fe(III)-chelate is to Fe(II) then the Fe(II) is then absorbed by IRT (Palmgren et al. 2008). This mechanism is called a reduction-based strategy (Strategy-I) by dicotyledonous and nongraminaceous monocotyledonous species, which performs (1) soil acidification due to the release of protons that increase Fe solubility, (2) release of reductants (ferric reductase) to reduce of $Fe^{3+}$ to $Fe^{2+}$ in the rhizosphere, and (3) uptake of $Fe^{2+}$ across the root plasma

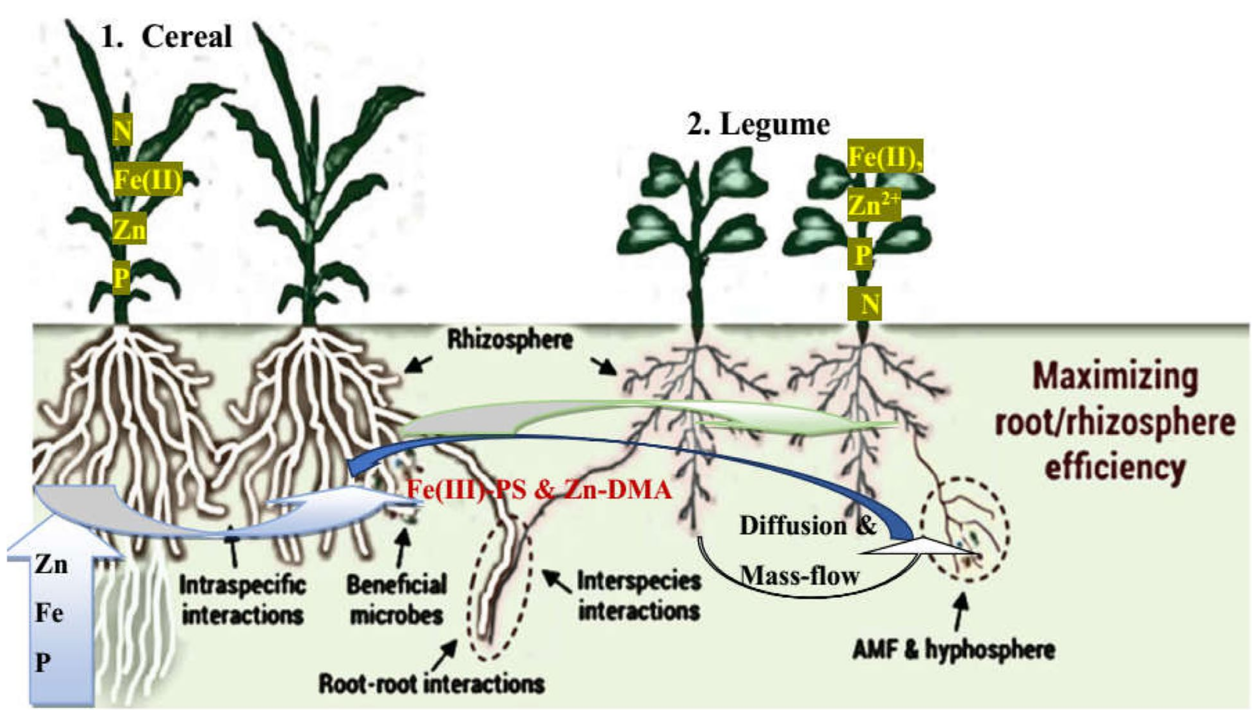



**Fig. 1** Changes in rhizosphere processes in cropping systems result in higher Fe, Zn, and P availability, absorption, and translocation (modified from, (Wang and Shen 2019))

membrane (Forieri and Hell, 2014; Rakshit et al. 2015). The Strategy-I plant also releases protons and phenolic compounds to enhance the bioavailability of Fe (Guerinot and Yi 1994; Tsai and Schmidt 2017). Acidification, ferric reductase, and chelation increase the bioavailability of $Fe^{3+}$ in plants (Lurthy et al. 2021). Hu et al. (2021) showed increasing $N_2$ fixation gene expression under intercropping.

In contrast, Graminaceous species deployed Strategy-II (a chelation-based strategy) and secreting mugineic acid-family (MAs) by their root cap and epidermal cells that have a high affinity for Fe(III) in the rhizosphere. Then root absorbs Fe(III)-MAs form (Rose et al., 2013) using the yellow stripe 1-like (YSL) gene transporter family in the plant roots (Curie et al., 2001; Inoue et al., 2009). In a similar manner roots also absorb Zn- DMA (phytosiderophore deoxymugineic acid) and improve Zn nutrition. The process of Fe acquisition by Strategy-II plants is divided into; (1) biosynthesis of magnetic acids (MAs) called phytosiderophore (PS) inside the roots; (2) secretion of MAs to the rhizosphere; (3) solubilization of sparingly soluble inorganic Fe(III) in soils by chelation of MAs; and (4) uptake of MA-Fe complexes [MA- Fe(III)] by the roots without Fe(III) reduction, which are effectively regulated by intracellular Fe level (Ma and Nonnoto 1996). This is function due to the high chelation affinity and solubilizing efficiency of MAs for Fe other than for polyvalent ions such as $Al^{3+}$, $Ca^{2+}$, and $Mg^{2+}$ and results in fast uptake 100-1000 times the rate from synthetic Fe chelators (EDTA, HEDTA) (Ma and Nonnoto 1996). Such fast uptake of ferric-MA complexes is a strategy that avoids decomposition by microorganisms. PS indirectly enhances the uptake rate of heavy metals such as Zn, Cu, and Mn by increasing their mobility in the rhizosphere and the root apoplast through intercropping systems (Li et al. 2014).

In the dicotyledonous and gramineous species, intercropping system release of PS by strategy-II plants helps to solubilize Fe and Zn in the form of PS-metal complexes in the rhizosphere not only for their own (Zhang et al., 2010) but also for intercropped cereal to that of legumes (Xue et al. 2016). PS–Fe (III) is reduced by FRO localized to the membrane surfaces of the root cells of dicotyledons that is $Fe^{2+}$ is the take-up by the strategy-I pathway. In the case of Zn, locally enhanced PS–Zn concentration in the rhizosphere of the intercropped dicotyledons would also increase the $Zn^{2+}$ activity through dissociation and enhancing Zn uptake (Zhang et al. 2010).

Strategy-II Fe uptake mechanisms are more efficient than Strategy-I plants such as dicotyledonous and non-graminaceous monocotyledonous plants, which are severely inhibited by high pH and bicarbonate concentrations in calcareous soils (Ma and Nonnoto 1996). Because, gramineous species released PS into the rhizosphere of dicot plants and helped to make much more PS-Fe available to dicot plants in intercropping; however, there is no PS-Fe available to dicot plants in monoculture (Guo et al. 2014; Zuo and Zhang 2009). Another possible reason may be, that Fe-solubilizing activity (Fe-SA) and ferric reducing (FR) capacity of the roots were generally higher in mixed culture relative to their monoculture, which improved Fe, Zn, and Mn nutrition of legumes (Inal and Gunes 2008). Additionally, in the mixed cropping system, root-secreted acid phosphatases (RS-APase), and rhizosphere P concentration (RS-P) activities, which is significantly higher in mixed cropping (Inal and Gunes 2008). Similarly, (Zuo and Zhang 2009) showed an increase in available Fe and P concentrations in the rhizosphere compared to the bulk soil. Furthermore, a higher ferric reduction capacity of dicot plant roots for a long time in intercropping may assist the mobilization of sparingly soluble Fe(III) compounds from the rhizosphere so that the dicot plants remain green. Cereals and legumes absorb Fe–PS and Zn–PS complexes in mixed culture (Fig. 1) (Dissanayaka et al. 2021). This suggests that intercropping of dicotyledonous (Strategy-I) and gramineous (Strategy-II) plants

**Table 1** Summary of studies showing the potential of cereal/legume intercropping those contribute to alleviating micronutrient deficiency

| Type of intercropping | Part of plants | Contribution to Biofortification | Reference |
|---|---|---|---|
| Peanut/maize, Wheat/chickpea, Peanut/barley, Peanut/oats | Shoot and grain | Fe and Zn | (Zuo and Zhang 2009) |
| Graminaceous/Leguminosae | Root, other | Fe | (Dai et al. 2019) |
| pearl millet/legumes | grain and stover | N, P, and protein | (Sharma and Gupta 2002) |
| Peanut/maize | Shoot | Fe, Zn, P, and K, | (Inal et al. 2007) |
| Cucumber/green garlic | Root and shoot | N, P, K, Ca, and Mn | (Xiao et al. 2013) |
| Sorghum/cowpea | Seed | Ca, Mg, Cu, Mn, and Fe | (Musa et al. 2012) |
| Rice-water spinach | Shoot | Si (silicon) | (Ning et al. 2017) |

mutually improve Fe, Zn, P, and K uptake system (Inal et al. 2007; Zhang et al. 2004) by increasing their solubility and bioavailability in alkaline and calcareous soils through soil pH modification (Marschner 2012; Odunze et al. 2017). Chongloi and Sharma (2018) also proposed that the N, P, K, Zn, and Fe content of oats is higher in pea/oat intercropping over the sole cropping of oat. Likewise, Sharma and Gupta (2002) showed that the accumulation of N, P, and protein in grain and stover of pearl millet is significantly improved by intercropping with legumes. Thus, intercropping Strategy-II with the Strategy-I is the main reason for the improvement of Fe and Zn nutrition to dicots due to the root interaction of the two species and exudates from graminaceous species by creating a favorable condition in the rhizosphere for dicots (Zheng et al. 2003; Li et al. 2014). It contributes to better nutrition of plants with Zn, P, K, Mn, and Fe as well by affecting biological and chemical processes in the rhizosphere (Table 1) (Zuo et al. 2000; Inal et al. 2007; Zuo and Zhang 2009; Dai et al. 2019) then mitigate malnutrition. This process led to 2–2.5-fold higher tissue concentrations of Fe and Zn in peanut and 0.2-to-two-fol higher tissue P and K concentrations in peanut and maize (Inal et al. 2007). From these premises, it is possible to suggest that legumes facilitated P nutrition of its own and associated cereals, while grasses improve Fe and Zn nutritional quality of harvested dicot grain.

## Modification of rhizosphere processes

Soil nutrients are modified and taken up by plant root hair in the rhizosphere, which is the critical zone of interaction influencing nutrient transformation, mobilization, and acquisition by plants (Shen et al. 2013). The term rhizosphere (root-soil interface) refers to the volume of soil near the roots, which links plants with soil and microorganism interactions and is the hub for controlling the nutrient transformation and plant uptake (Zhang et al. 2004; Zhang et al. 2010). Plants can sense changes in their surrounding environment and will be able to optimize the absorption of water and nutrients by modifying rhizosphere processes (Fig. 1) (Wang and Shen, 2019). Intercropped plants might increase nutrient uptake capacity by increasing the number of absorptive roots or density of root hairs or through the physiological adjustment of resource uptake kinetics (Homulle et al. 2022).

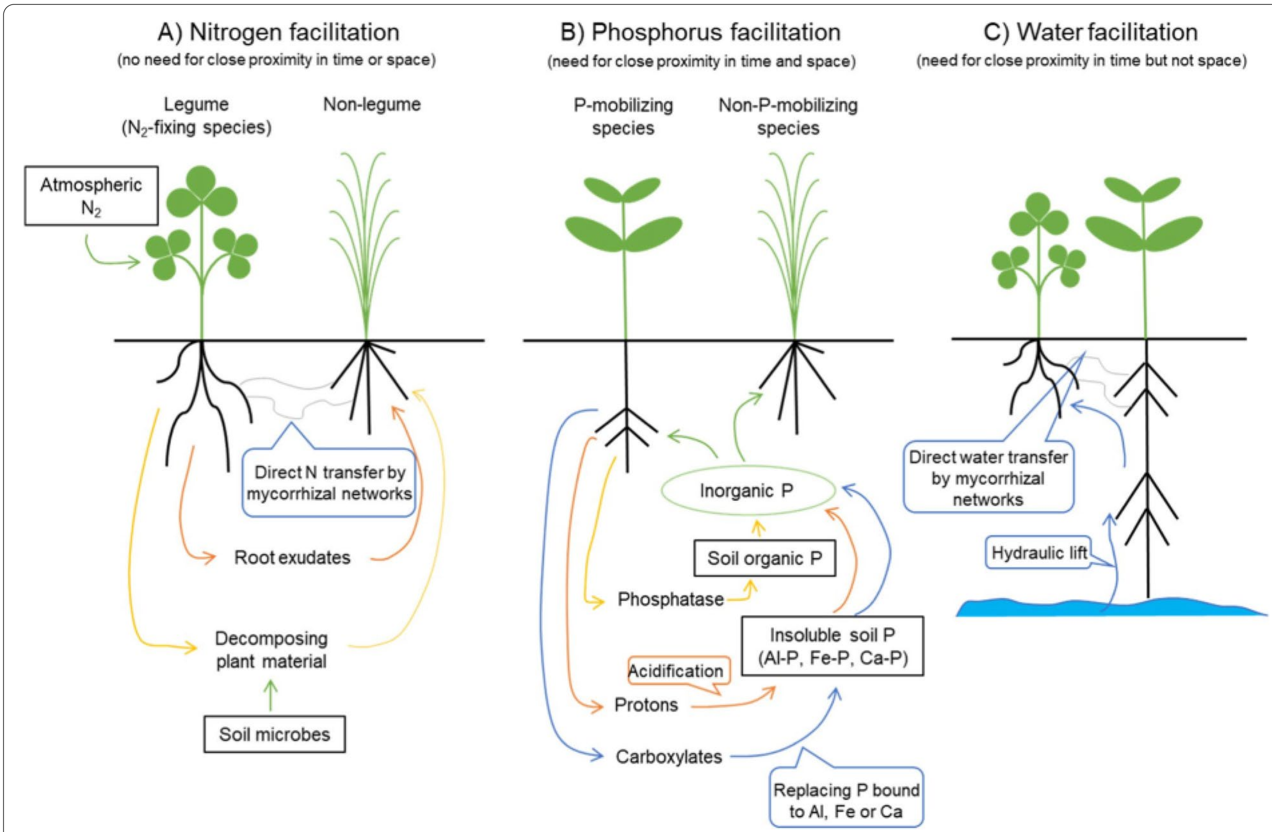



**Fig. 2** The physiological mechanism underlying interspecific facilitation of nitrogen (N), phosphorus (P), and water acquisition (adapted from (Homulle et al. 2022))

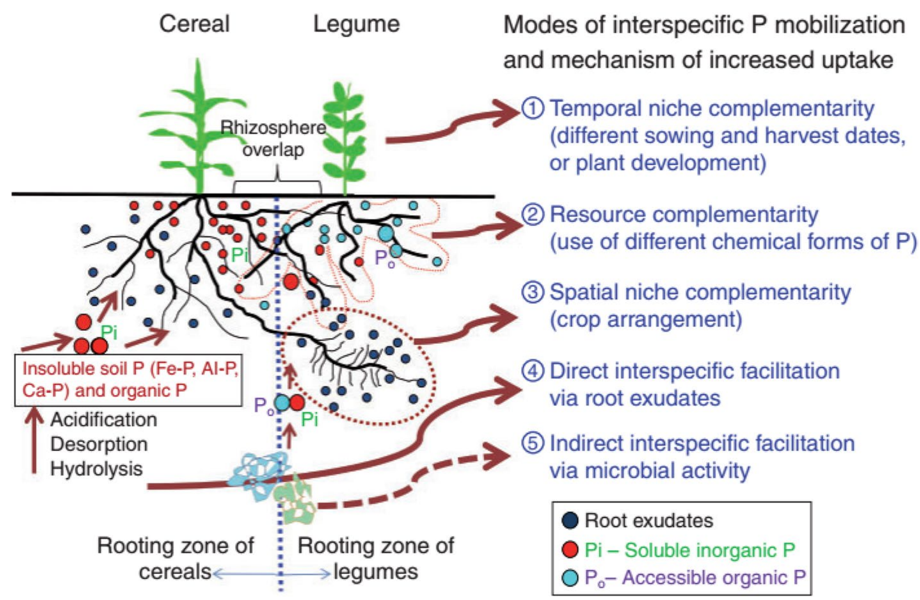



**Fig. 3** Direct and indirect modes of increased phosphorus (P) uptake in cereal/legume intercropping (adapted from (Xue et al. 2016))

Rhizosphere processes reflect dynamic changes in rhizosphere biochemistry for the interactions between plants and soils and play a vital role in controlling crop productivity and quality (Shen et al. 2013; Wang and Shen 2019). The major rhizosphere processes include bio-physicochemical processes such as mechanical root penetration, root exudation of carboxylates, enzyme secretion, proton release into the rhizosphere, and microbial interaction to mobilize sparingly available nutrients such as P, Zn, and Fe (Hinsinger 2001; Zhang et al. 2010; Jing et al. 2010; Marschner 2012; Shen et al. 2013) and improve yield and nutritional status the crops (Inal and Gunes 2008; Sharma and Gupta 2002). Recently several reports have described the role of intercropping in the improvement of nutritional status through modification of rhizosphere chemistry and biochemistry (Gunes et al. 2007; Inal and Gunes 2008). This modification affects the availability of salt ions (Na, Cl, and B) and other nutrients such as P, K, Mg, Fe, Zn, and Mn. Root intermingling and rhizosphere sharing between intercropped species might highly facilitate diffusion of Fe(III)–PS, N, and Zn facilitation in all directions (Fig. 1) (Dissanayaka et al. 2021).

## Enhance complementarity and facilitation

Complementarity and facilitation are two major ecological principles leading to improved resource use efficiency, which simultaneously occurs in intercropping systems empirically (Li 2020). The complementarity mechanism (better use of resources) refers to partitioning resources and reducing competition between species. The facilitation mechanism refers to the positive interaction by which one species increases the growth, reproduction, or survival of the other species by modifying the biotic or abiotic environment (Duchene et al. 2017; Li 2020).

Complementarity can be categorized as (i) *temporal* (a significant time lag between their needs e.g. relay-intercropping), *(ii) spatial* (niche differentiation due to different rooting patterns), (iii) *chemical* (the ability of one species to mobilize different chemical forms of nutrients) (Duchene et al. 2017). Chemical complementarity occurs when legumes crops fix nitrogen from the atmosphere and intercropped species tap into different pools of soil P (Fig. 3), such as inorganic and organic pools where legumes can mobilize soil organic P and leave more inorganic P available to the intercropped cereals (Xue et al. 2016). Complementarity of nutrient uptake (N, P, Fe, and Zn) in cereal-legume mixed-cropping systems provides a unique advantage for the system to be sustainable in the long run (Dissanayaka et al. 2021), which was the key underlying mechanism for improving nutrient-use efficiency and improving the nutrition of crop particularly P (Li et al. 2016; Wang et al. 2020). The best indicator of complementarity of the use of resources is Land Equivalent Ratio (LER) (Andersen 2004).

Facilitation can also categorize as (i) Indirect facilitation: which refers to the changes in physicochemical occurred in the rhizosphere and alteration of light, temperature, and soil moisture that enhance nutrient availability (Li et al. 2014), (ii) Direct facilitation: refers to the improvement in plant nutrition through the transfer of nutrients from one plant to another via stimulation of beneficial soil microbes during mineralization of organic matter, mobilization of sparingly soluble inorganic nutrients, or transfer of nutrients through mycorrhizal networks linking co-cultivated crop plant species (Duchene et al. 2017; Li et al. 2014). This facilitation includes rhizodeposition of different organic substances and direct transfer of P and N by association with soil microbes through the decomposition of plant material, such as dead roots and plant litter (Fig. 2) (Homulle et al. 2022). It occurs when legume species mobilize soil organic P (that is poorly available to cereal) through exudation of protons (in alkaline soils only), the release of carboxylates (in all soils), enhancement of phosphatases activity, and change in root morphology and physiology then resulted in facilitation of P acquisition by the cereals in the mixture (Fig. 3) (Li et al. 2014; Zhang et al. 2019; Li 2020; Wang et al. 2020).

Legumes intercropping systems promote complementarity between plants and facilitation processes in the soil to reduce interspecific competition, which leads to better exploitation of soil resources (Duchene et al. 2017; Xue et al. 2016). Interspecific facilitation is caused mainly by the complementary use of resources, especially water, nitrogen, and phosphorus in intercropping (Yang et al. 2021). Consequently, intercropping contributes to increased P, Fe, and Zn uptake as a result of increasing yield and improving grain nutritional quality due to niche complementarity and interspecific facilitation of intercropping system (Li et al. 2004; Xue et al. 2016). The critical mechanism underlying facilitation is the ability of some crop species to chemically mobilize and solubilize unavailable soil nutrients (P, Fe, Zn, and Mn) by releasing acid phosphatases, protons, carboxylates, and chelating substances into the rhizosphere and increasing their availability to non-mobilizing species (Hinsinger 2001; Li et al. 2014; Xue et al. 2016). Xue et al. (2016) stated that the concentrations of carboxylates in the rhizosphere of faba bean were 10 or 20 times higher than that of wheat, indicating a critical capacity of soil P mobilization and facilitation of wheat P uptake by faba-bean (Fig. 3).

Nitrogen fixation by legume is enhanced when associated with cereal as the excessive nitrate released in the root zone is utilized by the nearest plant, which otherwise decreases N fixation (nodulation) (Akhtar et al., 2013). Several studies demonstrated that intercropping system significantly led to an increase in grains nutrient concentrations of cereals and legumes (Zuo et al. 2000; Zuo and Zhang 2009; Nasar et al. 2020). Such complementarity and facilitation in nutrient use are predominantly vital in low-input farming systems, which ensure food security and grain production by compensating for potentially low fertility of cultivated land. Therefore, intercropping with appropriate component crops may be the pillar for improving the micronutrient concentration in the targeted crop by increasing the soil availability of micronutrients (Singh et al. 2016).

#### Modulating plant growth promoting microorganisms

Plant Growth Promoting Microbe (PGPMs) includes beneficial soil microorganisms such as bacteria (Azospirillum, Bacillus, Enterobacter, Gluconacetobacter, Paenibacillus, and Pseudomonas) and mycorrhizal fungi species that colonize plant roots. Intercropping favors the development of different types of microorganisms (Hinsinger 2001; Song et al. 2007; Weisany et al. 2016; Duchene et al. 2017; Li et al. 2018; Zhao et al. 2022) through diverse litter quality, litter types or root exudates entering the soil (Hooper et al. 2000; Maitra and Ray 2019; Wang and Shen 2019) regulating plant hormones (Chen et al. 2022), which are described as ecosystem engineers (Zhang et al. 2010; Kudoyarova et al. 2015; Duchene et al. 2017; Kumar and Verma 2018; Neina 2019). Among microbiota, arbuscular mycorrhizal fungi (AMF) symbiosis is arguably the essential symbiosis on earth (Bücking et al. 2012) and serves as 'biofertilizers and bioprotectors' in environmentally sustainable agriculture and plays a crucial role in nutrient cycling, absorption and translocation of nutrients (Qiu and Wang 2006; Soka and Ritchie 2014) that can be occurred through the direct pathway (by roots) and the AM fungal pathway (Smith and Smith 2011; Lurthy et al. 2021).

PGPMs enhance the bioavailability of soil P, K, Fe, Zn, and Si to plant roots (Hafeez et al. 2013; Maitra and Ray 2019; Karnwal 2020) and have the potential to substitute for inorganic fertilizers and pesticides (Kumar and Verma 2018). They also play essential roles in rhizosphere biochemical processes such as acidification, chelation, decomposition of organic matter, and suppression of soil-borne pathogens (Maitra and Ray 2019; Karnwal 2020). Thus, it modifies solubility and availability of nutrients for the host plant (Lurthy et al. 2021). Furthermore, they influence the direction and quality of energy and nutrient flow in the rhizosphere and play a key role in controlling the availability of soil nutrients (Zhang et al. 2010; Wang and Shen 2019). This improvement of plant growth and quality by PGPMs is related to their mechanisms of increased production of plant hormones, availability of mineral nutrients and/or water for plants, and enhanced resistance to drought, oxidative stress, and phytopathogens (Fahad et al. 2014; Dinesh K. Maheshwari 2015). For example, different studies showed that greater soil microbial diversity has been observed in intercropping systems compared with conventional monocropping systems such as *Rhizobium hainanense, Rhizobium leguminosarum, Frankia, and Pseudomonas* (Xiao et al. 2013; Chen et al. 2018; Li et al. 2018). Soil available nutrients in the intercropping system could have also been increased

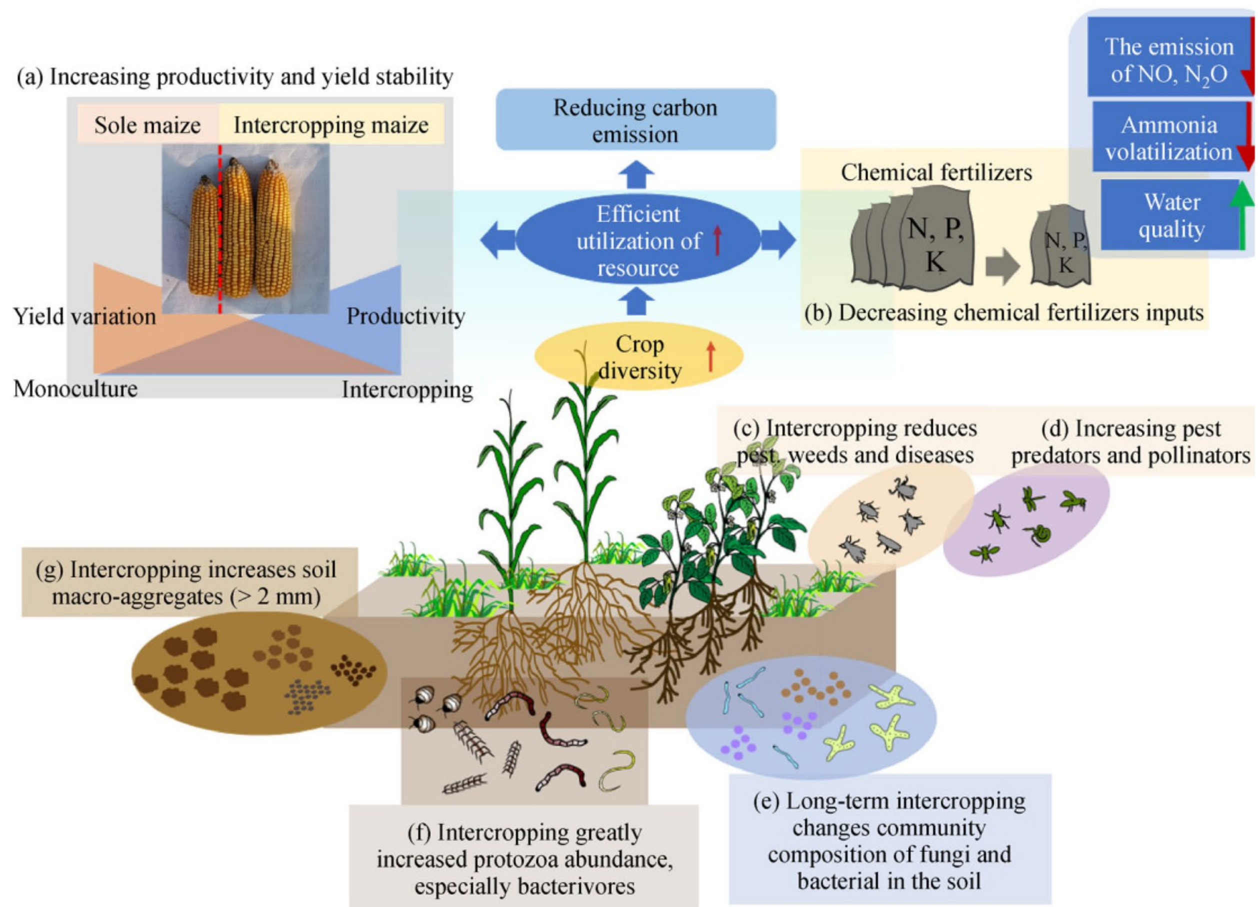



**Fig. 4** Mechanism and integration of intercropping for increasing soil fertility and yield stability (adopted from (Yang et al. 2021))

by the available bacterium (rhizobia, phosphate-solubilizing, and potassium-solubilizing bacteria), which helps improve soil quality (Xiao et al. 2013). The uptake of Fe, Zn and other micronutrients by the plant roots is improved due to the secretion of phytosiderophores and phytohormones by microorganisms present in the soil rhizosphere (Rakshit et al. 2015). Intercropping sorghum with cowpea increase the Ca, Mg, Cu, Mn, and Fe contents of sorghum seeds (Musa et al. 2012).

## Another role of intercropping system in nutritional security

### Regulate soil fertility status and nutrient use efficiency

Soil organic matter depletion is one of the main factors causing loss of ecosystem resilience and the degradation of ecosystem services as it is a good source of many essential plant nutrients (Kumar et al. 2021) while enhancing soil fertility and agricultural sustainability (Maitra et al. 2021). High biodiversity leads to increased carbon storage in roots and soil, and increased biomass yields will mitigate climate change (Yang et al. 2018). Growing cereals in association with legumes offer the best opportunity for conserving soil fertility by returning more amounts of organic matter to the soil, thus improving its cation exchange capacity and physical conditions (Bodena 2018; Iqbal et al. 2018). They also improve soil fertility through deep rooting, nitrogen fixation, leaf shedding ability, and mobilization of insoluble soil nutrients to soluble form (Begam et al. 2020; Layek et al. 2018; Maitra et al. 2021). The existing evidence shows that the mixture of exudates released by legumes can play a critical role in modifying the chemical composition and transforming unavailable P, Ca, and Fe in the rhizosphere into available resources through solubilization or chelation (Duchene et al. 2017; Latati et al. 2019). Cassava/peanut intercropping system increased available N, exchangeable K, pH value, urease activity, and soil microorganisms (Tang, Hamid, et al. 2020), which play a pivotal role in improving crop productivity and quality.

Intercropping is an effective measure to improve the absorption efficiency of trace elements and make full use of soil and water resources (Xia et al. 2013). it is also P and K uptake by 43% and 35% compared to pure stands (Richardson et al. 2011) and such enhancement was due to more dry matter production. The presence of maize increased the secretion of carboxylates from alfalfa roots, suggesting that the root interactions between maize and alfalfa are crucial for improving P-use efficiency (Wang et al. 2020). Subsequently, Sun et al. (2019) reported that decreasing rhizosphere pH and increasing organic anion exudation played key roles in soil P mobilization of maize and alfalfa, with little contribution of acid phosphatase. Generally, intercropping has the highest potential to increase above- and belowground biodiversity of various taxa at the field scale; consequently, it enhances ecosystem services affecting food security and food safety worldwide (Fig. 4) (Yang et al. 2021).

## Boosting diet diversification and yield stability

### *Yield stability*

One of the reasons for food insecurity in the developing countries is the instability of yield in the current monocropping system due to its less resilient ability against environmental perturbations (Lithourgidis et al. 2011; Raseduzzaman and Jensen 2017). Yield stability is a common term used to measure superiority and adaptability (Raseduzzaman 2016). Cereal-legume intercropping systems offer higher productivity and economic return by reducing the yield variability that helps for boosting future global food security and livelihood for the farmers (Bitew et al. 2021; Raseduzzaman 2016). The sound mechanisms for yield stability are a buffer against pests and diseases, resilience to abiotic factors, compensation of the loss, and complementarity or facilitation among the crops (Raseduzzaman 2016). Thus, diversification of cropping systems in time and space through intercropping can enhance yield stability and food security, which is considered an efficient way to achieve sustainability in global food production (Raseduzzaman and Jensen 2017).

### *Diet diversification*

Food and nutritional security are a headache task for smallholders under subsistence farming. This malnutrition is caused by the consumption of a cereal-based diet affecting about 2 billion people worldwide, particularly in Asia and Africa (Augustine and Kalyanasundaram 2020; Panneerselvam and Craufurd 2020; Singh 2016). Increasing dietary diversification is one of the decisive strategies to combat food security and malnutrition (Fischer 2021; Kumar et al. 2019). In the long term, dietary diversification is likely to ensure a balanced diet that includes the necessary micronutrients (Bouis et al. 2017).

Besides being an excellent source of proteins and vitamins, legumes provide a key tool for addressing micronutrient malnutrition in SSA compared to cereals (Singh et al. 2015). They also are an excellent reservoir of dietary fiber and complex carbohydrates and complement the starches derived from cereals and root crops (Kumar and Pandey 2020; Roorkiwal et al. 2021). Bouis and Welch (2010) suggested that increasing the consumption of a range of non-staple foods is the best and final solution to eliminating undernutrition as a public health problem in developing countries. Thus, dietary diversification through multiple cropping systems would seem a straightforward and sustainable way to combat micronutrient deficiency (Dayegamiye et al. 2015; Khoshgoftarmanesh et al. 2010) and improve household nutritional status and have positive links to better health conditions. Because the cereal-legume intercropping system increase N availability for the cereal, which results in increasing protein content than dry matter production and changes grain quality parameters (Bedoussac et al. 2015; Dayegamiye et al. 2015). They also increase the average concentration of all macronutrients through interspecific interaction in intercropping systems such as peanut/maize, wheat/chickpea, guava/sorghum, or maize (Zuo and Zhang 2009), giving the possibility of effective cereal grain biofortification (Głowacka et al. 2018). Intercropping also increased Zn contents in roots, stems, leaves, and shoots of maize seedlings by 30.76% more than monoculture (Zhang et al. 2016). Furthermore, cereal and legume/oilseed combinations provide a large portion of the family requirement (calorie intake) (Maitra et al. 2021).

A cropping system with alfalfa increased the wheat grain concentration of N (10%), S (17%), Cu (20%), Mg (18%), and Zn (50%) (Smith et al. 2018). Growing cereals and legumes on the same land not only supplies dietary carbohydrates, proteins, and vitamins to households but also c improves the income and livelihood of smallholder farmers (Nyagumbo et al. 2020). Therefore, intercropping gives food and nutritional security to smallholders in drylands and natural insurance against crop failure (Dissanayaka et al. 2021; Maitra et al. 2021). These techniques provide a feasible means of reaching malnourished rural populations who have limited access to commercially marketed fortified foods and supplements.

## Increase crop resistance to stress

The biotic and abiotic stresses represent the major bottleneck affecting global food security and directly exacerbate hidden hunger. Intercropping significantly increases the Si (silicon) nutrition of rice and provides an environmentally sound approach to controlling disease and pests (Ning et al. 2017). They also reported that rice-water spinach intercropping significantly reduced the disease index of rice sheath blight by 17.3%–50.6% and the incidence of rice leaf folders by 5.1%–58.2% compared with rice monoculture. Furthermore, intercropping increases crop diversification and thus reduces the risk of crop failure due to drought, excessive rainfall, pests, and disease attacks leading to better food, nutrition, and incomes (Tilman et al.2002; Rusinamhodzi et al. 2012; Kiwia et al. 2019; Nyagumbo et al.2020). The enhanced use of light, water, and nutrient directly reduce their availability for the growth of weeds thus favoring the main crop and reducing damage to the crops (Duchene et al. 2017).

Interspecific plant interaction also stimulated the defense system of the intercropped peanut for environmental adaptation by enhancing the secretion of the defense hormones (salicylic acid, jasmonic acid, and methyl jasmonate) and modulating peanut root endophytic in intercropped peanut tissues (Chen et al. 2022). These hormones result in vigor crops growth, which can change in Fe, Zn, or phytate content of the crops (Blair 2013) and augment food security. Intercropping also favors the development of different types of microorganisms (Hinsinger 2001; Song et al., 2007; Duchene et al. 2017; Li et al.2018; Zhao et al. 2022), which enhanced resistance to drought, oxidative stress, and phytopathogens (Fahad et al. 2014; Dinesh K. Maheshwari 2015). It leads to increased crop resistance through improved nutrition, production of reactive oxygen species, allelochemicals release, and oxidative burst for stress tolerance (Kumar and Verma 2018). Hence, intercropping can be a sustainable, low-input method of farming with the potential to provide resilience in a future with uncertain climatic conditions (Homulle et al. 2022).

### Assist Heavy Metals (HM) phytoremediation efficiency

In recent decades, non-essential heavy metals such as Cd, Pb, As, Hg, and Cr are the most serious disaster affecting humans, plants, and the environment negatively (Mohebbi et al. 2012) since they are non-biodegradable (Ali et al. 2013). The conventional remediation methods cause high cost, intensive labor, irreversible changes in soil properties, and disturbance of native soil microflora. Thus, researchers obtain a novel approach called phytoremediation, which is an economically feasible and sustainable option to clean up heavy metal-contaminated fields. Phytoremediation refers to a green technology that uses plants and associated soil microbes to reclaim HM and radionuclides from contaminated soil by various mechanisms including phytoextraction, rhizofltration, phytostabilization, phytodesalination, photodegradation, and phytovolatilization; Mohebbi et al. 2012; Ali et al. 2013; Liu et al. 2013).

Several studies confirmed that the agronomic practice of intercropping is a valid approach for the removal of HM from contaminated soils through releasing root exudates, modulating soil microbial community, and production of more biomass (Bian et al. 2021; Hussain et al. 2021; Tang et al. 2020; Zou et al. 2021). Intercropping also increases the resistance of plants to heavy metals through the reduction of plant oxidative damage and increase of antioxidant activity. In addition, a wide range of heavy metal tolerant microorganisms associated with plants such as rhizobacteria, mycorrhiza, and firmicutes have to remove or transform contaminants into harmless substances through the release of chelating gents, acidification, phosphate solubilization, and redox changes, affect heavy metal mobility and availability to the plant (Kumar and Verma 2018; Lichtfouse2017). For example, intercropping native grasses in young vineyards is an effective strategy for phytoremediation of Cu-contaminated soil in addition to contributing to soil protection and nutrient cycling (De Conti et al. 2019). Likewise, mixed cultures of white lupin (*Lupinus albus* L.) affect with oat (*Avena sativa* L.) might be a powerful tool for enhanced phytoremediation of HM (Pb, La, Nd, Sc, Th, and U) and phytomining (Sc, La, Nd, Ge) by enhancing their mobility that leads to a depletion of trace metals in the soil rhizosphere (Wiche et al. 2016). Intercropping patterns of ryegrass and alfalfa can significantly reduce the Pb uptake from soil to achieve the purpose of phytostabilization (Cui et al. 2018). Recently study by Hussain et al. (2021) depicted that accumulation of Cd and Pb was much higher as a result of hyperaccumulation and absorption nature of garlic and higher plant-microbial associations in interplanting garlic. In general, well designed intercropping system of hyperaccumulators plants with potential cash crops those able to boost phytoremediation mechanisms is directed to a safe strategy for soil, harvest products, and cost of remediation (Tang, Zhong, et al. 2020). These strategies can be directly translated to the sustainable achievement of food and nutritional security.

## Conclusion

Deficiency of micronutrients particularly Zn and Fe deficiencies ranked fifth and sixth respectively severely affecting public health throughout Sub-Saharan Africa. Biofortification is suggested as the most promising crop-based strategy that enhances the amount and bioavailability of essential nutrients in the edible portion of the crops during plant growth through agronomic intervention, breeding practices or genetic modification, and microbiological changes. Several studies showed that intercropping is one of the feasible, eco-friendly, low-cost, and short-term approaches to tackling the crisis of micronutrient deficiency particularly Zn, Fe, and P in a nature-based and holistic manner. Plant evolves various strategies such as rhizosphere pH modification, carboxylate exudation, phosphatase secretion, change of root architecture, and mycorrhizal associations, which is used to mobilize, solubilize, and facilitate bioavailability of soil P, Fe, Zn, etc. improve grain quality of plants. Such improved plant and soil nutrient contents in cereals-legumes intercropping are directly related to the complementarity, facilitation of nutrient sharing, and rhizospheric modification that efficiently contribute to soil nutrient cycling and plant nutrition. These physiological mechanisms to increase P, Fe, and Zn uptake are summarized by the terms 'Strategy-I' and 'Strategy-II' while strategies such as deity diversification, yield stability, and enhancement of crop to stress conditions are another key role of intercropping in improving food and nutritional security for smallholder farmers in developing countries. Food diversification using crop species that are adapted to local conditions can be an important avenue to improve food security, particularly with increasing climate uncertainty. An interdisciplinary research team including human nutrition scientists, physiologists, and plant scientists holds great potential for developing end products with desired nutritional properties. Therefore, developing biofortified crops along with suitable agronomic management options are needed to eliminate micronutrient malnutrition in humans and ensure food and nutritional security. Therefore, in the future, more systematic steps in developing advanced intercropping systems rely on the selection of appropriate crops component, maintenance of soil quality, and best agronomic management for enhancing biofortification and elimination of micronutrient deficiency in a holistic manner. It is also requiring future multiple technical and socio-economic developmental interventions to further explore the knowledge gap of the direct link between the principle of intercropping and change in micronutrients in plant systems and consecutive results in human health for wide-scale implementation in sub-Saharan Africa. As far as most of the SSA countries are malnourished populations who may have limited access to diverse diets, supplements, and commercially fortified foods; it is vital to intensify integrated research on intercropping as biofortification to better address micronutrient deficiencies.

#### Abbreviations

AMF: mycorrhizal; DMA: deoxymugineic acid; EDTA: Ethylenediaminetetraacetic acid; HEDTA: hydroxyethylethylenediaminetriacetic acid; FR: ferric reducing; HM: heavy metal; MAs: mugineic acid-family; PGPMs: Plant Growth Promoting Microbe; PS: phytosiderophore; SSA: sub-Saharan Africa.

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#### Authors' contributions

Addisu Ebbisa participated in planning, selecting the title, drafting the manuscript, and revising it critically. The authors read and approved the final manuscript.

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#### Ethics approval and consent to participate

Not applicable for this section.

#### Consent for publication

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#### Competing interests

The authors declare no conflict of interest

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