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REVIEW

Plant nutrient dynamics: a growing appreciation for the roles of micronutrients

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Abstract
Micronutrients are essential for plant growth and play a key role in crop nutrition. Micronutrients such as zinc (Zn), iron (Fe), copper (Cu), and manganese (Mn) are necessary for plants and humans who rely on them directly or indirectly. These minerals are important for several important cellular functions, including respiration (Fe and Cu), photosynthesis (Fe, Cu, and Mn), and transcription (Zn). Micronutrient deficiencies have gained importance as a source of 'hidden hunger,' focusing on iron (Fe) and zinc (Zn). Enhancing the nutritional value of staple crops seems to be a simple and effective solution. We address the methods of absorption of numerous beneficial Micronutrients, their positive characteristics, and their involvement in improving crop yield. The importance of biofortification as a procedure to enhance crop yield and as an agricultural solution to solve nutritional security challenges is discussed in this review. Biofortification boosted crop yield to relieve hidden hunger and quality parameters, proving a sustainable and cost-effective strategy. Several novel and targeted biofortification strategies for nutrient enrichment of field crops, including cereals, pulses, oilseeds, and fodder crops, have been reviewed. With the information presented here, researchers can see that biofortification promises to increase agricultural production and provide the crops with additional nutrients to ensure human food security and nutrient quality.

Keywords Micronutrients · Nutrient homeostasis · Nutrient acquisition · Plant nutrition · Agronomic biofortification · Biotechnological approach

Introduction

The growth and development of agricultural plants are heavily influenced by nutrient availability; as a result, understanding the dynamics of nutrient absorption, transport, and assimilation, as well as their biological interactions, becomes more important to increasing crop productivity (Wawrzyńska and Sirko 2014). During the previous two decades, a plethora of data on plant morphological and physiological adaptations in response to variations in mineral nutrient availability has been accumulated (Krouk et al. 2011; Gruber et al. 2013; Zhao and Wu 2017; Krouk and Kiba 2020). To a certain degree, protein-coding genes involved in the absorption, mobilization, storage, and assimilation of macro/micro-nutrients have been identified; however, regulatory networks regulating their expression in response to changes in nutritional status are still being uncovered (Liu et al. 2009; Pilon-Smits et al. 2009; Hindt and Guerinot 2012; Briat et al. 2015; Chaiwong et al. 2020). Several metabolic systems in crop plants are affected when a nutrient imbalance occurs. On the other hand, plants have developed mechanisms to deal with nutrient deficits (Hindt and Guerinot 2012; Pilon-Smits et al. 2009). Even though the soil contains many components, only 17 are now recognised as critical for crops' normal growth and development (Bünemann et al. 2018).

Nutrients for plant growth and development are mostly derived from soils (Cogger and Brown 2016). Plants absorb the required nutrients from the soil in varying quantities depending on their requirements (Marschner 2012). An important role is played by the phyto-microbiome (plant-associated microbial population) in increasing nutrient

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Extended author information available on the last page of the article availability and crop productivity (Bhatt et al. 2020; Fendrihan and Pop 2021). In addition, agriculture and agricultural products directly impact the health of both animals and people (Brevik et al. 2020). Macronutrients are required in greater amounts by plants, while micronutrients (also known as trace elements) are required in lesser quantities; nonetheless, both nutrients play equally significant roles in plant growth and metabolism. Soil health, crop yield, the nutritional value of agricultural products, and ultimately human and animal health are all harmed when phyto-available nutrients are deficient (Shukla et al. 2018). Apart from nitrogen (N), phosphorus (P), and potassium (K) inadequacy, deficiencies of sulfur (S) and micronutrients (zinc (Zn), boron (B), iron (Fe), copper (Cu), and manganese (Mn)) have been recorded in many soils across the globe, including India (Kihara et al. 2020; Shukla et al. 2019; Piotrowska-Dlugosz et al. 2017). The essential micronutrients Zn, B, Fe, Cu, Mn, and molybdenum (Mo) are required for field crops.

Historically, various field crops that serve as a staple food on a global scale have been a key focus for biofortification. In 2004, the first biofortified crop was released in Uganda and Mozambique. The crop was vitamin A orange sweet potato variety. More than 400 varieties of 11 biofortified crops have been released for consumption in 30 countries. By 2021, almost 12 million farming households were growing biofortified crops, benefiting over 60 million people (https://biocropshplustst.ciat.cgiar.org/about/howToDevelop). Rice, wheat, maize, pulses, oilseed crops, and fodder crops tend to collect exogenously provided nutrients and have therefore been biofortified. So far, research on biofortified crops containing critical micronutrients such as Zn, Fe, I, Cu, and others has been extensive (Klikocka and Marks 2018). For instance, the Zn-efficient PBW 1Zn variety was introduced by PAU in 2017 and had high quantities of Zn (40.6 mg L^{-1}) and Fe (40.0 mg L^{-1}). Moreover, many biofortified crops have been released, including corn, orange, cassavas, sorghums, sweet potatoes, squash, Fe-enriched beans, Zn-enriched rice, and lentils supplemented with micronutrients. (Steur et al. 2017; Connorton and Balk 2019; Ligowe et al. 2021; Saeid et al. 2019). Deficits in micronutrients are substantial obstacles to raising the socioeconomic level of food nutrition in the twenty-first century. A straightforward method to raise the nutritional content of the average person's diet is bio-fortification (Jaiswal et al. 2022).

Genetic engineering, traditional breeding, and agronomic biofortification are current methods used to attain nutritional security (Bouis and Welch 2010; Bouis 2003). The conventional strategy entails choosing existing varieties of high-yielding crops and cross-breeding them with better nutritional content to generate staple crops with desired nutrient and agronomic features. In addition, specialized genetic modification may enhance the concentration of micronutrients in edible plant portions (Haun et al. 2014; Michno et al. 2015; Tang et al. 2016; Dodo et al. 2008; Bonfim et al. 2007). In the present global food landscape, there is an inadequate supply of various micronutrients in dietary crops; consequently, fortifying yields with a single nutrient is insufficient to provide nutritional security, particularly if the diet is based on a narrow variety of foods. Advanced research has been conducted to determine the efficacy of applying combined nutrients to crops. Selenium and iodine biofortification of food plants was recently described by Górniak et al. (Górniak et al. 2018).

This review aims to create awareness about micronutrient delivery to plants to promote agricultural sustainability and increase yield and rectify micronutrient deficiencies in the human population. Micronutrient biofortification of staple crops for nutritional security is summarised in this review.

Agricultural crops are a rich source of micronutrients

The dietary pattern must provide the bare minimum of important elements such as carbohydrates, proteins, lipids, vitamins, and minerals (Lean 2019). Globally, various crops are cultivated to supply this demand, including cereals, pulses, oilseeds, and fodder crops. Because developing nations lack diversified food, staple crops must include essential nutrients in an appropriate diet. Although there are more than 50,000 edible plants on the planet, just 15 of them produce 90% of the food. Two-thirds of the world's consumption of staple foods come from these three commodities: rice, maize (corn), and wheat (Shelef et al. 2017). Other important dietary intakes include millet and sorghum, potatoes, cassava, yams, dairy products, and animal items such as meat and fish. In low-income developing countries, the primary diet consists of wheat, rice, millet, corn, and sorghum (Shelef et al. 2017).

Cereals crops

Aside from reducing global food insecurity, cereal grains can absorb more mineral nutrients in their edible part. Rice (*Oryza sativa*) is the most widely consumed cereal grain by more than half of the world's population and accounts for more than 42% of calorie consumption (Huang et al. 2020). Rice is the fastest-growing staple food in Africa and Latin America, accounting for about 90% worldwide consumption. Rice contains various vitamins (such as vitamin B1, B2, B3, B6), phyto-molecules, and minerals such as sodium, zinc, iron, copper, potassium, magnesium, and phosphorus.

Wheat is the second most common food after rice in South Asia, Turkey, and China, accounting for more than 70% of daily calorie consumption. As a result, its nutritional content is critical for ensuring nutritional security. The testa, aleuronic layer, embryo, and endosperm are all parts of wheat grain. The embryo is the live component of the grain, and it has a high concentration of nutritional value. While the endosperm is largely starch, the aleuronic layer contains most nutrients (such as protein, minerals, and vitamins) (Rosa-Sibakov et al. 2015). Its versatility adds to its value, as its seeds may be processed into semolina, flour, and other fundamental components for pasta, bread, and pastry items. In addition to wheat and rice, corn, also known as maize, is the world's most important staple grain. Most of its popularity comes from the fact that it is a good source of food for both human and animals. It may be prepared in various methods, including boiling, roasting, frying, grinding, and fermenting, and is often used in gruel, bread, cakes, porridges, and alcoholic drinks. In industries, its use is in sweeteners, oils, food thickeners, and non-consumables. Its nutritional composition comprises 72% carbohydrate, 10% protein, and 4% fat. Except for vitamin B-12, maize includes a variety of essential vitamins (Rosa-Sibakov et al. 2015). Maize's germ and endosperm contain 80% and less than 1% of the total mineral content. In maize, the most common minerals are K, Mg, Zn, and P (in the form of phytate). Methionine and cystine are two sulphur-containing amino acids. In the state of methionine and cysteine, sulfur may be found in the body. Ca and Fe are present in negligible amounts, and other trace minerals include Mn, Se, Cu, and I (Nuss and Tanumihardjo 2010).

Pulses crops

Pulses are also known as a "superfood" because they have a lot of nutrients that can help you stay healthy. The FAO has designated nutrition security as its 2016 topic, and this shows that they acknowledge the importance of achieving this goal (Food and Agricultural Organization of the United Nations). After cereals, they are the second most important crop in the agricultural sector, with a large consumption (over 70%) of lentils, peas, beans, and chickpeas globally (Callens et al. 2019). They are also important for their social and economic impact because of their inter-cropping systems. Cereals have a significant socioeconomic influence because of the intercropping systems, including low fertilizer and water needs, great disease resistance, extended storage duration, and the capacity to adapt to extreme environments (Brueck and Lammel 2016). These characteristics, when combined, possess technological/functional features with broad industrial relevance for the production of functional foods. In recent years, six pulses, namely chickpea (*Cicer arietinum*), field pea (*Pisum sativum*), lupin (*Lupinus*), faba/broad bean (*Vicia fabae*), lentil (*Lens culinaris*), and mung bean (*Vigna radiata*), have acquired prominence owing to the large amounts of these crops produced worldwide (Callens et al. 2019). India is the largest producer in Canada, Myanmar, and China.

Furthermore, they are high in protein (up to 30% of their dry weight in protein), carbohydrates, dietary fiber, and calories. They are also high in important bioactive compounds and necessary minerals and vitamins needed by the human body (Rebello et al. 2014). Lentils and beans are the pulses with the highest Fe and Zn content, followed by peas and lentils. Beans often have the greatest concentrations of iron and other elements. It is, nevertheless, vital to remove phytate and other inhibitors since they reduce the digestion and bioavailability of minerals. Pulses, owing to their high mineral concentration, would become potential sources of Zn and Fe after decomposition (Venkidasamy et al. 2019). Although cooked seeds maintained about 70–75% of water-soluble vitamins, raw bean samples contained 0.49 mg vitamin B12 and 0.30 mg folic acid. The folate concentration of beans accounts for 95% of daily requirements.

Oilseed crops

Oilseed crops are generally planted to extract the oil contained inside the seeds. Vegetable oils are widely utilized in domestic cooking and other food products such as baked goods and snacks worldwide. Additionally, they serve as raw materials for a variety of oleo-chemical businesses. Canola, safflower, maize, sunflower, olive, soybean, and peanut crops are examples of oilseed crops. Oilseeds are a key vegetable oil source with greater production of oil when compared to other crops (Zafar et al. 2019). These crops are especially essential among low-income households in semi-arid tropical areas since they account for 40% of their total calorie consumption. Recent studies have demonstrated that rape oilseeds contain significant protein and minerals such as Zn, Fe, Ca, and other trace elements, making them a viable alternative to conventional crops for addressing nutritional stress (Kowalskaet al. 2020). Groundnut, soya bean, castor bean, and other temporary oilseed crops are separated from permanent oilseed crops such as coconut, oil palm, and olives. Permanent oilseed crops include coconut, oil palm, and olives. Soybean, which is readily accessible as a meal and is high in amino acids, is a commodity that is extensively traded across the world. Because of their low lignin level and high mineral and nutrient content, soybean hulls are an excellent fibre, protein, and energy source. Proteins, amino acids, vitamins, and minerals are included in canola meals with a high sulphur concentration. Hemp seed and mustard seed oil are fortified with good nutritional characteristics and minerals such as Ca, Mg, P, S, K, Fe, and Zn.

Similarly, various oilseeds are very nutritious for humans. Because of their high oil content, brassica crops, including mustard, canola, and rape, are receiving much attention in the bio-diesel business for creating feedstock oils. The large levels of phytic acid and other binding agents in oilseeds, on the other hand, restrict mineral bioavailability from the seeds. As a result, phytate removal methods are being developed to manage or eliminate mineral binding in oilseed products. Oilseed supplemented with minerals by biofortification, on the other hand, may help to reduce the mineral shortage. For example, under acidic conditions, foliar application of Na_2SeO_4 enhanced the Se concentration in the plant components of oilseed rape (Száková et al. 2017). However, the biofortification of oilseed crops has received little attention, and this area needs to be investigated more to improve their nutritional value.

Mineral acquisition and transport via molecular mechanisms

Plants require micronutrients. The absorption of micronutrients from the soil, diffusion throughout the plant, delivery to sink organs, and allocation to particular metalloproteins in plants are all optimized via a highly specialized and tightly controlled network in the plant. *Arabidopsis thaliana* and rice have been the primary models for studying the molecular processes of plant micronutrient absorption and usage efficiency (Sperotto et al. 2014; Xue et al. 2016). In the future, the knowledge gleaned from these models will need to be applied to other agronomically important crops.

Mineral uptake, transport, and accumulation in crop plants must be well understood to enhance nutritional bioavailability. These processes are probably regulated by genes, many of which are unknown. Several studies have found genes involved in translocation into numerous vegetative tissues and eventually to seeds (Sperotto et al. 2014; Jeong et al. 2017). But the genes expressed by phloem involved in mineral loading and mobilization to various sink tissues are only known to a very limited extent (Braun et al. 2014). As a result, although research on particular transporters may help us understand their function, whole-plant studies are needed to identify the most important transporters for seed mineral delivery. Mineral acquisition and mobilization in plants have been extensively researched (González-Guerrero et al. 2016; Xue et al. 2016). However, numerous stressors may result in the non-availability of critical nutrition elements, impairing crop development.

Uptake of micronutrients

The molecular processes of plant absorption of most micronutrients have been explored in recent decades (Connorton et al. 2017; Stanton et al. 2021). The involvement of rhizosphere acidity in acquiring metal micronutrients is well established. It has recently been shown that root exudates play an important role in mobilizing dicot micronutrients (Fig. 1.). While it was previously known that cereals acquire Fe through the secretion of phytosiderophores into the rhizosphere, the central role of secreted coumarins in mobilizing Fe in the vicinity of growing roots has been highlighted in several dicot species, with possible implications for the acquisition of other micronutrients and the shaping of the bacterial communities associated with the roots (Tsai and Schmidt 2017; Stringlis et al. 2018). These are known as strategies I (proton extrusion, reduction, and absorption of Fe (II)) and II (phytosiderophores). Additionally, the YS1 (Yellow Stripe Oligopeptide Transporters 1) transporter transports the ferric-phytosiderophores complexes from the rhizospheres into plant roots (Saini et al. 2016). Furthermore, current research has shown the presence of unique processes for metal absorption from arbuscular mycorrhizal fungi, which are particularly important in natural ecosystems and organic agrosystems (Senovilla et al. 2020). Up to 50% of plant Zn absorption is attributed to root mycorrhizal colonisation (Watts-Williams et al. 2015). Reducing root mycorrhizal colonisation resulted in significant cadmium (Cd) build-up in wheat (Yazici et al. 2021). Thus, it is critical to pay close attention to the number and activity of mycorrhizal fungi in agricultural soils to control micronutrient nutrition and prevent Cd build-up in crop plants (Ma et al. 2021).

Even though plants need micronutrients, too much of them is often toxic and causes harmful things to happen (Raffa et al. 2021), such as a decrease in photosynthetic pigments (Aslam et al. 2021), a decrease in the integrity and permeability of membranes (Stoyanova and Doncheva 2002), an increase in oxidative stress caused by the production and accumulation of reactive oxygen species (ROS), as well as an increase in the activity of antioxidant enzymes (Balafrej et al. 2020), and in the worst cases, cell death (Zhang et al. 2022). Excess micronutrients have negative consequences such as diminished photosynthetic pigments, oxidative stress, changes in membrane integrity and permeability, suppression of protein function, interference with absorption and use of other mineral elements, stunted development, and lower yields (Zhang et al. 2022; Raffa et al. 2021).

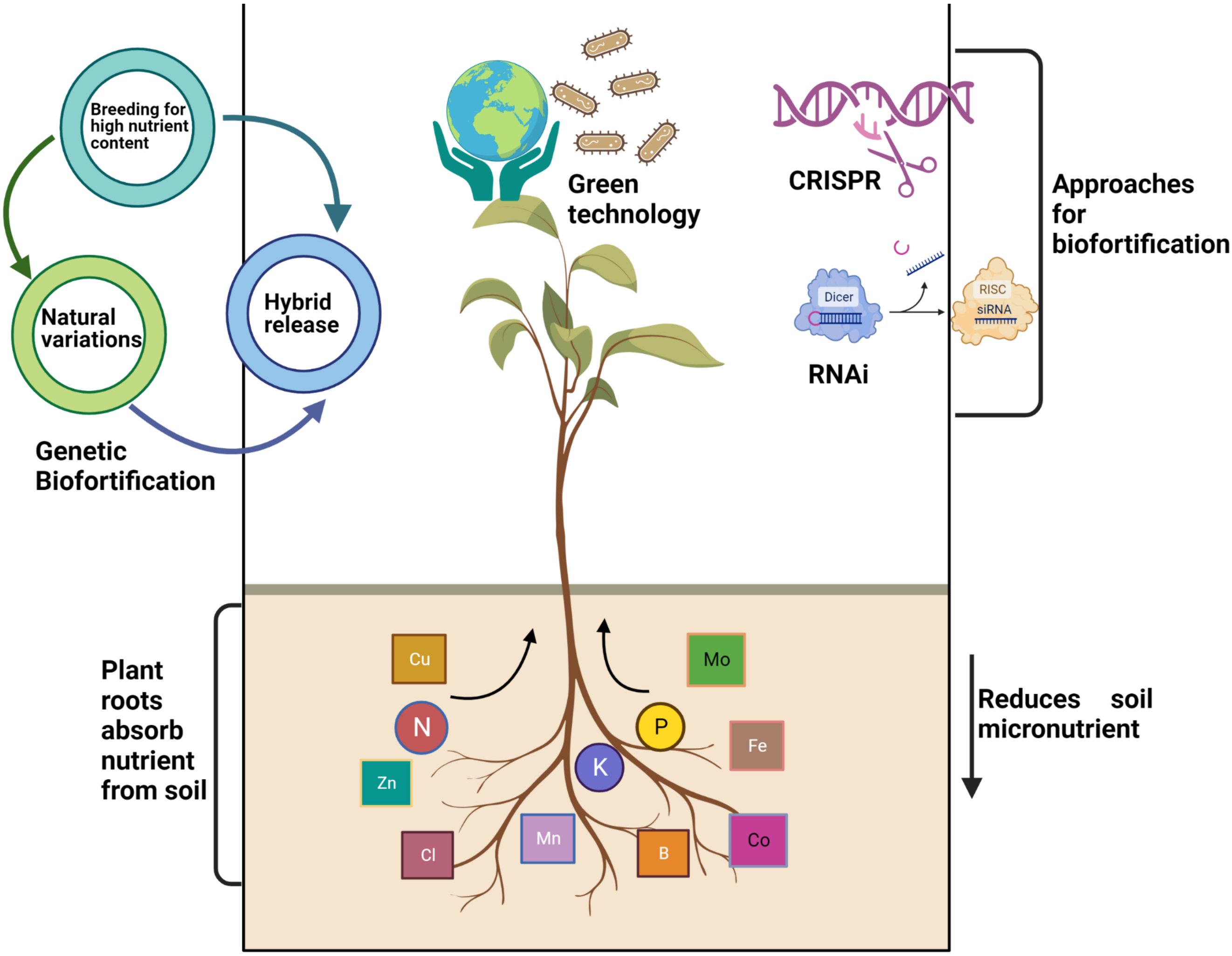

Fig. 1 Schematic illustration of micronutrients absorption in plants and different methods of biofortification. The absorption of micronutrients by plants results in the depletion of the soil micronutrients. Plants are deficient in micronutrients that can be biofortified through various approaches. Figure created with BioRender (biorender.com)

Distribution of micronutrients within the plant

Micronutrients are delivered to sink organs inside the plant through the sap, often the youngest leaves and seeds. This is accomplished by the movement of nutrients across membranes and the presence of tiny organic ligands that preserve the nutrients' solubility in solution and avoid mis-metallation (Olsen and Palmgren 2014; Connorton et al. 2017). While numerous genes involved in micronutrient mobilization and absorption from the soil have been discovered, the processes for loading micronutrients into the xylem and phloem and the ligands in conducting tissues are still largely unknown micronutrients. The transporters in the nodes and tiller buds of plants play important roles in the distribution of micronutrients in plants, especially in the delivery of micronutrients to the younger leaves and seeds, and should be studied further (Shao et al. 2018; Mu et al. 2021). Only a rudimentary understanding of the mechanics of micronutrient distribution to the edible organs exists (Andresen et al. 2018). To breed or engineer plants for targeted micronutrient allocation, a deeper understanding of the processes of micronutrient distribution to the organs and tissues would be required.

Additionally, metal recycling and reuse are mainly ignored during the shift from vegetative to reproductive development. According to preliminary findings, metal remobilization from senescing leaves looks to be a viable area for modulating metal accumulation in seeds (Mari et al. 2020). Wheat or Arabidopsis leaves with autophagy-mediated modification of leaf senescence and nutrient recycling change the levels of protein and mineral micronutrients in the seeds (Chen et al. 2019; Pottier et al. 2019). In addition, the method of mineral micronutrient loading into seeds is another important step that has to be investigated further. There is only a limited amount of information available on the penetration of micronutrients into seeds. Metal-pumping ATPases have been shown to play a crucial role in releasing Zn from the mother tissues before its entrance into the seed (Olsen et al. 2016). The production of ascorbate is utilized to lower Fe levels in the bloodstream and enable it to be absorbed by the embryo (Grillet et al. 2014). This study will need extensive characterization of the dynamics of micronutrient distribution in plant organs and tissues through the use of basic imaging methods and metal isotopes as tracers need to be developed further (Sheraz et al. 2021).

Micronutrient interactions

Aside from their relevance for nitrogen metabolism, micronutrients interact significantly with several macronutrients. Indeed, deficiency symptoms are often caused by dietary imbalances rather than a deficit of a specific micronutrient. Homeostasis of micronutrients and other mineral nutrients, such as inorganic phosphate (Pi) with Zn and Fe, have essential interactions (Dong et al. 2017; Hanikenne et al. 2021; Watts-Williams et al. 2015). On the other hand, Zn deficiency promotes Pi absorption, whereas root Zn absorption is inhibited by high Pi levels (Kisko et al. 2018). The uptake of Zn and Fe by the roots and their transport and remobilization from the roots to the shoots are positively affected by nitrogen fertilization (Kutman et al. 2011). In Arabidopsis, Iron-Regulated Transporter or Zrt-/Irt-like Proteins (IRT/ZIP) family and Yellow StripeLike (YSL) were identified (Kobayashi et al. 2019). Following this, the concentrations and distributions of zinc, iron, and proteins in seeds are highly connected (Cakmak et al. 2010). On the other hand, sulphur (S) fertilization has a detrimental effect on Mo absorption, resulting in Mo deficiency in plants (Maillard et al. 2016a, b). The metalloproteins involved and their biological functions must be explored to establish the molecular underpinnings of these interactions.

Enhancement of the accumulation of chemically identical hazardous trace elements is a key danger faced in biofortification techniques targeting mineral micronutrients (Kawakami and Bhullar 2021). Enhancing the expression of a transporter involved in Cd sequestration in root vacuoles or knocking down a gene involved in Cd absorption in roots have been effective techniques for preventing Cd accumulation-up in grains in rice. (Ueno et al. 2010; Ishikawa et al. 2012). Due to their chemical similarity, micronutrient metals compete with non-essential metals for transport and binding to ligands. It is necessary to have an extensive biochemical understanding of the substrate specificities and relative affinities of proteins and transporters for micronutrients and hazardous substances with comparable chemical characteristics to address these essential scientific problems in detail (e.g., Zn and Cd). To enhance the exclusion of non-biogenic metals, the factors of metal specificity, especially among divalent metals, must be well characterised (Pottier et al. 2015).

Specification of micronutrients

In plants, the most important metal ligands, like citrate or nicotianamine, and their involvement in micronutrient transport across cells and organs have been well established (Clemens 2019). For example, the bioavailability of Fe and Zn in rice grains was improved by increasing the concentration of the metal-binding molecule nicotianamine by activating the nicotianamine synthase gene (Lee et al. 2011). However, micronutrient speciation and subcellular distribution processes must be better understood to improve micronutrient content in edible crop plant parts and optimize metal distribution for photosynthetic and N metabolism. Identifying the metalloproteome and metallome for each essential metal using analytic and spectroscopic approaches and examining micronutrient speciation is critical to achieving this aim (Flis et al. 2016). Because metal speciation occurs in various cell parts, understanding the processes that govern micronutrient allocation is essential for controlling metal speciation. For instance, in the vacuole, Fe is generally stored as an insoluble compound with phytate, but in the plastids, it is stored as bioavailable ferritin (Mari et al. 2020).

Micronutrients in soil: global status

In many parts of the world, micronutrient insufficiency in soil has been tested using different analytical methods. High-yielding crops require many fertilizers, but there is not enough micronutrient supplementation to make up for it. Deficiencies of Zn and B were found to be 49% and 31%, respectively, in major regions of the world's soil (Shukla et al. 2021). Other mineral shortages were 15%, 14%, 10%, and 3% for Mo, Cu, Mn, and Fe. Boron, which is found in soils in the form of BO_3^{3-}, is important for mechanical resilience and cell membrane strengthening. Low B availability in soil indicators has been found in a few places in practically every nation, notably in Nepal, India, the Philippines, and Thailand. Cu well-known function as a catalyst is involved in the production of proteins and vitamin A and the activation of enzymes in a variety of plant-growth processes. Copper toxicity has been reported in soil samples from Brazil, the Philippines, Tonga, and Italy, among other places.

Iron (Fe) is well recognised as a component of haemoglobin and various other enzymes involved in nitrogen fixation, energy transmission, and lignin formation, among other processes. In Mexico, Malta, Turkey, and a few other nations' areas, there is a deficiency in Fe bioavailable form in soil. A different micronutrient, called Mo, is used to make nitrogenase, a key enzyme in the nitrogen fixation process in the rhizobium legume symbiosis (Lešková et al. 2017). In places with acidic soils, such as Africa (Zambia, Sierra Leone, Ghana, Nigeria), Nepal, Brazil, and New Zealand, Mo deficiency is more common. For the most part, the significance of the micronutrient Mn in photosynthesis and nitrogen metabolism is well-known. Still, it also helps plants use more P and Ca by increasing the number of water molecules that may be photolyzed (Lešková et al. 2017). Mn deficiency is found in alkaline soils, while Mn sufficiency is seen in acidic soils, indicating that soil pH influences Mn availability. A high Mn deficit has been recorded in alkaline soils in Syria, India, Egypt, Pakistan, Italy, and Lebanon. Even though Zn insufficiency has been reported regularly around the globe, it is more widespread in the following countries: Iraq; Pakistan, India; Turkey; Syria; Mexico, Italy, Lebanon, Nepal, Tanzania, and Thailand (Singh 2001).

Micronutrients are found insufficient concentrations in most Indian soils; however, their bioavailability for plant absorption is limited; as a result, soils in numerous Indian locations are deficient (Singh 2001). Indian grounds have a wide range of boron deficiencies, from 68% in red soils of Bihar to 2% in alluvial soils of Gujarat. Due to heavy rainfall, which causes a reduction in water-soluble B, maximum B insufficiency (54–86%) was recorded in the Alfisol soils of West Bengal and Assam. In the Indo-Gangetic plains with salty soil, there was a greater concentration of B, while the state of Rajasthan and Madhya Pradesh had a moderate amount. In addition, it was discovered that Kerala, the Himalayan Tarai zone, Bihar, Uttar Pradesh, and north Madhya Pradesh have copper-deficient soils (Singh 2001). Nutrient deficiency impairs the ability of the photosynthetic system to operate (Morales et al. 2020). Under a variety of stress conditions, a low stomatal aperture reduces photosynthesis. As a result, it is often observed in reaction to drought and extensively recorded in compacted soil-grown plants or soils causing deficits in the macronutrients K and P, as well as the micronutrients Zn and Cu. There is evidence of altered chloroplast ultrastructure and function in particular situations, such as plants lacking in K or micronutrients (Morales et al. 2018).

The alkali soils of the Indo-Gangetic area have low levels of plant-available iron, although iron is found in greater quantity in the earth's crust than in its soils. According to soil study studies, around 12% of Indian soils are deficient in Fe. According to research, manganese-deficient soil is very unusual in India, with approximately 1–5% of surface soil samples being confirmed to be Mn deficient. Manganese deficiency was prevalent in Haryana, Bihar, Punjab, and Madhya Pradesh, among other places. Furthermore, excessive lime treatment in red lateritic soils of Orissa resulted in Mn shortage (Singh et al. 2006). More than 11% of the soil in India doesn't have enough molybdenum. This is true for all types of soil, from hill soils in Andhra Pradesh to the coast of India's Malabar region and the north and northeast Himalayas (Bhupalraj et al. 2002; Singh et al. 2006).

Conversely, calcareous alkaline soils in the Punjab area have high accessible Mo concentrations, and as a result, possible toxicity in crops has been documented in several crops. Wheat straw, as fodder, was discovered to have a high Mo concentration and was consequently harmful to cattle. In India, 51.2% of soil samples were Zn deficient, making Indian soils the worlds most deficient throughout Zn, with a widespread deficiency in the Indo-Gangetic plains. States like Haryana, Punjab, Uttar Pradesh, Bihar, Andhra Pradesh, and Madhya Pradesh have shown a decrease in Zn deficiency (Bhupalraj et al. 2002; Singh et al. 2006).

Micronutrient enrichment in field crops includes several approaches

Biofortification raises the nutritional quality of a target crop by increasing the concentration of micronutrients in edible sections without compromising agronomic traits such as insect resistance, yield, or drought tolerance (Klikocka and Marks 2018; Murgia et al. 2013). Conventional biofortification, transgenic, and agronomic biofortification are three key ways to achieve nutritional security via biofortification (Waters and Sankaran 2011). The traditional approach is to select existing high-yielding crops with greater nutrients of interest and cross-breeding using standard procedures to generate staple crops with desired nutritional and agronomic qualities. Specific genetic modification may increase the concentration of micronutrients in edible plant portions, resulting in genetic biofortification. To boost the micronutrient content of food plants, non-genetic approaches like agronomic biofortification may be more effective. This method boosts grain yields and increases nutritional quality (Cakmak and Kutman 2017; Khoshgoftarmanesh et al. 2010). Using N, Zn, and Fe fertilization, Kumar et al. described the agronomic intervention as a sustainable and cost-effective technique to promote plant development, yield contributing characteristics, and Zn, Fe content in rice crops (Kumar et al. 2018).

Agronomic biofortification refers to the application of micronutrient fertilizers to the soil and/or plant to enrich the edible component of the field crop with micronutrients (Cakmak and Kutman 2017). Numerous biofortified crops, such as cereals, pulses, oilseeds, fodder crops, and others, have been grown across the globe till today. This technique gives the necessary nutrient externally before or during plant development. Foliar treatment improves the nutrient content in the leaf for transmission to other plant parts, while soil application maintains an adequate amount of food for root absorption. When applied to the soil, nutrients are ensured for root absorption, and however, when applied topically, nutrients are increased in the leaf, which may then be transported to other plant parts. The availability of the micronutrient and hence the success rate of biofortification is influenced by soil qualities such as pH, calcareous nature, etc. Therefore, the availability of micronutrients and the success rate of biofortification are influenced by soil qualities such as pH, calcareous nature, and other factors. Thus, the mineral enrichment in a given crop is affected by fertilization application technique, soil conditions, and additives.

Traditional approach

Agronomic biofortification

In this method, biofortification of crops (legumes and cereals) through foliar spray application of micronutrients. This application helps acquire more nutrients in reproductive parts, and hence healthier and natural biofortified grains are harvested. Micro nutrients are applied in liquid form in aerial parts of plants. After application, these micro nutrients are absorbed through stomata and epidermis, and finally become part of the food chain. Minerals such as selenium, zinc, calcium, etc., are supplied to crops alongside irrigation and are readily available for uptake. This results accumulation of these micronutrients in eatable parts of the plants. For the application of minerals through soils at the time of fertilization results perfect biofortification of crops that are usually completed through NPK. These are applied in the soil bed before sowing or seed using different seed cum fertilizer drills. In this way, they are absorbed and made part of the food chain through root uptake. Microbe-mediated enhanced uptake of nutrients for biofortification of vegetables and crops are also established techniques. Different microbial species, i.e., rhizobium bacteria, mycorrhizae fungi, etc., help plants in nutrient acquisition through mutualism.

Green technology (bacterial and endophytic biofortification)

Microorganisms are used in green technology to enhance the soil nutrient status by increasing nutrient accessibility to the crops. According to research, excessive usage of chemical fertilizers has negative consequences for the environment and human health. As a result, microorganisms (*Trichodesmium*, *Azospirillum* spp., *Pseudomonas* spp., *Mycorhiza, Bacillus* spp. *Enterobacter*, *Azoarcus* spp. etc.) harbouring biofertilizers may be a cost-effective and environmentally friendly alternative to chemical fertilizers for plant development and soil fertility (Fig. 1.). Plant growth-promoting microorganisms benefit plant health in various ways, including biological nitrogen fixation, the generation of numerous plant growth hormones, hydrolytic enzymes, siderophores, HCN, and the solubilisation of K, Zn, and P (Kaur et al. 2020). Bioavailability of nutrients cannot be achieved entirely by intrinsic plant-based mechanisms, including chelator secretion, organic acid synthesis, and phyto-siderophores. Microorganisms create chelating chemicals that form complexes with Zn and release them at the root surface, increasing Zn availability and resulting in Zn biofortification in plants. There have been several research on the positive impact of microorganisms in crop biofortification. Bacteria and fungus are the most common sources of biofertilizers.

Bacterial biofortification

The introduction of *Pseudomonas* and *Bacillus* sp. converted soluble zinc complex chemicals (ZnS, ZnO, and $ZnCO_3$) into zinc ions in broth culture (Praharaj et al. 2021). The application of *Arthrobacter* sp. DS-179 and *Arthrobacter sulfonivorans* increased the qualitative and quantitative parameters linked to Zn and Fe concentrations in wheat crops (DS-68) (Singh et al. 2018). Similarly, inoculation of siderophore-producing *Arthrobacter sulfonivorans* DS-68 and *Enterococcus hirae* DS-163 endophytes into soils with lower Fe content resulted in an increase in the average number of root tips and root surface area by 1.6 and 2 folds over the control, respectively, according to another study (Singh et al. 2017). However, in the presence of a high Fe concentration in the soil, the average number of root tips and root surface area increased by 1.2 and 1.5 times, respectively, compared to the control. Fortification of wheat grains in this way was made easier by the enlarged root parameters. They then inoculated wheat with *Bacillus subtilis* DS-178 and *Arthrobacter* sp. DS-179 and promising Zn-solubilizers and siderophore-producing endophytes (Enterococcus hirae DS-163 and Arthrobacter sulfonivorans DS-68) enhanced yield and micronutrient status (Singh et al. 2017).

Endophytic biofortification

Mycorrhizal fungus inoculation has a beneficial effect on the availability of micronutrients in soil via siderophore synthesis, rhizospheric acidification, and hyphal transfer of nutrients through the external mycelium. Additionally, increased grain Zn concentrations were detected after *Rhizophagus irregularis* colonisation under Zn-deficient circumstances through overexpression of *HvZIP13* (Watts-Williams and Cavagnaro 2018). The combined use of mycorrhizal fungi (MF) and plant growth-promoting bacteria (PGPB) resulted in improved yield-related measures, and increased Zn and Fe grain content in wheat compared to the control group. The PGPB increased the number of metabolic processes contributing to plant growth indices, including photosynthesis. However, AM is involved in several functions, including effective micronutrient absorption in plant tissues and encouragement of plant development through the production of signalling molecules and various other chemicals that alter agricultural plants' root shape and architecture. Along with PGPB and AM fungi, this combination improves stress tolerance, weed management, and better protection against pathogens (Yadav et al. 2020). According to previous studies, endophyte inoculation considerably lowered the phytic acid content in wheat grains by roughly 26% over the RDF, resulting in a rise in Fe and Zn concentrations (Singh et al. 2017).

New breeding technique (Genetic and genome engineering)

New breeding techniques are best strategy of biofortification. This strategy is based on group techniques where Overexpression of genes, Gene transfer, Gene silencing, Gene knockout is performed for biofortification of crops. Knocking out of genes is generally performed to stop the biosynthesis of anti-nutrient compounds. There are various anti-nutrient compounds which are involved in various pathways to restrict the bioavailability of essential micronutrients. These are lectins, phytic acid, saponins, pathogens, protease inhibitors, a-amylase inhibitors, and tannins. Hence, this results in mal-nutriated crops. Genes involved in the biosynthesis of anti-nutrients could be repressed through RNAi for reduced accumulation of these compounds. Tissue specific expression or overexpression of genes responsible for micronutrient accumulation in plants are the best way for the bioavailability of biofortification in transgenic crops. To improve the nutritional quality and quantity of micronutrients, gene transfer methods of biofortification is generally used. Different genes involved in the biosynthesis of provitamin A (*CrtB*), iron homeostasis (*Fer1-A*), and flavonoid production (*C1*) have been used for biofortification through various new breeding techniques and metabolic engineering (Shahzad et al., 2021; Blancquaert et al., 2017). These genes are transferred across the various crop species for enhancement of the nutritional supports. These genes help to biofortify the crops for better production of a micronutrient rich diet. In this way we can easily control the malnutrition and disease associated with hidden hunger. Previously, this technology has certain limitations, i.e., laborious, expensive, time-consuming, and regulatory issues but after historical and visionary decision of Govt. of India, SDN1 and few SDN 2 categories are now relaxed for tough regulation steps. It will become easy to develop, produce and transfer the biofortified crops in various cultivars.

Breeding for genetic biofortification

Plant breeding methods generate crops with greater micronutrient content, moderate to low levels of anti-nutrients, and enhanced amounts of compounds that encourage nutrient absorption via genetic biofortification (Bouis 2003). Breeding techniques can significantly boost micronutrient density by examining genetic diversity to generate nutrient-dense crop variants (Fig. 2). As a result of its long-term viability and lack of regulatory and political restrictions, biofortification through breeding seems to be the best method for biofortification (Saltzman et al. 2017). However, it is necessary to first establish a target micronutrient level for each crop before developing an agriculture crop genetic biofortification programme. Available genetic variability and information about genes that control the absorption of the element by roots, translocation to shoots, mobilization in different vegetative parts, and deposition of the element inedible parts in utilizable forms are among the factors that affect genetic biofortification (Bouis and Welch 2010). Aside from that, various environmental and cultural variables may influence micronutrient accumulation and dietary factors that influence mineral absorption and use by consumers (Bouis and Welch 2010). Breeding has been used to generate most biofortified goods in Asia, Africa, and Latin America, while new methods are being developed to manufacture biofortified products (Garcia-Casal et al. 2017). Biofortified food crops with high nutritional content are grown and marketed by HarvestPlus2 in collaboration with many CGIAR and National Agricultural Research Centers in Africa, Asia, and Latin America. Several biofortified crops, including yellow cassava, orange flesh sweet potato with high levels of β-carotene (over 200 mg/g), iron beans (50–70% more Fe content), orange maize, iron pearl millet, zinc rice, and zinc wheat developed through breeding, have been officially released in more than 30 countries and are in the testing stage in more than 50 countries, according to the HarvestPlus Annual Report (2015). Numerous studies have

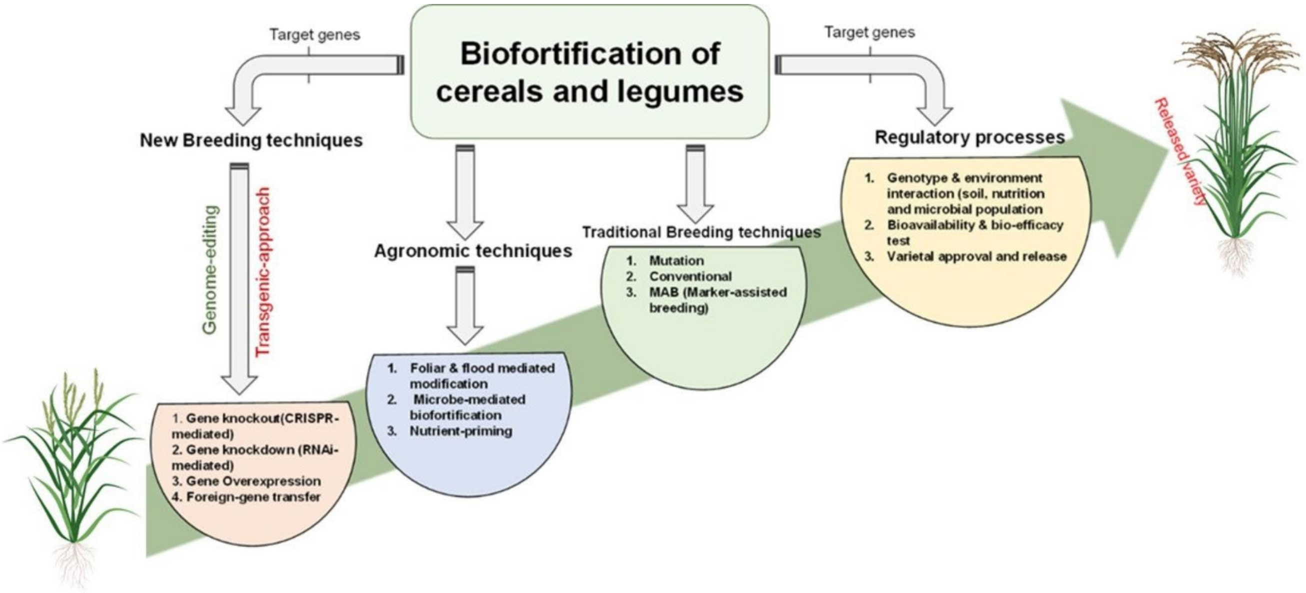

Fig. 2 Biofortification of cereals and legumes through different methodologies. These are broadly classified into three types, i.e., agronomic techniques, new breeding methods, and traditional breeding approaches. The regulatory process is the most essential stage in the release of a crop variety. Figure created with BioRender (biorender.com)

shown that these newly released biofortified cultivars effectively reduce micronutrient deficiencies in target groups (De Moura et al. 2014; Finkelstein et al. 2017).

In contrast to macronutrients, micronutrients account for a relatively small proportion of the overall weight of a grain crop; as a result, precision measurement is essential for efficiently measuring genetic variation to breed stable and high element concentrations. However, approaches for finding nutrient-dense genotypes that are rapid, precise, and economical have yet to be discovered. Pre-breeding procedures may be employed to create the parent for genetic biofortification if wild relatives are confirmed to be a source of micronutrients.

It is difficult to obtain genetic variation for the goal nutritional trait via selection and transgressive segregation of heterosis (Bouis and Welch 2010). It is necessary to have a basic grasp of genetics to successfully design a breeding programme and pick the appropriate parental line and breeding procedure. Furthermore, a greater understanding of the relationship between nutritional attributes and yield and yield-related traits will assist in the selection of nutrient-rich lines that produce higher yields while still exhibiting desirable characteristics (Bouis and Welch 2010). If, for example, there is a positive association between the Fe and Zn content in the seeds of common bean, peanut, mung bean, wheat, pearl millet, maize, and sesame, this implies the possibility of simultaneously improving these two traits (Pixley et al. 2011; Velu et al. 2012). A substantial negative correlation between Zn and grain yield across sites was identified in the case of chickpeas. In contrast, a significant negative correlation between Fe and grain yield was detected at one location in the case of chickpea (Diapari et al. 2014).

Genetic Architecture for the Accumulation of Nutrients

Even though genetic biofortification initiatives have been somewhat successful in addressing the problem of low nutritional content, they have not been as successful as expected in the long run. As a result, it's critical to use genomics ability to speed up the creation of nutrient-dense enhanced cultivars. The details of key crop genetic and genomic resources have been thoroughly studied (Bevan et al. 2017; Varshney et al. 2018; Roorkiwal et al. 2020). Recent advances in next-generation sequencing (NGS) technology have resulted in a dramatic decrease in the cost of sequencing agronomically important crops, allowing the use of NGS-based approaches for allele mining, candidate gene discovery, and high-resolution genetic mapping. Despite cost-effective genotyping systems for applying genomics-assisted breeding (GAB) in agronomically important crops, the expense of high throughput and accurate nutritional estimates remains a significant problem. The plant genome sequencing provides a chance to examine and comprehend the process for functional characterization of genes involved in nutrient absorption and mobilization.

Identification of QTLs/Genes

Linking genetic data with nutritional content data is a sophisticated and accurate way of identifying quantitative trait loci (QTLs) related to a characteristic of interest, and it is becoming more popular. Nutritional profiling of a broad group of genotypically defined germplasm (core collection, mini-core collection, reference set, composite set) may be used to establish a relationship between genetic data and global mineral nutrition (Ghandilyan et al. 2009; Norton et al. 2010). QTL mapping has become more popular for linking genetic variation to phenotypic variation and as a dependable technique for gene identification. QTL mapping may lead to the isolation or cloning of genetic markers (i.e., related regions or linked regions) that can be used to identify and analyse the genes in question. Many crops have had their genome regions that influence nutritional content/concentration mapped at the molecular level. Studies on understanding genes and processes to enhance seed nutritional composition by discovering QTLs were confined to a few nutrients in crop plants to improve seed nutritional composition. Seed element concentration QTLs have been found in *Lotus Japonicus*, *Medicago truncatula*, common bean, soybean, chickpea, and lentil, for example (Blair et al. 2010, 2011; Casañas et al. 2013; Zhang et al. 2009; Jegadeesan et al. 2010; Ramamurthy et al. 2014; Sab et al. 2020; Aldemir et al. 2017). The majority of research to date to map and tag the gene(s)/QTL(s) determining micronutrient status in crops has identified a quantitative mode of inheritance (Blair et al. 2010). Two genes (*PvIRT1* and *PvIRT2*) on chromosome-3 and two genes (*PvbZIP2* and *PvbZIP3*) on chromosome-11, for example, were linked with QTLs for Fe and Zn in *Proteus vulgaris* (Jiang et al. 2008).

Along with traditional bi-parental mapping populations, attempts have been undertaken to strengthen the available genetic variation for nutritional components via genome-wide association studies (GWAS). This strategy uncovered markers related to various critical nutritional parameters in common bean and chickpea varieties (unpublished) (Katuuramu et al. 2018; Caproni et al. 2020). Following confirmation, these newly discovered genes/QTLs may be used to generate nutrient-dense crops high in protein.

Biofortification via genome engineering

In the absence of natural diversity in the target crop's gene pool, transgenic techniques are required and preferable over breeding (Al-Babili and Beyer 2005). "Golden Rice" is the greatest example of genome engineering for a nutritional attribute since an advanced transgenic line with 37 mg/g carotenoid was generated (Al-Babili and Beyer 2005). Despite the positive side of transgenics, some researchers have raised concerns about allergies or intolerances caused by bioengineered or genetically modified crops, the environmental side effects, and the loss of biodiversity caused by these crops (Maghari and Ardekani 2011; Raman 2017). In agronomically important crops, recent advancements in molecular biology have drastically altered mutagenesis platforms for more focused and precise DNA modifications using transcription activator-like effector nucleases (TALENs), zinc-finger nucleases (ZFNs), and CRISPR–associated protein (Cas9) (Haun et al. 2014; Michno et al. 2015; Tang et al. 2016). Innovative technologies such as TALENs, ZFNs, RNA interference (RNAi), and CRISPR/Cas9 should be used to enhance nutritional characteristics in many crops plant.

RNAi seems to have an advantage over other genetic engineering methods. It is a sophisticated, particular gene silencing technique and a highly potent breakthrough that can help build nutritionally rich and antinutrient low crops (Tang and Galili 2004). In the past, RNAi technology has been utilised to lower the amount of BOAA in grass pea, reduce the quantity of Arah2, an allergy, by 25% in crude peanut extract, and generate peanut oils that include unique combinations of oleic acid. RNAi has also been utilised to develop common bean lines resistant to the *Golden Mosaic Virus*. (Dodo et al. 2008; Bonfim et al. 2007). Furthermore, the RNAi-mediated suppression of the SACPD gene has boosted soybean resistance to various diseases (Jiang et al. 2009). Because of lower lignin concentrations, RNAi treatments targeting genes involved in lignin synthesis improved soybean resistance to *Sclerotinia sclerotiorum* (Peltier et al. 2009). Additionally, the RNAi method has aided in enhancing oleic acid in soybean. Apart from legumes, it has improved maize, wheat, rice, cotton, jute, and tomato (Kusaba et al. 2003; Davuluri et al. 2005).

Biofortified crops released or testing by countries worldwide

In a global scenario, most of the countries are working to fight with hidden hunger using various techniques of biofortification. Figure 3 indicates that in which countries biofortified crop varieties had been released or were in testing by the end of the year 2021. Various crop varieties covered have been promoted by HarvestPlus or the International Potato Center, both of which are part of the CGIAR global research partnership for a food secure future. These biofortified varieties have been developed through conventional crop breeding for everyone in Africa, Asia, and Latin America. HarvestPlus promoted biofortified crops which include vitamin A cassava, maize, and sweet potato; iron beans and pearl millet; and zinc rice, maize, and wheat. Many experts in nutrition and agriculture work together to develop these

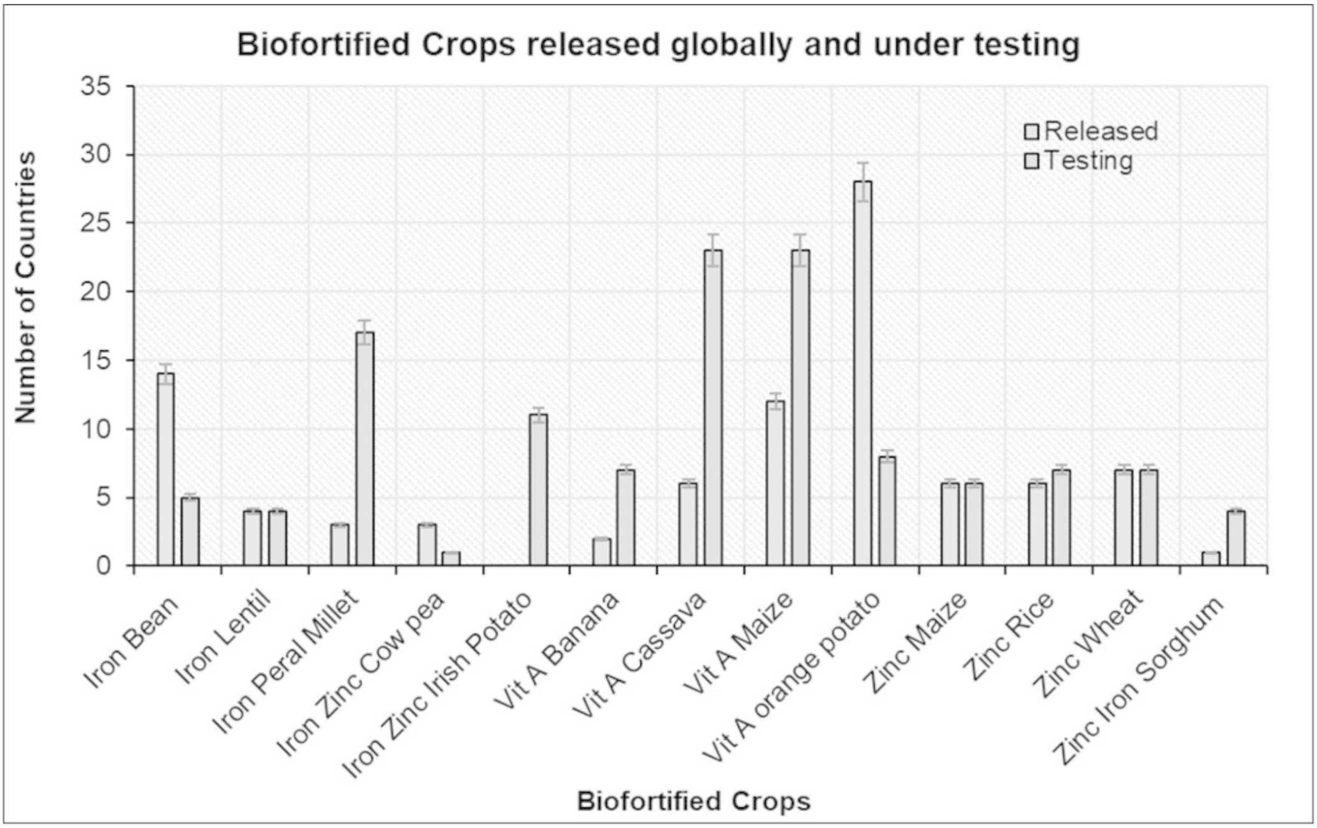

Fig. 3 Status of biofortified crops released or under testing by countries worldwide. More than 14 crop varieties released in 92 countries worldwide. Total 128 countries are still working on trails of these all 14 biofortified crops (https://biocropshplustst.ciat.cgiar.org/)

biofortified crops. They ensure that how these crops can develop high levels of nutrients to improve nutrition and health. They taste good and meet cooking requirements, and that they have agronomic traits farmers demand such as resistance to insects, diseases, and drought tolerance (Arun and Birol, 2020).

More than 48 million people in smallholder farming households are benefiting from conventionally bred biofortified crops facilitated by HarvestPlus. These crops improve nutrition and health status when eaten regularly. Most of the countries around the world now ready to adopt biofortification as part of their crop improvement programs using a wider strategy to combat micronutrient deficiencies (Fig. 3). HarvestPlus now anticipates that by 2030, around 1 billion people will be benefitting from biofortified foods.

Biofortified crops released or testing; an indian scenario

Govt of India have a defined program of biofortification through Indian Council of Agricultural Research for the nutritional biofortification of the staples crops and initiated many programmes in different crops. This body has intiated and recognized these programes in leadership of Dr. Trilochan Mohapatra, Director General, ICAR and Secretary DARE. National Agricultural Research System including ICAR and State Agricultural Universities (SAUs) made a significant progress in this area to develop of many biofortified varieties of cereals, pulses, oilseeds, vegetables and fruits along with staples. In the last 3–4 years these developments have published in the form of a report entitled, "Biofortified Varieties: Sustainable Way to Alleviate Malnutrition". This makes awareness among the stakeholders and consumers, through India and neighbouring countries. The details of released and tested varieties are summarized in Fig. 4.

Conclusion

Mineral micronutrient absorption and usage efficiency in plants are currently neglected traits in crop breeding projects, despite the fact that they have the potential to increase both the sustainability of agricultural yields and the quality of food and feed. Micronutrient supplementation and fortification procedures are generally advised strategies for alleviating micronutrient deficiency concerns in the human population and livestock. Efforts are being undertaken

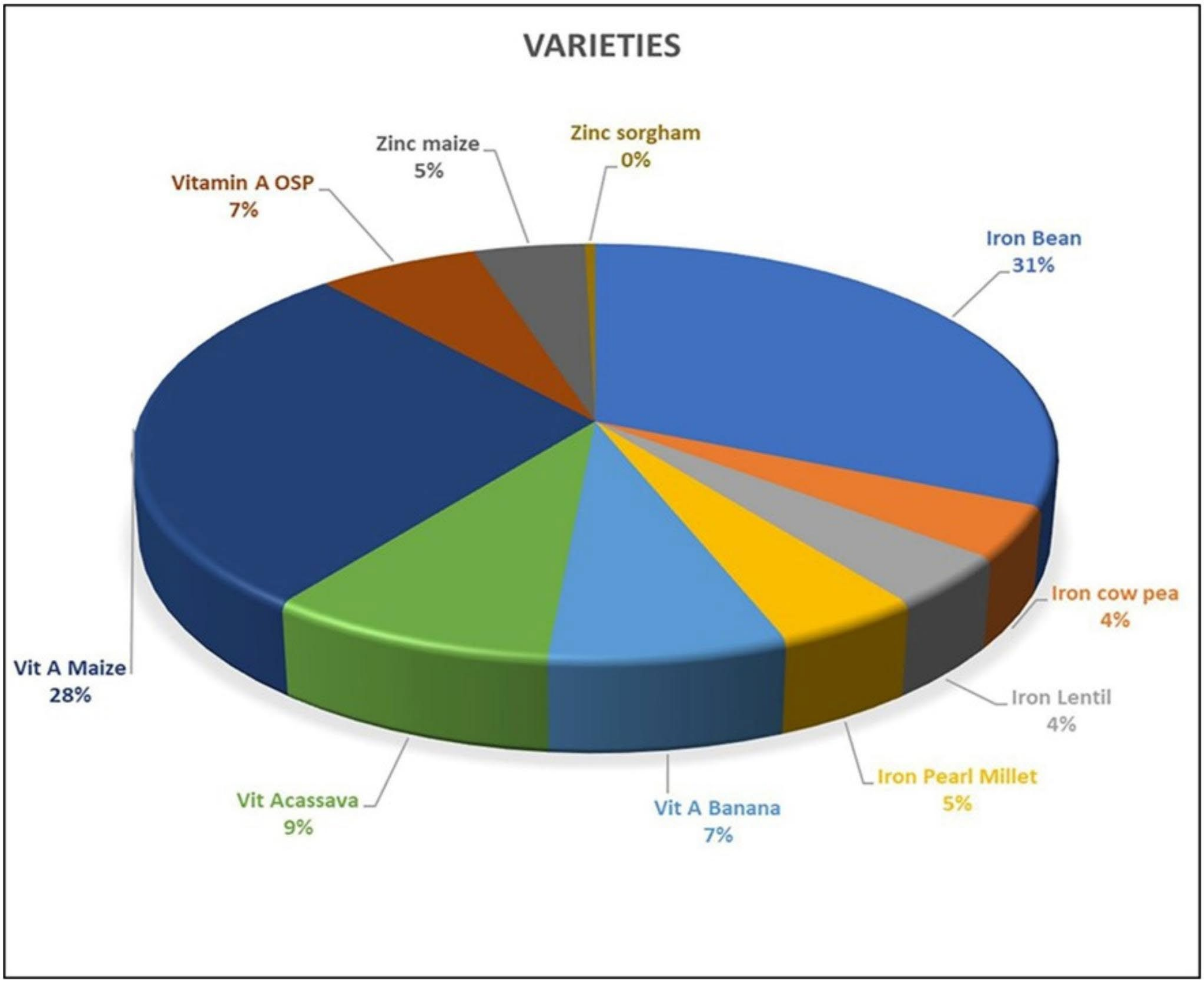

Fig. 4 Biofortified crops and their different varieties released by different countries. A total of 245 biofortified crop varieties has released by various countries for ten different crops (https://biocropshplustst.ciat.cgiar.org/)

worldwide to introduce nutrient-rich superfoods like staple grains and millets into mainstream agriculture. Although great progress has been made in producing transgenics for improved Fe and Zn nutrition in crop plants, further research into the holistic genetic circuitry of Fe and Zn intake, transport, and storage in grains is required.

Micronutrient deficiency is projected to rise as the population of developed nations' shifts toward more plant-based diets, and breeding food plants for high mineral micronutrient content looks to be a sustainable solution. Furthermore, breeding for mineral micronutrient efficiency will enable long-term crop production, which is necessary for light of global change. In this respect, it is required to stimulate research and innovation in this subject to protect the well-being of human populations while also maintaining the competitiveness of the agri-food business. As a first step in developing lasting solutions to micronutrient deficiency in human people, it is vital to understand the molecular and physiological processes underlying micronutrient homeostasis. There has been a plethora of information on the genes and promoters for target features in agronomically essential crop plants. It has been feasible to generate transgenic lines with improved micronutrients. Future studies should try to combine multiple genetic metabolic pathways to boost a variety of nutrients in a specific crop at the same time. Such genetically fortified crops for micronutrients may aid in the alleviation of nutritional issues.

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and the primary draft was revised by Milan Kumar Lal and Rahul Kumar Tiwari. The conceptualization, guidance and resources were provided by Abhijit Dey. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript."

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Declarations

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