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REVIEW

Microorganisms as a Sustainable Alternative to Traditional Biofortification of Iron and Zinc: Status and Prospect to Combat Hidden Hunger

Shaloo Verma[1] · **Hillol Chakdar**[1] · **Murugan Kumar**[1] · **Ajit Varma**[2] · **Anil Kumar Saxena**[1]

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Abstract

Despite the fact that the world has achieved adequate food grain production to fight the battle against caloric hunger, still, a significant fraction of population is suffering with deficiency of micronutrients like Fe and Zn. However, the dietary intake of these micronutrients could be sufficient to meet the nutritional demand if the bioavailability was not low due to the strong inhibition by phytic acid and phenolics. Another cause behind inadequate intake is the scarcity of plant-available micronutrients in soil and genetic makeup of plants impeding high accumulation. Postharvest fortification is the major strategy to enrich staple food crops with micronutrients, but biofortification of food crops using breeding and agronomic strategies is also gaining popularity. However, one important issue remained unaddressed as none of them could really increase the plant-available micronutrients like Fe or Zn which otherwise remain insoluble in soil. Microorganisms due to their enormous metabolic diversity are known to be key players in biogeochemical cycling. Their roles in improving the uptake of major nutrients by plants are well-known and understood. Enrichment of edible crops with Fe and Zn can be achieved through microorganisms by any of the three following strategies—(a) increased availability of micronutrients due to microbial activity such as production of acids, chelators, and phytohormones; (b) microbe-mediated modulation of micronutrient transporters; and (c) de-complexation of micronutrients from compounds like phytate through microbial activity during postharvest processing. Microbe-mediated biofortification can potentially complement the agronomic and genetic biofortification of staple crops.

Keywords Biofortification · Iron · Microorganisms · Siderophore · Zinc · Zn solubilization

1 Introduction

Since the inception of green revolution, productivity of cereal crops increased more than double to sustain the growing population demand of food supply. Development of high-yielding varieties with stress-tolerant traits had been the major means to increase the crop productivity. However, most of the early works on varietal development focused solely on productivity instead of quality. Our aim to combat caloric malnutrition (acute hunger) however undermined the so-called hidden hunger caused due to deficiency of some minerals and vitamins.

Micronutrients are low in majority of the staple crops such as rice, wheat, and potato on which more than half of the global population are dependent. Bioavailability (uptake) of Fe and Zn by the plant from the soil and bioavailability (absorption) by humans from the plant food are limited. Due to their involvement in multitude of biological functions, deficiency of Fe and Zn are widely distributed especially in developing nations. Apart from inherent low bioavailability of Fe and Zn in cereals, postharvest processes, viz. polishing, milling, and pearling, also lower the amount of these micronutrients (Borg et al. 2009). Moreover, anti-nutritional factors, for example, phytates and tannins, may further lower the absorption of Fe and Zn by humans from plant foods (White and Broadley 2005; Brinch-Pedersen et al. 2007; Pfeiffer and McClafferty 2007). It is estimated that more than 2.6 billion people are iron-deficient (WHO 2019; Cacoub et al. 2020) while approximately one-third of the world human

✉ Hillol Chakdar
hillol.chakdar@gmail.com

[1] ICAR-National Bureau of Agriculturally Important Microorganisms (NBAIM), Kushmaur, Mau, Uttar Pradesh 275103, India

[2] Amity Institute of Microbial Technology, Amity University, Noida, Uttar Pradesh 201313, India

population are at risk of zinc deficiency (Lilay et al. 2020). Application of specific micronutrient-bearing chemical fertilizers had been tried but was not effective as they form complexes in soil which cannot be taken up by plants efficiently. Among other interventions to combat micronutrient deficiencies in humans are supplementation with pharmacological (high) doses for treatment of deficiencies (Fe, Zn, vit A and D), and food fortification of cereals (Fe, folic acid) or oils, and margarine (vit A, vit D) for prevention of deficiencies. These strategies are frequently successful. Dietary diversification is often recommended but has had little success because the low-income populations usually cannot afford the recommended foods (e.g., animal source foods for Fe and Zn) and lack of robust distribution systems, and crop seasonality. Biofortification has now emerged as an efficient strategy to sustainably enhance the level of micronutrients in staple food crops and is cost-effective and nutrient reaches the target people in natural form. A number of strategies like conventional and molecular breeding, genetic modification, and agronomic and/or soil management have been applied to increase the micronutrient levels in food crops. As most of the micronutrients present in soil remain in inaccessible form, breeding strategies may not always work to make them available for plants as a variety/line may not achieve its genetic potential when the nutrients are not present in bioavailable form in soil. Microorganisms which remain in close association to the plants and key to the biogeochemical cycling hold considerable promise for biofortification. Application of microorganisms as a part of soil management can make the unavailable nutrients available to plants and can also modulate the specific transporters for enhanced uptake. However, the validated and published reports in this area are very few which warrant a significant emphasis to develop microbe-based effective strategies for micronutrient biofortification. In the present review, we will discuss the status and prospects of microbe-mediated biofortification in comparison to other available strategies.

2 Iron and Zinc in Human Nutrition

Iron is an essential component of hemoglobin and myoglobin. It is also required for a number of biochemical reactions and enzyme systems including energy metabolism, cell division, production of neurotransmitters, formation of collagen, and immune system function (Edison et al. 2008). The recommended dietary allowance (RDA) of iron among non-vegetarians based on an estimated iron bioavailability of 18% for a mixed diet which includes animal products ranges from 0.27 to 10 mg/day for children, 8 to 11 mg/day for adult males, 8 to 18 mg/day for adult females, and 9 to 27 mg/day for lactating and pregnant females (Institute of Medicine 2001). On the other hand, RDA for vegetarians is almost 1.8 times that of the non-vegetarians as meat-derived heme iron is more bioavailable than non-heme iron from plant-based foods due its lower (2–10%) absorption (Trumbo et al. 2001). RDA of iron among vegetarians ranges from 11.5 to 13.7 mg/day for children, 15.1 to 27 mg/day for teens, 16.3 to 18.2 mg/day for adult males, 12.3 to 32.4 mg/day for adult females, 48.6 mg/day for pregnant women, and 16.2 mg/day for lactating women (U.S. Department of agriculture 2012). People consuming a phytate-rich diet with little animal tissue food or vitamin C from fruits and vegetables are at higher risk of iron deficiency (ID). Pregnant women and children who have higher requirements for growth are also at risk of ID. It has been reported that almost 50% of the pregnant women worldwide are anemic due to ID where in country like India, almost 88% of pregnant women are anemic (Lopez et al. 2016).

Like plants, human also require Zn for growth and development. Kumssa et al. (2015) have reported that average per capita Zn supply is ~ 16.3 mg/capita/day while more than two billion people are at risk of Zn deficiency. Children and pregnant and lactating women require higher amounts of Zn and, hence, are at higher risk of zinc deficiency (Reeves and Chaney 2008; Boonchuay et al. 2013). Along with Fe, and vitamin A and I deficiencies, Zn deficiency was incorporated as a major global risk in 2002 (WHO 2002). Zn deficiency in human causes lack of taste, decreased fertility, impaired cognitive function, decreased work capacity, and stunting of growth and increases susceptibility to infections (Prasad 2009; Barnett et al. 2010; Cakmak et al. 2010).

3 Iron and Zinc in Crop Plants

Micronutrients are required in minute quantities by plants but play a significant role in plant nutrition as they are necessary as cofactors and involved in many metabolic functions. Iron is essential for a number of cellular functions in plants, involving in photosynthesis, respiration, biosynthesis of chlorophylls, DNA, hormones etc. (Hansch and Mendel 2009; Kobayashi and Nishizawa 2012). Ferric iron (Fe^{3+}) and ferrous iron (Fe^{2+}) are the most common forms of iron found in the earth crust (Hori et al. 2015). Fe^{3+} is insoluble and its uptake is difficult; Fe^{2+} is soluble and readily available to plants. In general, a neutral to alkaline soil pH (7.4–8.5) causes a low solubility and slow dissolution of iron-bearing minerals. Higher bicarbonate levels, which are prevalent in calcareous soils, reduce the iron uptake by plants grown on alkaline soils. Under aerated and alkaline soils, Fe is oxidized as insoluble iron oxides, but in flooded soils where oxygen diffusion is limited, pH decreases and ferric ions are reduced to ferrous forms (Morrissey and Guerinot 2009). Besides low iron availability and uptake from soils, partitioning of iron in shoots and seeds further reduces the Fe content in seeds especially in cereals. The level of remobilization from shoot to seed varies from plant to plant; for example, in rice, only 4% of shoot Fe is mobilized to the seeds.

Majority of the cereal staple crops are low to moderate in iron content (Fig. 1a). In whole grains of wheat, Fe is present in the range of 29–73 mg/kg (Rengel et al. 1999; Cakmak et al. 2004). As only 25% of these nutrients are localized in endosperm, major fraction of the nutrients present in other parts is lost during milling (Slavin et al. 2001; Ozturk et al. 2006). Iron concentration in brown rice ranges from 6.3 to 24.4 mg/kg, and thus, the iron intake will be 3.78–14.64 mg assuming a maximum of 600-g rice consumed daily while polished rice contains only ~ 2 mg iron/kg; thus, the iron intake will be 1.2 mg/day (Lichtenstein et al. 2006). The amount needed in a country like India, with higher RDA values, would likely be even higher, making postharvest fortification of rice a more potential strategy than biofortification. Other cereal flours have a much higher Fe concentration than rice which makes biofortification with plant breeding and agronomic techniques a more plausible strategy.

Zinc is essential for a number of metabolic functions in plants such as oxidative reactions, structural and catalytic activities, membrane stability, DNA replication, translation, and energy transfer reactions (Broadley et al. 2011; Gurmani et al. 2012). A number of key enzymes, viz. hydrogenase, carbonic anhydrase, Cu/Zn super oxide dismutase (SOD), and RNA polymerase, also require Zn for their catalytic activity (McCall et al. 2000). While Zn deficiency is quite common in plants, Zn toxicity is rare. Zinc deficiency during plant growth and development results in lower Zn content in fruits and grains. To fulfill the human nutritional requirement, the optimum grain Zn concentration should be 50 μg g^{-1} dry weight; however, the current status is 20–30 μg g^{-1} dry weight (Cakmak 2008) (Fig. 1b). Therefore, biofortification strategies are required to double the zinc concentration in the grains to provide the daily amount of zinc needed. Low plant-available Zn was reported for soils of various characteristics: extreme pH, high and low organic matter, calcareous, sodic, sandy, wetland or ill-drained, limed acid soils, etc. Reducing

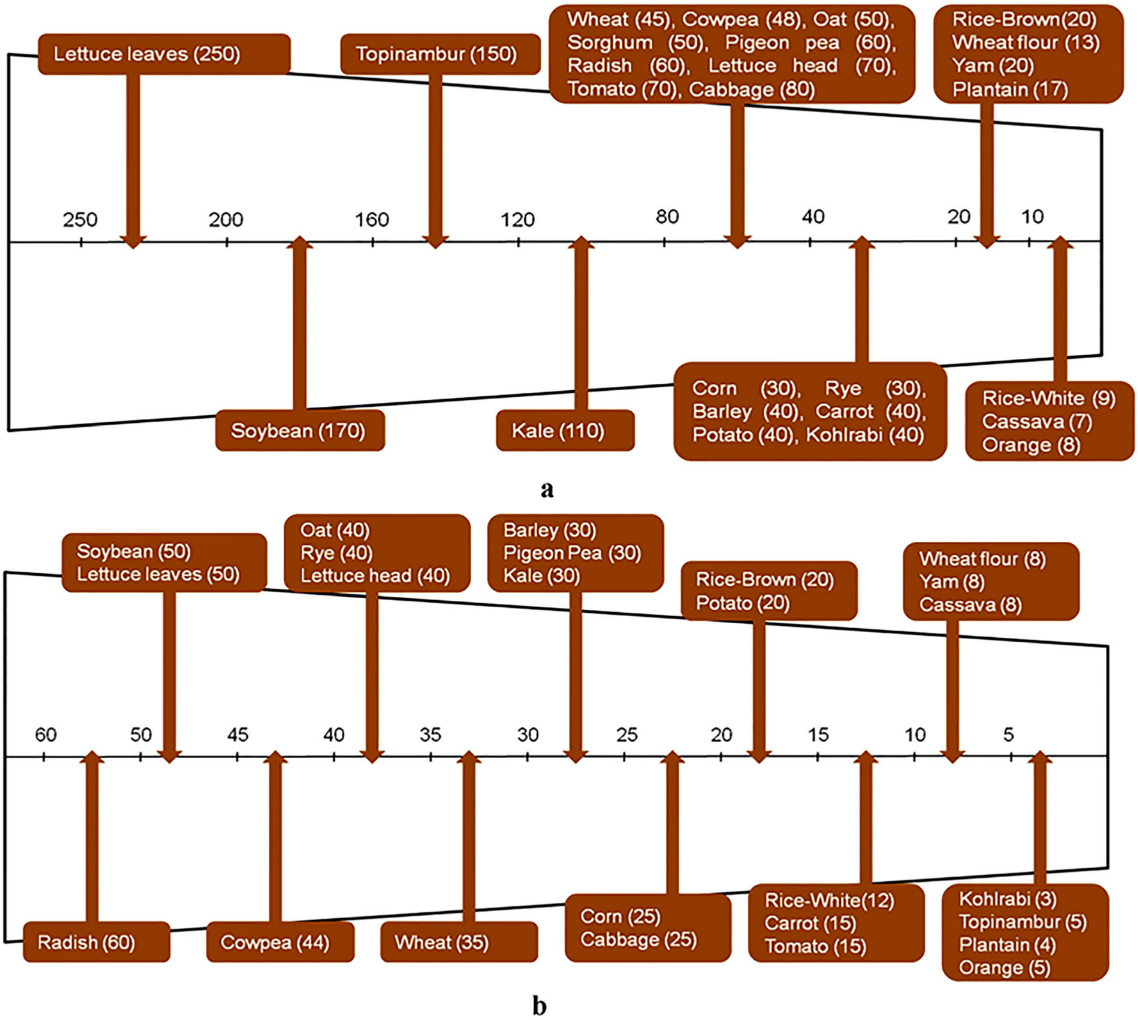

Fig. 1 Diagrammatic representation of **a** iron and **b** zinc content in edible parts of different grains, leaf blades, roots/tubers, and fruits. Units are in milligrams per kilogram dry weight. Numbers inside the parenthesis represent the iron and zinc content of that particular food product

conditions as well as low pH favors conversion of non-available (non-toxic) Fe^{3+} into plant-available Fe^{2+} ions (Genon et al. 1994) that is toxic if present at high ionic activity (Rengel 2002; Khabaz-Saberi and Rengel 2010).

4 Biofortification of Iron and Zinc Levels in Crop Plants: Strategies and Issues

Different plants show differential ability to uptake Fe and Zn, for example, rice, maize, and sorghum are known to be highly susceptible to zinc deficiency while wheat, oat etc. have been reported to be zinc-efficient. High phytic acid in food crops is reported to inhibit the absorption of Fe and Zn by human from these foods (Graham et al. 2001). Negatively charged phytic acids strongly chelate with divalent micronutrients such as Zn^{2+}, Fe^{2+}, Ca^{2+}, and Mg^{2+} and reduce the bioavailability of these micronutrients for humans due to the absence of phytase enzyme in their digestive tract. Food processing can also decrease the level of iron and zinc in the grain when the outer layers are removed. For example, in rice, Zn and Fe are localized in aleurone layer and embryo of grains, which is removed during polishing and milling, thus reducing the amount of available Zn and Fe in the edible part of rice (endosperm) (Haas et al. 2005; Zimmermann and Hurrell 2007). However, this can also lead to better absorption of iron as phytic acid is also localized in the outer layers. The most economical approach to alleviate micronutrient deficiency in crop plants is biofortification, a process through which the content and bioavailability of essential nutrients in staple crops are increased during plant growth through agronomic approaches, conventional or molecular breeding, genetic engineering, or any other means (Petry et al. 2010; Tiwari et al. 2010; Bouis et al. 2011; El-Mekser et al. 2014). Biofortification has been mainly focused on starchy staple crops (rice, wheat, maize, sorghum, millet, sweet potato etc.) (Hussain et al. 2012; Saltzman et al. 2013). Agronomic biofortification is achieved through soil or foliar application of micronutrients in the form of chemical fertilizers while genetic biofortification involves either conventional breeding or genetic engineering to enhance micronutrient sequestration or reduction in inhibitors (Saltzman et al. 2013). Agronomic biofortification for Fe and Zn has been reviewed earlier in detail by others (Cakmak 2008; Prasad et al. 2014; de Valenca et al. 2017; Cakmak and Kutman 2018).

Crop biofortification by breeding has been a popular means to develop biofortified varieties in developing countries (Graham et al. 2007). Genotypic variation in major crops showing broad range of Fe and Zn content has been exploited through breeding programs to develop Fe- and Zn-rich crop varieties. Different genotype of various crops have been reported with varying concentration of micronutrients in grains, for example, rice genotypes vary from 6 to 24 μg/g iron in their grains (Gregorio et al. 2000; White and Broadley 2005) while in wheat, iron concentration ranges from 25 to 56 μg/g (Monasterio and Graham 2000). Table 1 presents a list of some prominent biofortified crop varieties developed and released globally. Breeding for biofortification has made a significant impact on alleviating micronutrient malnutrition in many Asian and African countries. Globally coordinated initiatives like Harvest Plus have developed and released a large number of biofortified (for Fe, Zn, and vitamin A) varieties of 13 different crops in Asia, Africa, and Latin America (HarvestPlus 2019).

In the absence of genetic variation in micronutrient content among varieties, breeding approaches are not successful. Under such conditions, genetic engineering becomes more apt for biofortification (Brinch-Pedersen et al. 2007). However, this approach requires a deep understanding of metabolic pathways, enzymes, and genes involved in micronutrient transport and sequestration. Introduction of novel genes of prokaryotic or eukaryotic origin and engineering metabolic pathways are the key approaches for genetic engineering–guided biofortification. Genetic biofortification through breeding or genetic engineering has been reviewed in details by Rawat et al. (2013), Vasconcelos et al. (2017), and Cakmak and Kutman (2018).

Plant breeding approach of biofortification is comparatively a better approach for micronutrient fortification in grains, but it still depends on soil factors such as soil pH, moisture, and soil nutrient content. Although it is a sustainable and economical approach, it is still labor- and time-intensive. Stein (2006) estimated that breeding high Zn-accumulating varieties would be three times more cost-effective than agronomic fortification but the grain accumulation of Zn depends on the amount plant-accessible Zn stores in the soil. Genetic engineering may overcome the problem of low genetic variation but has low social acceptance. Different time taking regulatory processes in different countries have also hindered the adoption of genetically engineered crops (Garg et al. 2018).

Although agronomic and genetic biofortification are still the most practiced way for micronutrient enhancement in edible crops, they cannot be universally applied for all crops and all geographical regions. For example, agronomic biofortification using Zn- and Fe-containing fertilizers is highly influenced by soil types and conditions (Cakmak 2008). Low soil moisture, high pH, high $CaCO_3$ content, and low amount of organic matter severely decrease solubility and availability of Zn and Fe in the soil. Most of the soil-applied micronutrients are quickly fixed into plant unavailable form; as a consequence, sufficient uptake of Zn or Fe is hindered and grain mineral concentrations are significantly depressed (Cakmak 2008). Use of iron fertilizer is complicated due to low solubility of iron and low mobility through phloem. However, this can be tackled through use in large quantities or when expensively chelated to organic molecules. Many of

Table 1 Some of the prominent Fe- and Zn-fortified crop varieties released globally

Biofortified crop	Traits	Level (mg/kg)	Country	Year of release	Reference
Rice					
DRR Dhan 45	High Zn	22.6 ppm	India	2016	Yadava et al. (2017)
DRR Dhan 48	High Zn	24.0 ppm	India	2018	Yadava et al. (2018)
DRR Dhan 49	High Zn	25.2 ppm	India	2018	Yadava et al. (2019)
Zinco Rice MS	High Zn	27.4 ppm	India	2018	Yadava et al. (2020)
CR Dhan 311	High Zn	20.1 ppm	India	2018	Yadava et al. (2020)
CR Dhan 315	High Zn	24.9 ppm	India	2020	Yadava et al. (2020)
BRRI Dhan 64	High Zn	24 mg/kg	Bangladesh	2014	Bashar (2018)
BRRI Dhan 62	High Zn	22 mg/kg	Bangladesh	2013	Islam et al. (2016)
BRRI Dhan 72	High Zn	22.8 mg/kg	Bangladesh	2015	Bashar (2018)
BRRI Dhan 74	High Zn	22.7 mg/kg	Bangladesh	2015	Bashar (2018)
BU Hybrid Rice 1	High Zn High Fe	Zn: 21.8 mg/kg Fe: 9.75 mg/kg	Bangladesh	2016	Bashar (2018)
BU Dhan 2	High Zn High Fe	Zn: 22.2 mg/kg Fe: 11 mg/kg	Bangladesh	2016	Bashar (2018)
BRRI Dhan 84	High Zn	27.6 mg/kg	Bangladesh	2017	Bashar (2018)
BINA Dhan 20	High Zn	27.5 mg/kg	Bangladesh	2017	Bashar (2018)
Wheat					
WB 02	High Zn High Fe	Zn: 42.0 ppm Fe: 40 ppm	India	2017	Yadava et al. (2017)
HPBW 01	High Zn High Fe	Zn: 40.6 ppm Fe: 40 ppm	India	2017	Yadava et al. (2017)
Pusa Tejas (HI 8759) durum	High Fe High Zn	Fe: 41.1 ppm Zn: 42.8 ppm	India	2017	Yadava et al. (2018)
Pusa Ujala (HI 1605)	High Fe	43.0 ppm	India	2017	Yadava et al. (2020)
HD 3171	High Zn	47.1 ppm	India	2017	Yadava et al. (2020)
HI 8777 (durum)	High Fe High Zn	Fe: 48.7 ppm Zn: 43.6 ppm	India	2018	Yadava et al. (2020)
MACS 4028 (durum)	High Fe High Zn	Fe: 46.1 ppm Zn: 40.3 ppm	India	2018	Yadava et al. (2020)
PBW 757	High Zn	42.3 ppm	India	2018	Yadava et al. (2020)
Karan Vandana (DBW 187)	High Fe	43.1 ppm	India	2018 and 2020	Yadava et al. (2020)
DBW 173	High Fe	40.7 ppm	India	2018	Yadava et al. (2020)
DDW 47	High Fe	40.1 ppm	India	2020	Yadava et al. (2020)
PBW 771	High Zn	41.4 ppm	India	2020	Yadava et al. (2020)
HI 8805 (durum)	High Fe	40.4 ppm	India	2020	Yadava et al. (2020)
HD 3249	High Fe	42.5 ppm	India	2020	Yadava et al. (2020)
HI 1633	High Fe High Zn	Fe: 41.6 ppm Zn: 41.1 ppm	India	2020	Yadava et al. (2020)
Zincol-2016	High Zn	40 mg/kg	Pakistan	2016	Baloch et al. (2018)
BARI Gom 33	High Zn	55 mg/kg	Bangladesh	2017	BARI (2017); Mottaleb et al. (2019)
Pearl millet					
HHB 299	High Zn High Fe	Zn: 73.0 ppm Fe: 41.0 ppm	India	2017	Yadava et al. (2017)
Dhanshakti	High Fe High Zn	Fe: 81 mg/ kg Zn: 43.0 mg/kg	India	2013	Rai et al. (2014)
ICMH 1201	High Fe High Zn	Fe: 75 mg/ kg Zn: 40.0 mg/kg	India	2015	Govindaraj and Rai (2016)
AHB 1200Fe	High Fe	73.0 ppm	India	2017	Yadava et al. (2017)
AHB 1269Fe	High Fe High Zn	Fe: 91.0 ppm Zn: 43.0 ppm	India	2018	Yadava et al. (2019)
ABV 04	High Fe	Fe: 70.0 ppm	India	2018	Yadava et al. (2019)

Table 1 (continued)

Biofortified crop	Traits	Level (mg/kg)	Country	Year of release	Reference
Phule Mahashakti	High Zn High Fe	Zn: 63.0 ppm Fe: 87.0 ppm	India	2018	Yadava et al. (2019)
RHB 233	High Zn High Fe	Zn: 41.0 ppm Fe: 83.0 ppm	India	2019	Yadava et al. (2020)
RHB 234	High Zn High Fe	Zn: 46.0 ppm Fe: 84.0 ppm	India	2019	Yadava et al. (2020)
HHB 311	High Zn High Fe	Zn: 46.0 ppm 83.0 ppm	India	2020	Yadava et al. (2020)
Finger millet					
VR 929 (Vegavathi)	High Fe	131.8 ppm	India	2020	Yadava et al. (2020)
CFMV1 (Indravati)	High Fe High Zn	Fe: 58.0 ppm Zn: 44.0 ppm	India	2020	Yadava et al. (2020)
CFMV 2	High Fe High Zn	Fe: 39.0 ppm Zn: 25.0 ppm	India	2020	Yadava et al. (2020)
Little millet					
CFMV1	High Fe High Zn	Fe: 59.0 ppm Zn: 35.0 ppm	India	2020	Yadava et al. (2020)
Lentil					
Pusa Ageti Masoor	High Fe	65.0 ppm	India	2017	Yadava et al. (2017)
IPL 220	High Fe High Zn	Fe: 73.0 ppm Zn: 51.0 ppm	India	2020	Yadava et al. (2020)
BRRI Mosur-6	High Fe High Zn	Fe: 86.0 ppm Zn: 63.0 ppm	Bangladesh	-	Bashar (2018)
BRRI Mosur-7	High Fe	Fe: 81.0 ppm	Bangladesh	-	Bashar (2018)
BRRI Mosur-8	High Fe High Zn	Fe: 72–75 ppm Zn: 58–60 ppm	Bangladesh	-	Bashar (2018)
Common bean					
RWR 2245	High Fe	76.0 ppm	Rwanda	2010	Mulambu et al. (2017)
RWR 2154	High Fe	71.0 ppm	Rwanda	2010	Mulambu et al. (2017)
MAC 44	High Fe	78.0 ppm	Rwanda	2010	Mulambu et al. (2017)
RWV 1129	High Fe	77.0 ppm	Rwanda	2010	Mulambu et al. (2017)
RWV 3006	High Fe	78.0 ppm	Rwanda	2012	Mulambu et al. (2017)
RWV 3316	High Fe	87.0 ppm	Rwanda	2012	Mulambu et al. (2017)
RWV 3317	High Fe	74.0 ppm	Rwanda	2012	Mulambu et al. (2017)
MAC 42	High Fe	91.0 ppm	Rwanda	2012	Mulambu et al. (2017)
RWV 2887	High Fe	85.0 ppm	Rwanda	2012	Mulambu et al. (2017)
Cowpea					
Pant Lobia-1	High Zn High Fe	Zn: 40.0 ppm Fe: 82.0 ppm	India	2008	Singh (2014)
Pant Lobia-2	High Zn High Fe	Zn: 37.0 ppm Fe: 100.0 ppm	India	2010	Singh (2014)
Pant Lobia-3	High Zn High Fe	Zn: 38.0 ppm Fe: 67.0 ppm	India	2013	Singh (2014)
Pant Lobia-4	High Zn High Fe	Zn: 36.0 ppm Fe: 51.0 ppm	India	2014	Singh (2014)
Pomegranate					
Solapur Lal	High Fe High Zn	Fe: 5.6–6.1 mg/100 g Zn: 0.64–0.69 mg/100 g	India	2017	Yadava et al. (2018)
Greater yam					
Sree Neelima	High Zn	49.8 ppm	India	2020	Yadava et al. (2020)
Da 340	High Fe	136.2 ppm	India	2020	Yadava et al. (2020)

the chelates are expensive while many are toxic and non-biodegradable. For iron, foliar applications have been reported to be the most effective. But foliar application of micronutrients is strongly influenced by factors such as wind (which may cause variability in spray deposition) and soil moisture. Furthermore, it is not always possible to target the micronutrient into fruits, seeds, or grains, and sometimes, they may accumulate in other parts, for example, leaves; therefore, this technique is only successful in certain minerals and specific plant species (Cakmak et al. 1999).

5 Microorganisms—a Promising Option for Micronutrient Biofortification

Due to their immense metabolic diversity, microorganisms are present in any habitat we can imagine. Microbial activities influence primary productivity, plant and animal diversity, and Earth's climate (Nazaries et al. 2013). In soil, microorganisms are the key players in biogeochemical cycling of the nutrients essential for the survival of any living entity on the earth. The role of microorganisms in decomposition of organic matters, biological nitrogen fixation, denitrification, phosphate solubilization etc. is well-known. By virtue of their metabolic multiplicity, microorganisms can produce a number of metabolites such as phytohormone, antibiotics, organic acids, and siderophores, helping in plant growth directly or indirectly.

Rhizospheric soil harbors more number of microorganisms in comparison to the bulk soil due to secretion of sugars, amino acids, vitamins etc. in the root zone. The microorganisms colonizing the rhizosphere help in nutrient mobilization, root growth, protection from abiotic, and biotic stresses. Microbial production of organic acids and siderophores has been implicated as major means of nutrient solubilization in soil. Reduction of pH in microhabitats due to secretion of organic acids by microorganisms helps to solubilize nutrients such as P, K, and Zn which are complexed with other metals or ions. Siderophores produced by microorganisms can increase the solubility of Fe by chelation to form siderophore-Fe complex, and this process has been regarded as the key microbial process involved in Fe uptake by plants (Desai and Archana 2011). Production of phytohormones, for example, IAA and cytokinin, by microorganisms can significantly influence root architecture and anatomy, thereby enabling the plants to uptake nutrients efficiently. Apart from the rhizospheric microorganisms, endophytes also play similar functions which can help to enhance the uptake of nutrients in plants. Since last one decade, there are increasing numbers of reports on microbe-mediated Zn and Fe biofortification (Table 2). In comparison to other biofortification strategies, microbe-mediated biofortification is an environment-friendly, cheaper, and sustainable alternative to enrich food crops with micronutrients. Moreover, microbe-mediated fortification strategies can offer additional advantages like overall improvement in growth and protection from stresses.

The following sections will discuss the potential of microbe-mediated biofortification with specific examples along with their possible mechanisms. Figure 2 presents different mechanisms employed by microorganisms to improve uptake of Fe and Zn in plants. The major mechanisms related to microbe-mediated Fe and Zn uptake are presented below.

5.1 Production of Siderophores and Other Chelators

Under iron-depleted conditions, microorganisms produce siderophores which are low molecular weight organic compounds with strong affinity to Fe. At first, the siderophores form complex with Fe^{3+}, and then, this complex moves into the cell through specific receptors located in cell membrane. Siderophore-iron complex transport in the cell membranes of gram-positive bacteria is assisted by siderophore-binding proteins, permeases, and ATPases while in gram-negative bacteria, the same is mediated by an outer membrane receptor, a periplasmic binding protein, and a cytoplasmic ABC-transporter (Ahmed and Holmstrom 2014). Once this siderophore-iron reaches the cytoplasm, the ferric iron gets reduced to ferrous form and released from the siderophore. Siderophores of microbial origin have conclusively been shown to be an important factor in iron nutrition of plants (Bar-Ness et al. 1992; Desai and Archana 2011). Fe-siderophore complex can be reduced by the plants using strategy I for Fe uptake and thus the released Fe^{2+} becomes accessible to plant transport system. The Fe-Siderophore complex can directly be taken up by the plants and afterwards reduced by extracellular reductases (Wang et al. 1993). In some cases, the Fe-siderophore complex may be taken up directly and transported to the shoot (Manthey et al. 1996). Reports also suggested that some plants may have specific transporters for such siderophore complexes. It has also been reported that the Fe-siderophore complex may enter to the plant system through the cracks developed due to lateral root emergence. In strategy II plants where phytosiderophores are produced by plants, it has been suggested that microbial siderophores can also exchange the bound ligand with the phytosiderophores. Rasouli-Sadaghiani et al. (2014) reported that *Pseudomonades* could enhance the iron nutrition of wheat either by increasing the Fe supply on root surface or ligand exchange with wheat siderophores. Similarly, Scagliola et al. (2016) reported that siderophores produced by *Enterobacter* sp. BFD160 and *Pseudomonas* sp. TFD26, complex ferric ion, and via a ligand exchange with plant siderophores, make it available to the plasma

Table 2 Potential of microorganisms to enrich food crops with Fe and Zn

Sl. no.	Crop	Scientific name of crop	Inoculant	Isolation source of inoculant	Enhancement level of Fe/Zn	Reference
1	Wheat	*Triticum aestivum* var. WR 544	Rhizospheric bacteria: *Providencia* sp. PW5	Wheat (*T. aestivum*)	106% increase in Fe content	Rana et al. (2012)
2	Wheat	*T. aestivum* var. PBW 373	Rhizospheric bacteria: *Pseudomonas* sp.	Rice (*Oryza sativa*)	31% increase in Zn	Joshi et al. (2013)
3	Japonica rice	*O. sativa* L. var. Nipponbare	Endophytes: *Sphingomonas* sp. SaMR12, *Enterobacter* sp. SaCS20	*Sedum alfredii*	21.9% increase in Zn content in brown rice	Wang et al. (2014)
4	Durum wheat	*T. turgidum* var. cv. *durum* HI 8691	Rhizospheric bacteria: *E. cloacae* subsp. *dissolvens* MDSR9	Soybean (*Glycine max*) var. PK1024	36.56% and 21.11% increase in grain Zn and Fe content, respectively	Ramesh et al. (2014a)
5	Soybean	*G. max* var. cv. JS 95-60	Rhizospheric bacteria: *E. cloacae* subsp. *dissolvens* MDSR9	Soybean (*G. max*) var. PK1024	32.78% and 25.03% increase in grain Zn and Fe content, respectively	Ramesh et al. (2014a)
6	Chickpea	*Cicer arietinum* L. var. cv. Sultano	Arbuscular mycorrhizal fungi	Agricultural field	Fe: 5% Zn: 16%	Pellegrino and Bedini (2014)
7	Wheat	*T. turgidum durum* var. cv. HI 8691	Rhizospheric bacteria*: Bacillus aryabhattai* MDSR 7	Soybean (*G. max* L. *merrrill*) var. PK472	45% increase in Zn content in grain	Ramesh et al. (2014b)
8	Soybean	*G. max* var. cv. JS 95-60	Rhizospheric bacteria: *B. aryabhattai* MDSR 14	Soybean (*G. max* L. *merrrill*) var. NRC 7	36% in increase in seed Zn content	Ramesh et al. (2014b)
9	Maize	*Zea mays* L. var. COMH5	Arbuscular mycorrhizal fungi: *Glomus intraradices* TNAU-11-08	Not available	Increased grain Zn content by ~30%	Subramanian et al. (2013)
10	Rice	*O. sativa* var. Basmati	Rhizospheric bacteria: *Bacillus* sp. SH10 and *B. cereus* SH17	*O. sativa* var. Super Basmati and Basmati 385	22–49% increase in Zn translocation to grain	Shakeel et al. (2015)
11	Wheat	*T. aestivum* var. HD2851	Rhizospheric bacteria: *P. fluorescens* strain Psd	Mung bean (*Vigna mungo*)	85% increase grain zinc content	Sirohi et al. (2015)
12	Chickpea and pigeonpea	*C. arietinum* var. ICCV 2 and *Canjanus cajan* var. ICPL 88039	Rhizospheric bacteria: *P. plecoglossicida*, *B. antiquum*, *E. ludwigii*, *Acinetobacter tandoii*, *P. monteilii*	Rice (*O. sativa*)	Zn: 5–23% Fe: 12–18%	Gopalakrishnan et al. (2016)
13	Wheat	*T. aestivum* var. 4HPYT-414, 4HPYT-404	Endophytes: *B. subtilis, Arthrobacter* sp.	Wheat (*T. aestivum*)	2-fold increase of Zn content in grain	Singh et al. (2017)
14	Wheat	*T. aestivum* var. Faisalabad-2008	Rhizospheric bacteria: *P. fragi* EPS1	Wheat (*T. aestivum*)	More than twofold increase in grain Zn content	Kamran et al. (2017)
15	Wheat	*T. aestivum* var. Gw-366 and LK-1	Rhizospheric bacteria: *Exiguobacterium aurantiacum* MS-ZT10	Agricultural field	Sixfold enhancement in grain iron and zinc	Shaikh and Saraf (2017)
16	Maize	*Z. mays* var. Monsanto DK-6142	Rhizospheric bacteria: *B. subtilis* ZM63 and *B. aryabhattai* ZM31	Maize (*Z. mays*)	68% and 78% increase in grain Zn and Fe, respectively	Mumtaz et al. (2017)
17	Bread wheat	*T. aestivum* cv. Lasani-2008 (LS-2008) and Faisalabad 2008 (FSD-2008)	Endophytes: *Pseudomonas* sp. MN12	Maize (*Z. mays*)	-	Rehman et al. (2018)

membrane FCR. Sah et al. (2017) reported increased accumulation of iron in maize grains upon inoculation with siderogenic *Pseudomonas aeruginosa* which could enhance the amount of plant-available Fe in soil through

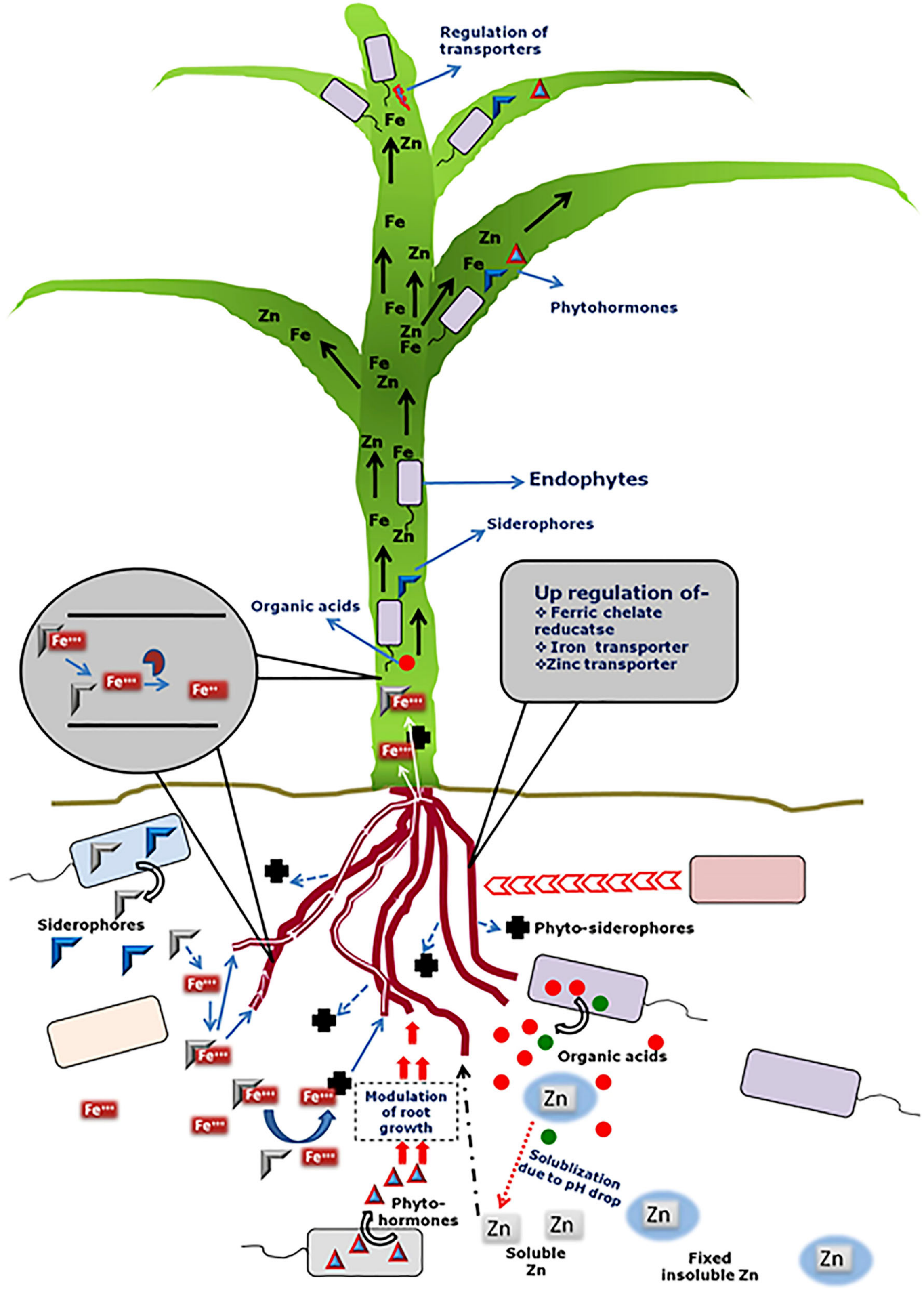

Fig. 2 Diagrammatic representation of various mechanisms used by microorganisms present inside or outside the plants to improve Fe and Zn uptake and translocation

production of siderophores. Rice endophytic *Streptomyces* sp. has also been reported to be involved in the iron nutrition of rice (Rungin et al. 2012). Gopalakrishnan et al. (2016) also implicated siderophore-mediated Fe solubilization in Fe fortification in chickpea and pigeon pea upon inoculation with plant growth-promoting bacteria.

Apart from siderophores, microbes are known to produce other metal chelators which can increase the availability of certain metal ions. Whiting et al. (2001) suggested that many bacteria produce Zn-chelating metallophores for increasing water-soluble Zn (bioavailable) in soil. Mastropasqua et al. (2017) reported that *Pseudomonas aeruginosa* produce a metallophore which is released outside the cell and mediates zinc uptake through a receptor. Lhospice et al. (2017) implicated pseupaline metallophore as primary mediator of Zn uptake in chelating environment. Chelators have also been attributed towards increased mobilization and bioavailability of Zn in rice by *Azospirillum lipoferum*, *Pseudomonas* sp., and *Agrobacterium* sp. (Tariq et al. 2007).

5.2 Zinc Solubilization

In soil, Zn is present in the form of sulfates, oxides, carbonates, silicates, sulfides etc. pH is an important factor which governs the proportion of plant-available zinc forms in soil. In general, Zn solubility increases with a reduction in soil pH. At alkaline pH, Zn becomes fixed in the form of insoluble carbonates, sulfides, phosphates etc. and proportion of the bioavailable zinc pool decreases. Microbe-mediated solubilization of Zn can be accomplished by a range of mechanisms such as excretion of organic acids, proton extrusion, or production of chelators (Goteti et al. 2013). Additionally, inorganic acids, viz. sulfuric acid, nitric acid, and carbonic acid, can also facilitate the solubilization process. Microorganisms can produce an array of organic acids which can reduce the soil pH in and around the rhizosphere, thereby releasing the Zn to make it bioavailable to plants (Table 3). Mostly, gluconic and ketogluconic acid has been reported to be associated with Zn solubilization (Fasim et al. 2002; Saravanan et al. 2007a; Saravanan et al. 2007b; Sunithakumari et al. 2016). Gluconic acid has been reported to be produced by bacteria across various phyla like Firmicutes, Protobacteria, and Actinobacteria (Table 3). However, production of citric acid, malic acid, oxalic acid, tartaric acid, formic acid, and acetic acid has also been reported to be associated with Zn solubilization by bacteria from different phyla (Martino et al. 2003; Li et al. 2010; Sah et al. 2017). Increased zinc uptake by plants can lead to enhancement in grain zinc accumulation. For example, organic acid production has been implicated in enhanced uptake and accumulation of zinc by *Enterobacter cloaceae* MDSR9 in soybean (Ramesh et al. 2014a); by *Pseudomonas fluorescens* strain Psd in wheat (Sirohi et al. 2015); and by *Exiguobacterium aurantiacum* in wheat (Shaikh and Saraf 2017).

5.3 Modulation of Plant Nutrient Uptake Systems

Microorganisms can produce an array of signals which can modulate the expression of the genes involved in nutrient uptake and transport. A number microorganisms including endophytes and mycorrhiza have been reported to possess the capability to modulate the uptake systems for a variety of plant nutrients especially N, P, and Na (Zhang et al. 2009; Saia et al. 2015; Liu et al. 2018). There are reports on microbial influence on plant transporters of micronutrients like Zn and Fe which are, however, lesser in number as compared to N and P. Zhang et al. (2009) showed that activation of iron-induced transcriptional regulator (FIT) by *Bacillus subtilis* GB03 in *Arabidopsis* resulted in upregulation of ferric chelate reductase (FRO) and iron-regulated transporter (IRT1), thereby increasing the iron absorption. Similar observations were also made by Zhou et al. (2016) in *Arabidopsis* plants when inoculated with *Paenibacillus polymyxa* BFKC01, which activated FIT leading to upregulation of FRO and IRT1. Pii et al. (2016) reported upregulation of CsFRO (ferric chelate reductase) and CsHA1 (PM H^+ ATPase) in cucumber upon inoculation with *Azospirrilum brasiliense* which resulted in increased Fe uptake through iron reduction on root surface and rhizosphere acidification. Krithika and Balachandar (2016) reported that inoculation of Zn-solubilizing bacteria, *Enterobacter cloaceae*, resulted in modulation of ZIP (ZRT, IRT-like proteins) genes in rice. Likewise, endophytes have also been reported to potentially modulate the metal transporters in crop plants. For example, over expression of TaZIP (Zn-Fe transporter like protein in wheat) genes was implicated in endophytic *Arthrobacter*-mediated Fe and Zn uptake in wheat (Singh et al. 2017). Endophytic fungi *Phomopsis liquidambari* has been reported to upregulate FRO and IRT1 genes which was also associated with significant increase in Fe accumulation in the roots, stems, and leaves of groundnut (Su et al. 2019).

5.4 Microbe-Mediated Dephytinization of Food Crops

Phytates vary from ~ 0.4 to 2.0% in cereals and legumes (Reddy et al. 1982). Six phosphate groups of phytates carry twelve negative charges which can bind to cations such as Ca, Mg, Fe, Zn, Cu, and Mn to form stable complexes resulting in low bioavailability of these minerals to humans. Phytases can be used to remove the phosphate groups from phytic acid which prevents binding of Fe and Zn in the digestive tract of humans and thus making these minerals available for absorption.

Diverse microorganisms produce diverse phytases, viz. cysteine phytases (CPhy), histidine acid phosphatases (HAP), beta propeller phytases (BBP), and purple acid phosphatases (PAP). HAPs are more predominant in filamentous fungi while BBPs are most prevalent in bacteria (Jorquera

Table 3 Production of organic acids by different bacteria for solubilization of Zn

Group of bacteria	Name of bacteria	Organic acids	Reference
Firmicutes	*Bacillus* sp.	Gluconic acid	Dinesh et al. (2018)
	Bacillus sp. AZ6	Cinamic acid, ferulic acid, caffeic acid, chlorgenic acid, syrirgic acid, gallic acid	Hussain et al. (2015)
	B. megaterium	Gluconic acid	Dinesh et al. (2018)
	Exiguobacterium aurantiacum	2-Ketogluconic acid	Shaikh and Saraf (2017)
	Lysinibacillus sp.	Gluconic acid	Dinesh et al. (2018)
Proteobacteria	*Acinetobacter* sp. SG2	Gluconic acid	Vaid et al. (2014)
	Burkholderia sp. SG1	Gluconic acid	Vaid et al. (2014)
	Burkholderia lata	Gluconic acid	Dinesh et al. (2018)
	Burkholderia latens	Gluconic acid	Dinesh et al. (2018)
	Pseudomonas sp.	Acetic acid, gluconic acid	Jaivel et al. (2017)
	P. aeruginosa	2-Ketogluconic acid	Fasim et al. (2002)
	P. fluorescens	Gluconic acid	Di Simine et al. (1998)
	P. chlororaphis	Gluconic acid, malonic acid, oxalic acid	Costerousse et al. (2018)
	P. moraviensis	Gluconic acid, malonic acid, oxalic acid	Costerousse et al. (2018)
	P. syringae	Gluconic acid, malonic acid, oxalic acid	Costerousse et al. (2018)
	Gluconacetobacter diazotrophicus	5-Ketogluconic acid	Saravanan et al. (2007b)
	Gluconacetobacter diazotrophicus	Gluconic acid	Intorne et al. (2009)
	Stetnotrophomonas rhizophila	Gluconic acid, malonic acid, oxalic acid	Costerousse et al. (2018)
Actinobacteria	*Plantibacter flavus*	Gluconic acid, glutamic acid, oxalic acid	Costerousse et al. (2018)
	Streptomyces narbonensis	Citric acid, malic acid, 2-oxoglutaric acid, succinic acid	Costerousse et al. (2018)
	Curtobacterium ocenosedimentum	Citric acid, malonic acid, 2-oxoglutaric acid, succinic acid	Costerousse et al. (2018)

et al. 2008; Singh and Satyanarayana 2015). Among bacteria, Proteobacteria have been reported to possess all different types of phytases. A number of studies have reported exogenous application of microbial phytases in feeds for enhancing mineral availability in animals, fish, and birds (Mohanna and Nys 1999; Brenes et al. 2003; Baruah et al. 2005; Nwanna et al. 2008). Similarly, it has also been used in human foods for improving mineral absorptions (Troesch et al. 2013). Hurrell et al. (2003) reported that dephytinization using Finase (a commercial phytase from *Trichoderma reesei*) in various cereal porridges increased iron absorption from rice, oat, maize, and wheat porridge by ~ 3-, ~ 8-, ~ 5-, and ~ 11-folds. Dephytinization of wheat- and soy-based foods also resulted in higher zinc absorption in adult human subject from Switzerland (Egli et al. 2004). However, in all of these studies, microbial phytase have been used either during food processing or as an ingredient of the food. Microorganisms such as *Lactobacillus pentosus* have been successfully used to remove phytates from seed coat matter (SCM) of finger millets ultimately resulting in increased bioavailability of Zn (Amritha et al. 2018). Phytate-degrading microorganisms have been reported as endophytes in different plant parts including seeds (Mehdipour-Moghaddam et al. 2010; Costa et al. 2018; Zhu et al. 2019). Especially, phytate-degrading seed endophytes can be very useful in dephytinization. Phytase activity has been reported by endophytic bacteria isolated from seeds of bean (*Rhizobium endophyticum*) and maize (*Pantoea stewartii*) (Lopez-Lopez et al. 2010; Hafsan et al. 2018). However, adequate studies have still not been carried out with specific focus on microbe (especially endophytes)-mediated dephytinization of food grains despite sufficient scientific evidences suggesting their significant potential.

5.5 Modification of Root Architecture

Root is the main nutrient-absorbing part of the plants, and mineral nutrition is a function of root growth. Higher numbers of fine roots is very important for mineral absorption. Plants with more fine roots can explore a large volume of soil to efficiently take up small amounts of immobile micronutrients. Longer and finer root systems in early growth stage have been reported as the two characters associated with Zn-efficient genotypes (Dong et al. 1995).

It is a well-known fact that microbial activity can greatly influence the root growth and development through production of phytohormones and other metabolites. Moreover, mycorrhizal infection of roots is also known to enhance the nutrient uptake capacity of the plants. Wang et al. (2014) reported modulation of root morphology as one of the mechanisms involved in endophyte-enhanced metal uptake and accumulation in rice plants which was evident from the improved architecture of rice roots in presence of endophytic bacteria. In this study, the Zn content in brown rice from inoculated plants ranged from 30.0 to 31.0 mg/kg which is ~ 25% improvement over normal Zn content (6.3–24.0 mg/kg) in brown rice. Singh et al. (2017) observed that inoculation of endophytic bacteria, viz. *B. subtilis* and *Arthrobacter* sp., resulted in significant improvement in root length, surface area, volume, and diameter which might have helped the wheat plants to accumulate more zinc in grains. They reported that the grain Zn content in inoculated plants ranged from 50.0 to 66.2 mg/kg which was well beyond the target of 50 mg Zn/kg.

Mycorrhizal association with plants and their contribution in plant nutrition are well-known. Ninety percent of plant species are known to establish a mycorrhizal association (Smith and Read 2008). The most common type of mycorrhiza is the arbuscular mycorrhiza with fungal members of Glomeromycota. The fungus forms an appressorium penetrating the root cortex where it moves through the intercellular spaces and develops a network with formation of arbuscules. Nutrients are exchanged across the periarbuscular and host cell membranes, with which arbuscules make a close contact (Rausch et al. 2001; Javot et al. 2007a; Javot et al. 2007b). It is estimated that mycorrhiza can transfer more than 90% of the P and more than 50% of the fixed N to their host in exchange of photosynthates (Smith and Smith 2011). Besides translocation of major nutrients, arbuscular mycorrhizal roots are also known to help in micronutrient transportation in plants. For instance, zinc content in tomato fruits was 50% higher in mycorrhiza-colonized plants (Cavagnaro et al. 2006). Furthermore, it has been reported that during mycorrhiza-mediated micronutrient delivery, expression of nutrient transporter genes in plant decreases. For example, cortical ZIP in *Medicago truncatula* gets downregulated upon mycorrhization (Burleigh et al. 2003). The contribution of the mycorrhiza in plant metal nutrition may range from 20 to 50% (Ortas 2012; Lehmann et al. 2014). In addition, AMF genome encodes several metal transporters (Tamayo et al. 2014), some of which could be involved in metal uptake. *Piriformospora indica* (belonging to order Sebacinales of family Serandipitaceae) which resembles AM fungi, owing to its ability to colonize and interact with a wide variety of unrelated host plants, holds a tremendous practical application as nutrient mobilizer. It offers multiple benefits to its host plants such as nutrient uptake, growth promotion, abiotic stress alleviation, growth promotion, and disease resistance (Unnikumar et al. 2013). Inoculation with *P. indica* under zinc supplementation has been shown to increase Zn concentration in lettuce plants (Padash et al. 2016). Improved iron uptake has been observed in a medicinal herb *Chlorophytum* sp. inoculated with *P. indica* and *Pseudomonas fluorescens* (Gosal et al. 2010). Although there are only two reports on biofortification using *P. indica*, the beneficial roles played by this endophyte such as root development and nutrient uptake indicate that *P. indica* can be a potential candidate to be used for biofortification.

5.6 Improving Overall Plant Growth and Nutrition

Microorganisms are well-known for their role in biogeochemical cycling of nutrients and improvement of plant growth through various direct and indirect mechanisms. Microbes are the key mediators of nutrient cycling in soil and responsible for maintaining the soil fertility. In soil, the macro- and micronutrients interact in a complex way interfering with each other's uptake by plant. It is known that level of nitrogen in soil can significantly influence the uptake of micronutrients such as Fe and Zn. Kutman et al. (2011) reported that nitrogen nutrition was critical for uptake and allocation of Fe and Zn in wheat. Similar findings were also reported by Xue et al. (2014). Excessive application of phosphorus can reduce the micronutrient uptake and allocation (Nyoki and Ndakidemi 2014; Zhang et al. 2017). Zribi et al. (2015) showed that symbiosis of *Sinorhizobium meliloti* with *Medicago sativa* resulted in higher accumulation of zinc in roots. Studies carried out by Kumar et al. (2014) revealed that inoculation of siderogenic bacteria along with diazotrophic *Arthrobacter* resulted higher gain accumulation of iron in wheat as compared to inoculation only with siderogenic bacteria. Praburaman et al. (2017) showed that N2-fixing plant growth-promoting *Herbaspirillum* sp. GW103 can enhance Zn accumulation in maize. Rana et al. (2012) reported grain Fe content of 271.93 mg/kg in wheat upon inoculation of *Providencia* sp. PW5 and attributed this improvement towards better N nutrition due to inoculation. It is evident from such studies that microbial inoculation can achieve the micronutrient levels in grains well beyond the desired level.

6 Future Prospects

Deficiency of micronutrients particularly Fe and Zn is a grave concern for the entire world, especially for the Asian and African countries. Efforts are being made to enrich the foods including the staple crops with iron and zinc through agronomic or genetic biofortification. Agronomic biofortification is not any permanent solution to this problem while genetic methods including breeding strategies are time- and cost-intensive. Microorganisms due to their huge metabolic diversity, known role in biogeochemical cycling, and intricate interaction with plant and soil can be a better choice to mobilize micronutrients to the plants. From various reports of microbe-mediated biofortification around the globe, it is clear that microbial inoculation can improve grain Zn content in a range of 20–50% in rice, 30–80% in wheat, and 80–100% increase in grain Fe content in wheat depending on type of soil and plant. This level of enhancement of Fe and Zn can definitely help to combat deficiency. If we assume a conservative 30% increase in Zn content of brown rice achieved by microbial inoculation, then it can supply additional 1.05–4.35 mg Zn daily assuming consumption of 600-g rice.

Enrichment of edible crops with Fe and Zn can be achieved through microorganisms by any of the three following strategies—(a) increased availability of micronutrients due to microbial activity like production of acids, chelators, and phytohormones; (b) microbe-mediated modulation of micronutrient transporters; and (c) de-complexation of micronutrients from compounds such as phytate through microbial activity during postharvest processing. However, higher micronutrient availability alone may not be effective enough to fortify the edible parts as the activity of specific transporters should be modulated to accumulate higher amounts of micronutrients. Soil or rhizosphere inhabiting microorganisms seem to be more potent to increase the soil availability of micronutrients and their uptake by plant roots while the endophytic microorganisms may be more suitable to influence the uptake and transportation. Furthermore, endophytes can also be helpful for degradation of anti-nutritional factors like phytate in seeds/grains and thus improving the bioavailability upon consumption. Endophytes from wild plants having high Fe and Zn content need to be explored for such activities. Application of microorganisms for biofortification should be carried out after thorough examination of interaction among potential microbes, crop genotypes with varying accumulation pattern, and soils with differing micronutrient status. Breeding approaches can also be focused on selecting genotypes preferentially harboring higher population of potential endophytes or rhizobacteria with micronutrient-mobilizing capability. However, the application of microorganism cannot be the sole solution for combating the hidden hunger. Integration of genetic as well as agronomic biofortification should be explored to work out a viable, economical, and sustainable option for biofortification.

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Declarations

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Consent to Participate Not applicable.

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