



Potential of microbes in the biofortification of Zn and Fe in dietary food grains. A review

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Abstract

Micronutrients are essential factors for human health and integral for plant growth and development. Among the micronutrients, zinc (Zn) and iron (Fe) deficiency in dietary food are associated with malnutrition symptoms (hidden hunger), which can be overcome through biofortification. Different strategies, such as traditional and molecular plant breeding or application of chemical supplements along with fertilizers, have been employed to develop biofortified crop varieties with enhanced bioavailability of micronutrients. The use of microorganisms to help the crop plant in more efficient and effective uptake and translocation of Zn and Fe is a promising option that needs to be effectively integrated into agronomic or breeding approaches. However, this is less documented and forms the subject of our review. The major findings related to the mobilization of micronutrients by microorganisms highlighted the significance of (1) acidification of rhizospheric soil and (2) stimulation of secretion of phenolics. Plant–microbe interaction studies illustrated novel inferences related to the (3) modifications in the root morphology and architecture, (4) reduction of phytic acid in food grains, and (5) upregulation of Zn/Fe transporters. For the biofortification of Zn and Fe, formulation(s) of such microbes (bacteria or fungi) can be explored as seed priming or soil dressing options. Using the modern tools of transcriptomics, metaproteomics, and genomics, the genes/proteins involved in their translocation within the plants of major crops can be identified and engineered for improving the efficacy of plant–microbe interactions. With micronutrient nutrition being of global concern, it is imperative that the synergies of scientists, policy makers, and educationists focus toward developing multipronged approaches that are environmentally sustainable, and integrating such microbial options into the mainframe of integrated farming practices in agriculture. This can lead to better quality and yields of produce, and innovative approaches in food processing can deliver cost-effective nutritious food for the undernourished populations.

Keywords Micronutrients · Deficiency · Hidden hunger · Biofortification · Microorganisms · Rhizosphere · Zn/Fe transporter

1 Introduction

In the pursuit of increasing food grain production and feeding the ever increasing global population, agricultural research in the last few decades mainly focused on cultivation of high yielding varieties of crops and intensive cropping systems, mainly involving the imbalanced use of chemical fertilizers (Elkoca et al. 2010; Foley et al. 2005; Gliessman 2014;

Singh 2000). It is well-documented in literature that the intensive use of chemical fertilizers has a negative impact on soil ecology, as it disrupts nutrient equilibrium in the soil, leading to impaired soil structure and functioning. Imbalances in fertility lead to harmful impacts on the proliferation of communities and health of macro/micro fauna, flora, and human beings (Lockhart et al. 2013; Wu and Ma 2015). In order to understand the relationship between micronutrient supply and human health, there is an urgent need to understand the level of micronutrient deficiencies in soils and their influence on crop physiology. Millions of hectares of land in the world, including India, have low availability of micronutrients. In Indian soils, the deficiency of Zn has gone as high as 47% and that of Fe to 13% (Singh 2009). Micronutrient deficiency in soil is mainly attributed to high levels of more than the recommended dose of fertilizers (RDF), soil erosion, and other agronomic practices that interfere with the translocation of

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micronutrients. This causes imbalances in the amounts of organic matter and phosphorus in soil, which is particularly accentuated in soils such as calcareous type, water-logged, peat, arid, alkaline, sandy, and saline soils, which also limit Fe mobilization (Alloway 2008). The mobilization of Fe in plants often occurs via chelating with phytosiderophores, citrate, nicotianamine, and mugineic acid (strategy II), or in the form of free iron ions— Fe^{2+} (both strategy I and strategy II plants) (Zhang et al. 2019). Fe^{2+} is the free form of iron in the soil which is limited in soil. Fe^{2+} is a more soluble form and can be taken up by the roots of all types of plants. But it is readily oxidized into Fe^{3+} due to chemical reactions. Fe^{3+} is the most dominant form of iron in soil but it is insoluble, therefore not available to plants (Mahender et al. 2019). In this regard, plants have developed different mechanisms to acquire sufficient iron under deficient conditions. Nongraminaceous plants, known as strategy I plants, use a reduction-based strategy to reduce the ferric ions (Fe^{3+}) to free form of Fe ions (Fe^{2+}). Graminaceous plants, known as strategy II plants, have a chelation-based strategy for acquisition of Fe^{3+} . Strategy II plants secrete phytosiderophore (PS) in the rhizosphere which form PS-Fe^{3+} soluble complex, taken up by plant roots (Kobayashi and Nishizawa 2012; Römheld and Marschner 1986). Micronutrients are essential for plant growth and development, and their presence in sufficient amounts is important for proper human and animal health (Welch and Graham 2004). In the last two decades, the concept of hidden hunger (deficiency of certain vitamins and micronutrient) has been well-documented (Nilson and Piza 1998). Low availability of micronutrients in soils not only reduces crop yields, but also leads to poor nutritional quality of the edible parts of crops, resulting in malnutrition in human populations, particularly in developing and underdeveloped countries (Hurst et al. 2013; Kumssa et al. 2015). The micronutrients Fe and Zn are important for all organisms. Fe is an important cofactor for various enzymes involved in plant and human metabolism; its deficiency causes stunted growth and anemia (Hentze et al. 2004). About 25% of the world's population suffers from anemia (Ministry of Health and Family Welfare 2016; World Health Organization 2008), and the Global Burden of Disease Study (2015) reported that Fe-deficiency anemia led to 54,000 deaths in 2015 (Forouzanfar et al. 2016). Low Zn levels lead to stunted growth and development of neonatal, immune dysfunction, hypogonadism, and impairment in cognition (Sauer et al. 2016). An average of 17.3% of the world population is affected by Zn deficiency (Wessells and Brown 2012) and about 433,000 children perish due to Zn malnutrition (World Health Organization 2009). Iron deficiency in humans is relatively easy to quantify, as hemoglobin is the most commonly used biochemical indicator of population response, which is reliable. On the other hand, zinc deficiency is difficult to quantify, as no reliable biochemical indicator is currently available to denote zinc status (Mei et al. 2005; Wieringa et al. 2015).

Biofortification is a promising and sustainable agriculture-based strategy to minimize Zn and Fe deficiency in dietary food substances (Garcia et al. 2016; Petry et al. 2016; Vasconcelos et al. 2017). Among the different strategies deployed, the plant breeding approach to develop biofortified crops and agronomic supplementation of micronutrients, such as foliar/soil application along with chemical fertilizers, have received maximum attention (Cakmak et al. 2010; Di Tomaso 1995; Rengel 2001).

A less investigated approach, which is promising, involves exploring plant–microbe interactions, which are known to have a crucial role in improving the nutritional status of soil and enriching micronutrients through metal solubilization, mobilization, and translocation to different parts of the plant (Chen et al. 2014a, 2014b; Kothari et al. 1990; Rana et al. 2012) (Fig. 1). Therefore, microorganisms can be used to enhance the accumulation of micronutrients in the grains of staple cereal crops; this has been successful in rice and wheat (Mader et al. 2011; Prasanna et al. 2016; Rana et al. 2012, 2015; Singh et al. 2017a, b, Singh et al. 2018, Singh et al. 2020; Vaid et al. 2014; Zhang et al. 2012a, b). However, its potential is still to be explored across other crops, ecologies, and farming systems.

In this review, an attempt has been made to collate and critically analyze the available information on the major mechanisms employed by microorganisms for the enrichment of micronutrients in the plant, and in particular, their prospects for the biofortification of Fe and Zn.

2 Zn and Fe deficiency in soil—a global concern

Zn deficiency is one of the important nutritional constraints in cereal crops, especially rice and wheat, and Zn-deficient cereal-based diets create serious problems for human health. Zn deficiency was found to be prevalent in 50% of the soil samples collected from different countries (Dharejo et al. 2011; Hansen et al. 1996; Manyevere et al. 2017). Fageria et al. (2002) observed that under such deficiencies, cereal crop yields can exhibit growth and yield a reduction, up to 80%, along with a reduced grain Zn concentration. Mark et al. (2016) reported that micronutrient deficiencies are predominant in the low income South Asian countries, including India.

Deficiency of Zn is the most widespread among the micronutrients, in almost 50% of soils surveyed from India (Reza et al. 2017; Shukla et al. 2017, 2018). Analyses of 0.25 million surface soil samples collected from different parts of the country revealed the predominance of Zn deficiency in divergent soils (Singh et al. 2005). The magnitude of Zn deficiency varies widely among soil types and within the various states in India. In India, the extent of deficiency of Zn was to the tune of 86% in Maharashtra, 72.8% in Karnataka, 60.5%

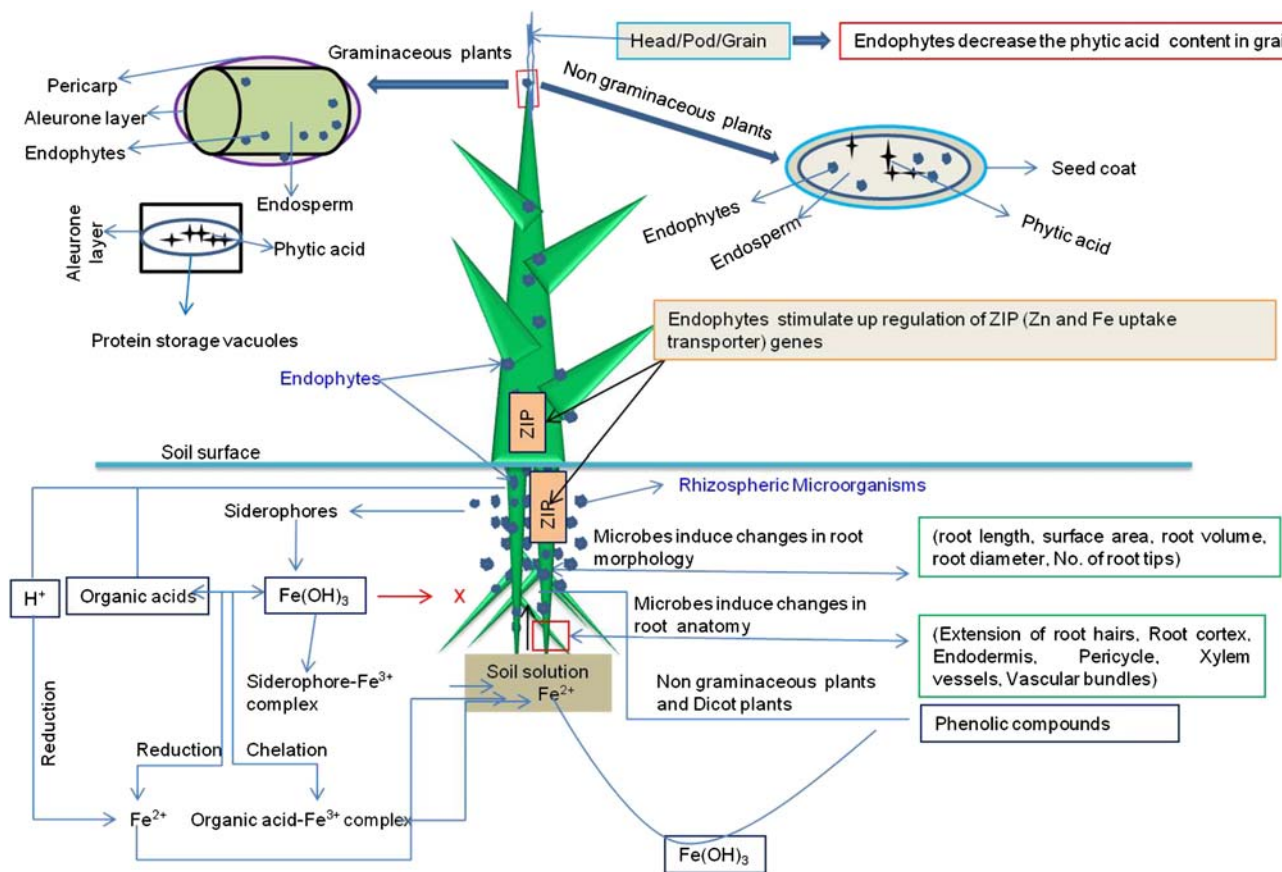


Fig. 1 Microbe-mediated iron transformations in the rhizosphere and its uptake toward biofortification in grains in crop plants

in Haryana, 58.4% in Tamil Nadu, 57% in Meghalaya, 54% in Bihar and Orissa, 49.4% in Andhra Pradesh, and 48.1% in Punjab (Shukla et al. 2015, 2016, 2017, 2018; Singh 2009). Such an alarming prevalence is a crucial issue.

Low availability of DTPA (diethylenetriamine pentaacetic acid) extractable Fe in soils is also of global concern. Fe deficiency-mediated interveinal chlorosis in crops is a widespread phenomenon in arid and semiarid soils or calcareous soils worldwide, including India, which causes a significant loss in yield (Mortvedt 1991). In India, Fe is mainly deficient in the soils of Karnataka (35%), H.P. (27%), Maharashtra (24%), Haryana (20%), Tamilnadu (17%), and Punjab (14%) (Shukla et al. 2015, 2016, 2017, 2018; Singh 2009).

3 Causes of micronutrient deficiency in soil

Different environmental and edaphic factors, such as organic matter content in soil, soil pH, cation exchange capacity, clay content etc., and soils more prone to water logging, or peat/calcareous soils are characteristics that affect the bioavailability of micronutrients (Ibrahim et al. 2011; Lindsay 1984; Ramzan et al. 2014). The critical limit of DTPA-extractable Fe and Zn in soil are 4.5 and 0.6 mg kg⁻¹,

respectively (Alloway 2009; Sillanpaa 1982). The critical limit for the soil is defined as minimum soil test value which is associated with maximum crop yield. It represents the concentration below which deficiency manifests as it designates the lower end of the sufficiency range.

A major percentage of Fe on the earth's crust is present as Fe^{3+} which is not readily accessible to plants. Fe^{2+} is the more soluble form of iron but readily oxidized to ferric form (Fe^{3+}), which is precipitated in oxide/hydroxide, phosphate, carbonate, and other unavailable complex forms in the soil (Lindsay and Schwab 1982). A large amount of Fe is present in soils, but its bioavailability is very low. Chirwa and Yerokun (2012) and Harter (1983) suggested that Zn bioavailability decreased in soil, with increasing soil pH due to precipitation or adsorption of Zn on the surface of $CaCO_3$ and Fe oxides. There is a negative correlation between available Zn or Fe and cation exchange capacity (CEC) of soil (Yoo and James 2002). Sidhu and Sharma (2010) reported that with increasing clay content in the soils, there was a lower availability of Zn. The available Zn was negatively correlated with electrical conductivity (EC) (Chattopadhyay et al. 1996). Gao et al. (2011) also stated that the availability of Zn is negatively correlated with phosphorus content in soil.

4 Role of Zn and Fe in plant growth and development

Among the micronutrients essential for the proper growth and development of plants, animals, and human beings, Zn and Fe are the most important elements. Even though they are needed in trace amounts, they are involved in critical functions and play an important role in the maintenance of the structural integrity of biological membranes, gene expression, and regulation (Hänsch and Mendel 2009; Mahender et al. 2019; Mousavi et al. 2013). Additionally, they are also involved in mediating several processes such as carbohydrate metabolism, protein synthesis, nucleic acid synthesis, phytohormone levels, photosynthesis, fertility, seed production, and defense against abiotic/biotic stresses (Brown et al. 1993; Kobayashi and Nishizawa 2012; Rout and Sahoo 2015). Romheld and Marschner (1991) illustrated that Zn is essential for carbohydrate metabolism, protein synthesis, nucleic acid synthesis, and phytohormone synthesis and also as a cofactor for all six classes of enzymes. Fe is an important constituent of enzymes like peroxidase, catalase, and nitrogenase (Kerkeb and Connolly 2006), and along with Mo, plays an important role in nitrogen fixation (Kim and Rees 1992). Fe deficiency decreases chlorophyll production, leading to interveinal chlorosis, which is exhibited as sharp distinctions between veins and chlorotic areas in young leaves (Kobayashi et al. 2003), followed progressively by the entire leaf becoming whitish-yellow and necrosis, along with slower plant growth (Follett and Westfall 1992). White and Broadley (2009) recommended a serious concern towards the alleviation of micronutrient deficiency in soil, as it not only leads to declining crop yields but also contributes to poor quality of produce, leading to dietary micronutrient deficiencies in human beings.

5 Role of Zn and Fe in human health

Zn has an important structural and functional role in biological systems (Parkin 2004), as it plays a significant role in reproductive, catalytic, and anabolic processes in human beings (Bonaventuraa et al. 2015; Corvol et al. 2004; Cummings and Kovacic 2009). Zn deficiency causes stunted growth of human beings, immaturity of sexual organs, and distortions of the immune system and central nervous system (Welch 2001). Ross et al. (1985) reported that women who receive Zn supplements of 4–13 mg day⁻¹ delivered babies with low birth weight compared to the control group. Shankar and Prasad (1998) also reported infertility in Zn-deficient men. Zn deficiency may cause congenital diseases like Acrodermatitis enteropathica (Moynahan 1974). The recommended daily allowance (RDA) for Zn is 15 mg day⁻¹ for adults (Food and Nutrition Board 2001).

Fe is a crucial element for human fitness, as it is involved in a wide variety of metabolic processes, including deoxyribonucleic acid (DNA) synthesis, catalase and peroxidase enzyme synthesis, oxygen and electron transport, etc. (Abbaspour et al. 2014). The recommended dietary allowance (RDA) for Fe for adults of 19–50 years age is 8 mg day⁻¹ for males and 18 mg day⁻¹ for females, but during the pregnancy period, it is 27 mg day⁻¹ (Food and Nutrition Board 2001). In the 2013 Global Burden of Diseases Study, Fe deficiency anemia was predominantly implicated in nearly 200,000 deaths and 45 million disability-adjusted life-years (DALYs) lost annually (4.5% of all risk-attributable DALYs; Forouzanfar et al. 2016). Fe biofortification in India is essential, where over 50% of women and 74% of children are anemic (International Institute for Population Sciences and ORC Macro 2000), attributed largely to the insufficient intake or bioavailability of Fe. Stevens et al. (2013) showed that anemic prevalence was highest in pre-school age children, pregnant, and nonpregnant women in Western Pacific, Southeast Asia, and Africa. In a nationwide study in India, Chellan and Paul (2010) found a moderate to severe Fe deficiency anemia in 47.9% pre-school children (below 6 years), 74.8% in adolescent girls (10–19 years), and 41.5% in pregnant women (15–44 years).

6 Strategy of Zn and Fe biofortification in food grains

Biofortification is a bouquet of approaches that focus on improving the availability of micronutrients biologically in staple food products like wheat, maize, pearl millet, rice, and others. This could be achieved genetically or through soil management practices, agronomic approaches, or by using microbiological interventions or a combination of these. Although plants can take up higher amounts of micronutrients from soil, their availability in edible parts may be low, because of anti-nutritional factors, thus having no influence in alleviating human malnutrition (Frossard et al. 2000). Some of the possible interventions include the subsections that follow.

6.1 Agronomic interventions

Applying mineral fertilizers to the soil for maintaining soil health and improving plant quality is an age old practice (Rengel et al. 1999). In general, it is observed that the response to an applied nutrient, in terms of its translocation to grains, is more pronounced when there is a deficiency of that particular element in the soil or the characteristics of the particular element allow its rapid mobilization. Micronutrient supplementation with chemical fertilizers has been an effective measure employed by farmers to gain maximize crop yield. However, micronutrient-use efficiency in crops is low and only 2–5% of

total applied fertilizer dose is utilized (Tian et al. 2008). Some of the methodologies for improving use efficiency of micronutrients, such as foliar application or granular/dust-type formulations of Zn or modulating dose and frequency of applications or enrichment of urea and other fertilizers, have shown promising results in several crops, particularly cereals (Prasad et al. 2013; Shivay et al. 2008, 2015; Wissuwa et al. 2008).

6.2 Genetic approaches

Genetic biofortification involves classical breeding approaches to characterize and exploit the genetic variation for mineral content, as well as new approaches involving gene discovery and marker-assisted breeding (Grusak 2002). Hindu et al. (2018) used genome-wide association studies (GWAS) for identification of different genomic regions in maize for kernel Zn and Fe biofortification. Velu et al. (2016) suggested that genomic selection (GS) may be a potential breeding method for Fe and Zn biofortification in wheat. In terms of sustainability, the nutrition-oriented breeding of crop plants has several advantages. Recent advances empower us to modulate signaling pathways, although breeding, by and large, relies on long and repetitive cycle of hybridization and selection, which are time-consuming and labor-intensive. Nevertheless, in recent years, modern molecular tools like DNA markers and marker-assisted selection (MAS) technologies are expediting the development of nutrient-rich genotypes. Kumar et al. (2018) reported quantitative trait loci (QTLs) for Fe and Zn biofortification in pearl millet using diversity array technology (DArT) and simple sequence repeat (SSR) markers. Literature reported that many Fe- and/or Zn-biofortified varieties of rice, wheat, and maize have been released in the world, including in India, to alleviate malnutrition (Table 1). Besides the genetic or plant breeding approach, several transgenic interventions have been applied for successful biofortification of food crops. Transgenic techniques permit the exchange of genes between totally irrelevant species or bring new genes into food or cash crops. Ramesh et al. (2004) developed a novel approach for increased seed zinc and iron content, through the overexpression of a zinc transporter in *Hordeum vulgare* cv. Golden Promise, facilitated by a ubiquitin promoter. Goto et al. (1999) were able to enhance the iron content in rice grains 3-fold using an *Agrobacterium*-mediated transfer of complete coding sequence of the ferritin gene from soybean plants. Lucca et al. (2002) developed transgenic rice plants, with higher iron content, which was rich in phytase and cysteine-peptides; this can facilitate better iron intake and bioavailability. Vasconcelos et al. (2003) were able to engineer the expression of the soybean ferritin gene, under the control of the glutelin promoter in an elite Indica rice line that has highly desirable agronomic and field performance traits; enhanced grain nutritional levels

were recorded not only in brown grains but also in polished grains. Liu et al. (2004) developed ferritin-incorporated rice varieties that showed 64% higher iron content in the milling, and this ferritin gene could be specifically expressed in the endosperm of transgenic rice with a high level.

Genetic approaches can be a challenging task for breeders in soils inherently low in Fe and Zn micronutrients. To realize the full potential of biofortified varieties, there is a need to also give simultaneous attention toward other factors, like soil pH and organic matter, which influence root exudation and enzyme activities in the rhizosphere, and thereby micronutrient uptake and accumulation (Cakmak 2008).

6.3 Microbe-based approaches

The mechanisms of Fe acquisition by higher plants under Fe deficiency have been categorized into two groups (Kobayashi and Nishizawa 2012; Römhild and Marschner 1986): strategy I in nongraminaceous plants and strategy II in graminaceous plants. The two main processes in the strategy I response are (1) the reduction of ferric chelates at the root surface with the help of Ferric reduction oxidase gene (*FRO2*) and (2) the absorption of the generated ferrous ions across the root plasma membrane by the Iron-regulated transporter gene (*IRT1*). Other processes involved in strategy I include extrusion of proton and phenolics compounds from the roots to the rhizosphere, which increases the solubility of ferric ions or supports the reduction capacity of ferric Fe on the root surface. Strategy II plants take up Fe under Fe deficiency by the excretion of phytosiderophores (PSs), which are low molecular weight Fe chelating compounds, i.e., mugineic acids (MA) and nicotianamine (NA) have strong affinity for Fe (III) and form an Fe–phytosiderophore soluble complex. The Fe–phytosiderophore complex is then transported into root cells through a high affinity uptake system. Suzuki et al. (2006) reported that barley plants secreted mugineic acid (MA) phytosiderophore under Zn deficiency and the form Zn (II)–mugineic acid complex and Zn (II)–mugineic acid complex absorbed more than Zn^{2+} by the roots of a Zn-deficient plant. The amounts and kinds of phytosiderophores secreted by plants into the rhizosphere vary from species to species (Mori 1999).

There are large amounts of Fe and Zn present in the earth's crust but unavailable to plants, as they are present in the form of insoluble salts. Plant-based intrinsic strategies like phytosiderophore or organic acid production or secretions of chelators are not always sufficient to make micronutrients available in micronutrient-deficient soils. With our improved understanding of crosstalk between soils, plants, and microorganisms, greater insights into the rhizosphere environment have been gained (De Santiago et al. 2011; Mishra et al. 2011; Pii et al. 2015; Zaidi et al. 2003). Plant growth-promoting microorganisms play a crucial role in the

Table 1 Promising biofortified varieties developed

Crop	Varieties	Country	References
Rice	CR Dhan 310 (protein-rich variety)	India	Yadava et al. (2017)
	DRR Dhan 45 (zinc-rich variety)	India	Yadava et al. (2017)
	Zhongguangxiang (iron-rich variety)	China	Saltzman et al. (2013)
	GR2 events (provitamin A-rich transgenic biofortified variety)	USA	Saltzman et al. (2013)
	BRR1 Dhan 62 (zinc-rich rice variety)	Bangladesh	Andersson et al. (2017)
Wheat	WB 02, HBPW 01 (zinc- and iron-rich varieties)	India	Yadava et al. (2017)
	Zhongmai 175 (iron- and zinc-rich variety); Pusa Tejas MACS 4028 (protein-, iron-, and zinc-rich varieties)	China	Saltzman et al. (2013)
	BHU-3 and BHU-6 (zinc-rich varieties)	India	Andersson et al. (2017)
Maize	Pusa Vivek QPM9 improved (provitamin A, lysine- and tryptophan-rich hybrid), Pusa HQPM-5/7 improved (provitamin A, tryptophan, lysine rich)	India	Yadava et al. (2017)
	Pusa HM4 improved, Pusa HM8 improved, and Pusa HM9 improved (lysine- and tryptophan-rich hybrid)	India	Yadava et al. (2017)
Pearl millet	HHB 299 (iron- and zinc-rich hybrid)	India	Yadava et al. (2017)
	AHB 1200 (iron-rich hybrid)	India	Yadava et al. (2017)
	ICTP8203-Fe/"Dhanashakti" (iron-rich variety)	India	Saltzman et al. (2013), Rai et al., (2014)
	ICMH-1201/Shakti-1201 (iron-rich hybrid)	India	Andersson et al. (2017), Govindaraj et al. (2016)
Lentil	Pusa Ageti Masoor (iron-rich variety)	India	Yadava et al. (2017)
	BARImasur-7 in 2012, BARImasur-8 in 2015 (zinc- and iron-rich varieties)	Bangladesh	Andersson et al. (2017)
	ILL 7723	Nepal	Andersson et al. (2017)
	L4704	India	Andersson et al. (2017)
Sweet potato	Nanshu 0101 (provitamin A rich)	China	Saltzman et al. (2013)
Cow pea	Pant Lobia-1 and Pant Lobia-2 (iron-rich cowpea varieties)	India	Saltzman et al. (2013)

List is not comprehensive, only selected varieties given

fortification of macronutrients and micronutrients in food crops, through various mechanisms such as siderophore production, transformations, nitrogen fixation, and phosphorus mobilization (Khan et al. 2019; Singh et al. 2018). Figure 1 illustrates the diverse microbe-mediated mechanisms involved in the biofortification of Fe.

Microorganisms are known to have crucial roles in the biofortification of Zn and Fe in cereal grains (Gosal et al. 2010; Rana et al. 2012; Sharma et al. 2012). Both rhizospheric and endophytic microorganisms have significant impacts on micronutrient bioavailability to plants. However, endophytic microorganisms are considered more promising agents to enhance Fe and Zn uptake and translocation, because endophytic microorganisms can indirectly influence the regulation of metal transporters (Reiter et al. 2002; Weyens et al. 2013). Bacterial and fungal endophytes have been implicated in the biofortification of grains of wheat and rice with Fe and Zn (Abaid-Ullah et al. 2015; Ramesh et al. 2014). Balakrishnan and Subramanian (2012) revealed that the inoculation of mycorrhizal fungi (arbuscular mycorrhiza) improves the availability of micronutrients, particularly Zn in soils, as a consequence of rhizospheric acidification and siderophore

production besides hyphal transport of nutrients through the external mycelium. Gosal et al. (2010) reported that an endophytic fungus *Piriformospora indica* had a significant impact on plant growth, biomass, and micronutrients uptake. Wang et al. (2014) also found a positive influence of endophyte inoculation on Zn accumulation in rice grains. In earlier studies, *Bacillus subtilis* (DS-178) and *Arthrobacter* sp. (DS-179) were able to increase the Zn content by an average of 75% over the control in Zn-deficient soils. Similar results were also found with *Arthrobacter sulfonivorans* (DS-68) and *Enterococcus hirae* (DS-163), with respect to Fe availability in wheat grains (Singh et al. 2017a, 2018). Utilization of PGP rhizobacterium *Pseudomonas fluorescens* was found to be suitable towards Zn biofortification in wheat grains (Sirohi et al. 2015). Rana et al. (2012) reported that Fe content in wheat grains increased significantly due to inoculation of *Providencia* sp. PW5. Similarly, Prasanna et al. (2015) and Tariq et al. (2007) also found a significant effect of rhizospheric microorganisms on Zn biofortification in maize and rice, respectively.

Both rhizospheric and endophytic microorganisms play crucial roles in metal solubilization in soil and redistribution

in the plant parts. Bacteria capable of solubilizing insoluble sources of Zn can enhance uptake of Zn by 21% in soybean plants (Sharma et al. 2012). There are different mechanisms through which microbes increase the availability of Zn and Fe in soil and enhance their mobilization in plant parts or increase the bioavailability of Fe and Zn in food grains. These include the following:

- 6.3.1 Production of siderophores and other chelating substances
- 6.3.2 Organic acid secretion and proton extrusion
- 6.3.3 Modification in root morphology and anatomy
- 6.3.4 Upregulation of Zn and Fe transporters
- 6.3.5 Reduction of phytic acids or anti-nutritional factors in food grains
- 6.3.6 Secretion of phenolics and related reducing moieties
- 6.3.7 Secretion of phytohormones like signaling molecules

6.3.1 Production of siderophore and other chelating substances

Siderophores are low molecular weight Fe chelating compounds that have high affinity toward Fe (III) (Ganz 2018). The literature suggests that many microorganisms secrete siderophores to overcome the Fe deficiency in soil (Schalk et al. 2011). Fe (III) is insoluble in soil, but siderophores form siderophore–Fe (III) complexes and increase the availability of Fe in the environment (Saha et al. 2012). Because of their solubilizing effect on Fe hydroxides, the production of siderophores in the rhizosphere is the key microbial activity that benefits plant Fe acquisition (Desai and Archana 2011; Hayat et al. 2012). Khalid et al. (2015) reported that the inoculation of siderophore-producing fluorescent *Pseudomonas* was effective in enhancing Fe content in chickpea grains. In our earlier field experiments, inoculation with siderophore-producing endophytes (*Arthrobacter sulfonivorans* DS-68 and *Enterococcus hirae* DS-163) enhanced the Fe concentration in grains of low and high Fe accumulating wheat genotypes by 67 and 46%, respectively, over the uninoculated control, as compared to the application of RDF (recommended doses of fertilizers) + FeSO₄, in which 63 and 28% enhancement was recorded over the uninoculated control, respectively. The percent increase of Fe was more pronounced with low Fe accumulating wheat cultivars due to application of siderophore-producing endophytes or FeSO₄, as compared to high Fe accumulating wheat genotypes. It was interesting to note that microbial treatment was statistically on par with chemical fertilizer (FeSO₄) application, in terms of Fe content in wheat plant tissues (Singh et al. 2018).

Zn cations, being more reactive species in soil, are present in low amounts in soil solution (Alloway 2009); hence, the bioavailability of Zn ions in soil is meager. However, Zn chelating compounds (synthetic or plant and microbial derived) can enhance the mobilization and solubilization of Zn fractions in soil (Obrador et al. 2003). Such chelators form soluble complexes with Zn²⁺ (Tarkalson et al. 1998) and decrease their interactions with soil constituents. Whiting et al. (2001) observed the significant impact of Zn chelator metallophores, produced by bacteria (*Microbacterium saperdae*, *Pseudomonas monteilii*, and *Enterobacter cancerogenes*), on the bioavailability of Zn in soil and uptake by plant roots. Tariq et al. (2007) also reported that the *Azospirillum lipoferum* (JCM-1270, ER-20), *Pseudomonas* sp. (96-51), and *Agrobacterium* sp. (Ca-18) bioinoculants were able to solubilize the zinc hydroxide and zinc phosphate or other insoluble Zn salts and increase the availability of Zn to rice plants for a longer time in soil. This was found to be mediated by the production of natural chelating agents (Tariq et al. 2007). According to the reports of Kucey (1988), inoculation of *Penicillium bilaji* increased Zn solubilization and uptake in plants to a greater extent as compared to that achieved through ethylene diamine tetra acetate (EDTA) chelating mechanisms. Singh et al. (2018) reported a positive correlation between siderophore production and Fe accumulation in wheat grains by endophytes (Fig. 2a), which illustrates the important role of siderophores in iron acquisition and transport into the plant; however, its translocation within the plant, particularly to grains, involves several steps and mechanisms—transport, remobilization, and storage processes, mediated by membrane transporters, chelators, and regulatory proteins.

6.3.2 Organic acid secretion and proton extrusion

The plant root exudates significantly increase the soluble proportion of Zn in soil solution through different biochemical processes (Zhang et al. 2010); however, microorganisms can also modify the root exudation patterns and influence the activities in the rhizosphere (da Silva et al. 2014; Malinowski et al. 2004; Singh et al. 2017b; Subramanian et al. 2009). Plants mediate through mobilization and solubilization of metal cations through root exudates by several biochemical routes: (i) acidification of rhizosphere through proton ions or organic acids in root exudates; (ii) formation of soluble complex of metal ions with amino acids or organic acids and other chelators; (iii) enzymatic redox reaction reactions; or indirectly through (iv) biostimulation effect of root exudates on beneficial microbes in the rhizosphere (Pérez-Esteban et al. 2013; Sessitsch et al. 2013; Ström et al. 2002).

Organic acids represent the dominant moiety in the root exudates, particularly, in relation to metal solubilization in the rhizosphere region (Chiang et al. 2011; Luo et al. 2014). Kim et al. (2010) reported that oxalic and citric acids secreted

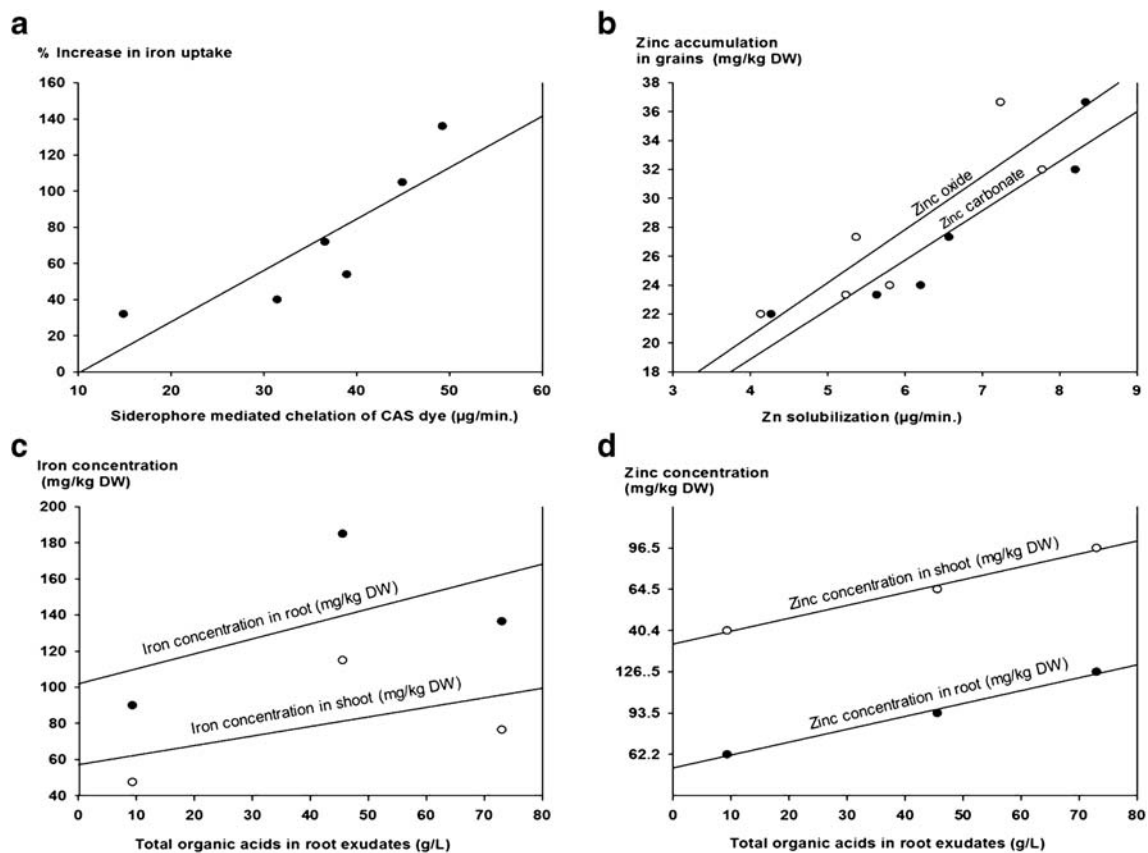


Fig. 2 Relationship between endophytic bacterial activities (siderophore secretion, organic acid production, and Zn solubilization) and Fe/Zn acquisition in wheat tissues. **a** Siderophore production and Fe

acquisition in grains. **b** Zn solubilization and Zn acquisition in grains. **c** Organic acid secretion and Fe accumulation in root and shoot. **d** Organic acid secretion and Zn accumulation in root and shoot

by *Echinochloa crusgalli* significantly increased the micronutrient uptake and translocation in plant tissues. The nature of soil affects the availability of micronutrients to plants. When chemical fertilizers are applied to soil, most of the phosphorus, potassium, Zn, or Fe precipitates in soil, making them unavailable for use by plants. Micronutrient availability is sensitive to soil pH; it has been reported that minimal changes in pH have drastic effects on the solubility of micronutrients in soil. Havlin et al. (2007) suggested that the availability of Zn decreases 100 times with one unit increase in pH. Similarly, Guerinot and Yi (1994) found that the availability of Fe decreased up to 1000-fold, when pH was increased by one unit. Several reports have been published on the positive contribution of organic acid-producing microorganisms in increasing the availability of nutrients (P, K, Zn) in the rhizosphere (Goswami et al. 2014; Meena et al. 2015; Sirohi et al. 2015). Chen et al. (2014a, 2014b) and Raja et al. (2006) observed significant changes in the root exudate pattern and solubilization of precipitated metals due to inoculation of plant growth-promoting rhizobacteria. Singh et al. (2018) also reported that the Zn solubilization activity of endophytic bacteria positively correlates with the accumulation of Zn in wheat grains (Fig. 2b).

In addition to organic acids, proton excretion by microorganisms may lead to acidification of the rhizosphere and an increase in the availability of nutrients. Asea et al. (1988) reported that the phosphorus solubilizing fungi—*Penicillium bilaji* and *Penicillium cf. fuscum*—significantly increase the phosphorus availability in soil by lowering the soil pH, as a result of secretion of protons. Besides phosphate-solubilizing bacteria (PSB), mycorrhizae also excrete H^+ . Thus, the presence of protons in micronutrient-deficient soils may help the crop plant in more efficient uptake of micronutrients.

In our earlier investigation, the inoculation of *Arthrobacter sulfonivorans* (DS-68) and *Arthrobacter* sp. DS-179 in wheat plants led to both qualitative and quantitative changes in organic acid profiles over the control, with several fold changes in the quantity of organic acids in inoculated treatments. This also positively correlated with increasing amounts of Zn and Fe in wheat root and shoot tissues (Singh et al. 2017b) (Fig. 2c and d).

6.3.3 Modification in root morphology and anatomy

Zn or Fe hyperaccumulator plants have various morphological, anatomical, and physiological adaptations, such as

elaborative root hairs or root surface area, and metal-mobilizing root exudates (Dong et al. 1995; Genc et al. 2007; Lynch 2007). Singh et al. (2005) also reported that a well-developed root system of plants can be an important strategy to enhance the uptake of micronutrients. Zn-efficient plants appear to employ a plethora of physiological mechanisms that allow them to withstand Zn deficiency stress better than Zn-inefficient plants. Zn-efficient plants have a greater proportion and longer length of fine roots ($\leq 0.2 \mu\text{M}$), and this plays an important role in the differential Zn efficiency observed among various genotypes (Rengel and Wheal 1997). In general, Zn-efficient plants have thinner roots with increased surface area, which increases the availability of Zn along with other nutrients, due to a more thorough exploration of the soil (Singh et al. 2005). Chen et al. (2009) for rice and Genc et al. (2006) for wheat showed that the Zn-efficient genotype developed longer and thinner roots ($\leq 0.2 \text{ mm}$) than a less Zn-efficient genotype. Available reports also illustrate that the inoculation of plant growth-promoting rhizobacteria and endophytic bacteria has notable effects on root morphology and architecture (Delaplace et al. 2015; Vacheron et al. 2013; Wang et al. 2014). Our earlier published work (Singh et al. 2017a) also supports this hypothesis that inoculation with a plant growth-promoting, Zn-solubilizing endophyte (*Bacillus subtilis* DS-178 and *Arthrobacter* sp. DS-179) enhances the root volume, surface area, root length, root diameter, and average number of root tips in a wheat crop. Inoculation of these Zn-solubilizing endophytes also enhanced Zn accumulation in wheat grains by 2-fold over the control, which, in turn, was better or equal to the application of $40 \text{ kg ZnSO}_4 \text{ ha}^{-1}$.

Investigations undertaken in low available Fe content soil with inoculation of siderophore-producing *Arthrobacter sulfonivorans* DS-68 and *Enterococcus hirae* DS-163 endophytes led to increases in the root surface area and average number of root tips by 2-fold and 1.6-fold, respectively, over the control (RDF). However, in high available Fe content soil, root surface area and average number of root tips increased by 1.5-fold and 1.2-fold, respectively, over the control (RDF). These increased root parameters directly facilitated Fe fortification in wheat grains (Singh 2016). Chen et al. (2014a, 2014b) reported that inoculation with endophytic bacterium *Sphingomonas* SaMR12 significantly improved the root length, root surface area, and average number of root tips in *Sedum alfredii* plant, as compared to uninoculated treatment. Batista et al. (2016) suggested that root morphological parameters, such as total root length and root surface area, play an important role in nutrient uptake, particularly under micronutrient-limiting conditions.

Besides root morphology, the internal structure of roots is also modified by plant growth-promoting microbes, as a consequence of which a higher amount of nutrients is taken up by roots from the soil (López-Bucio et al. 2007; Ortíz-Castro

et al. 2008). Rêgo et al. (2014) conducted an experiment with rice plants to understand the effect of the bioinoculant (bacteria and a fungus) on root anatomical features. They observed that inoculation of *Trichoderma asperellum*, *Burkholderia pyrrocinia*, and *Pseudomonas fluorescens* had a significant impact on root anatomy, particularly in terms of the diameter of the root cortex, dimension of vascular bundles, and numerical changes in the protoxylem and metaxylem vessels. Several reports suggest that well-developed root anatomical features, such as expansion of the root cortex and volume of xylem vessels, more elaborative root hairs, thickening of the endodermis, and vascular bundles, were positively correlated with nutrient uptake (Kotula et al. 2009; Kramer et al. 1980). In our earlier investigation, inoculation of both *Arthrobacter sulfonivorans* DS-68 and *Arthrobacter* sp. DS-179 individually enhanced the volume of xylem vessels, thickness of the root cortex, and diameter of vascular bundles and pericycle (Fig. 3). Inoculation of these microorganisms also enhanced the Fe or Zn uptake by 60 to 75% (Singh et al. 2017b). Thus, the modification of internal structure of roots, which leads to better anchoring and uptake system as a result of inoculation, can be one of the strategies that also results in biofortification of micronutrients in crop plants.

6.3.4 Upregulation of Zn and Fe transporters

Micronutrient uptake and translocation are both different processes; in some crop genotypes, micronutrient uptake efficiency is very high, but the translocation of micronutrients from root to shoot and shoot to grains is very poor (Singh et al. 2018). Therefore, nutrient translocation or redistribution in plant parts is an important phenomenon that needs to be modulated to increase the micronutrients in the edible parts of plant. Tables 2 and 3 provide details of Fe and Zn transporters identified in various crops.

Arbuscular mycorrhiza (AM) fungal inoculants were found to bring about significant variations in the uptake of nutrients and their accumulation in roots, shoots, and grains (Chatzistathis et al. 2009). This indicated the significant role of metal transporters in the translocation of nutrients from shoots to grains. There are several metal transporters in plants, including a zinc-regulated transporter (*ZRT*)/iron-regulated transporter (*IRT*)-like protein (*ZIP*) family, which is involved in the translocation of Zn and Fe, a cation diffusion facilitator (*CDF*) family, and a P-type ATPase family involved in xylem loading of Zn as well as other heavy metals (Colangelo and Gueriot 2006; Eide 2006). The *ZIP* family proteins have been reported in rice, wheat, maize, and *Arabidopsis thaliana* (Evens et al. 2017; Grotz et al. 1998; Ishimaru et al. 2005; Krämer et al. 2007; Xu et al. 2010). The overexpression of these proteins led to an accumulation of excess amounts of Zn in the cells of wild emmer wheat (Durmaz et al. 2011). The Zn-solubilizing *Enterobacter cloacae* strain ZSB14 has been

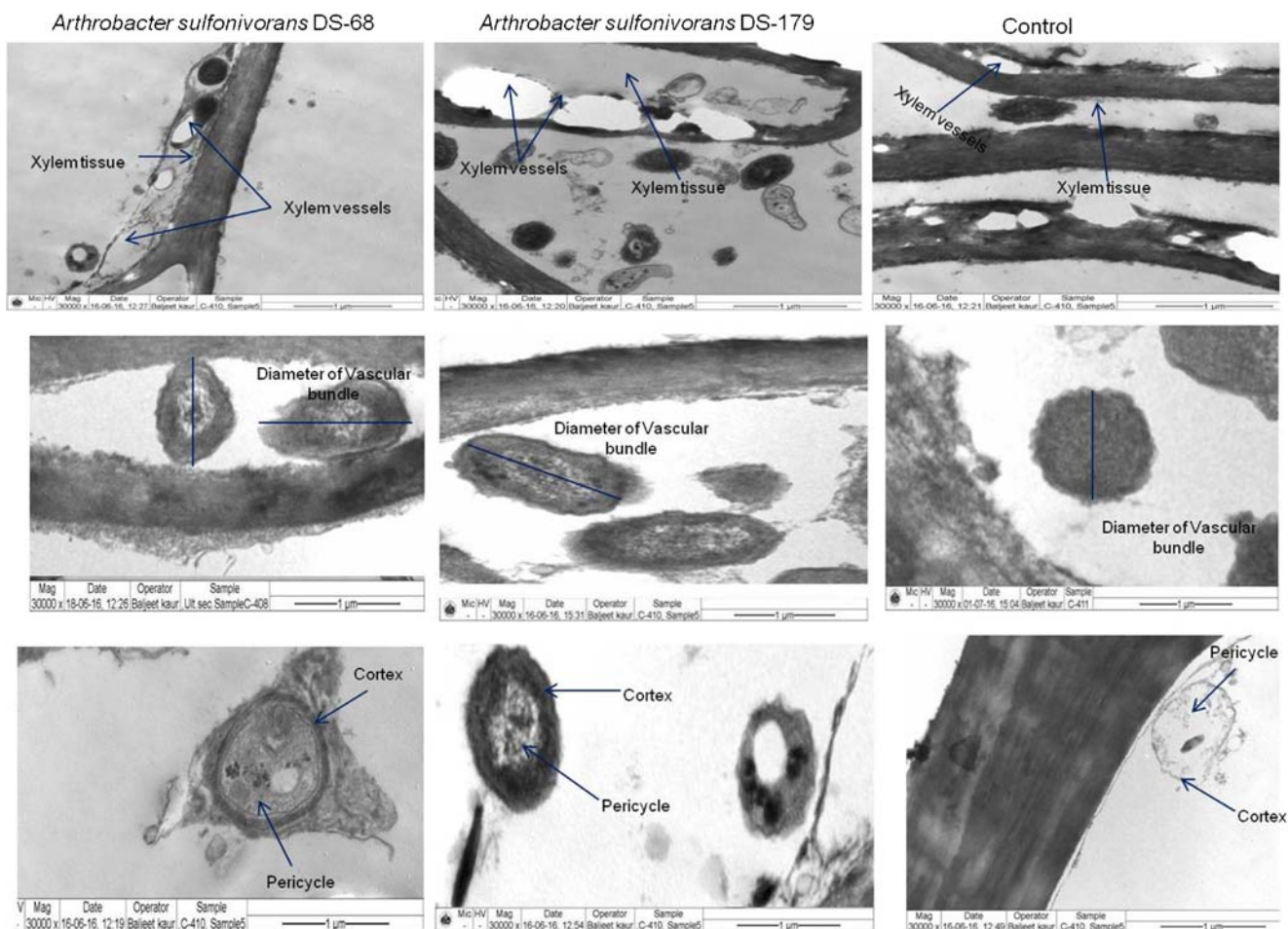


Fig. 3 Transmission electron microphotographs showing anatomical modifications after 30 days of sowing (in terms of volume of xylem vessels, thickness of root cortex, diameter of vascular bundles and pericycle) in wheat root architecture due to inoculation of endophytes

reported to upregulate *OsZIP1* and *OsZIP5* expression and downregulate *OsZIP4* expression in rice genotypes (Krithika and Balachandar 2016). In *Hordeum vulgare*, the colonization of *Rhizophagus irregularis* improved grain Zn concentrations under Zn-deficient conditions through upregulation of *HvZIP13* (Watts-Williams and Cavagnaro 2018).

Our recent published reports also support this hypothesis that microbes enhance the expression of ZIP genes. In the shoots, inoculation of Zn-solubilizing *Arthrobacter* sp. DS-179 endophyte led to 1.9- and 4.0-fold increase in *TaZIP3* and *TaZIP7* transcripts, respectively. The expression levels of *TaZIP7* in shoots due to siderophore-producing *Arthrobacter sulfonivorans* DS-68 endophyte inoculation were 2.6-fold higher than uninoculated control, and *TaZIP3* was not influenced by endophyte inoculation, whereas in roots, inoculation of *Arthrobacter* sp. DS-179 endophyte led to 1.7-fold increase in *TaZIP3* gene and 40% downregulation in *TaZIP7* gene with respect to uninoculated control. The expression level of *TaZIP3* and *TaZIP7* genes in roots due to *Arthrobacter sulfonivorans*

DS-68 inoculation was 1.5- and 2.2-fold higher than uninoculated control, respectively (Fig. 4) (Singh et al. 2017b).

6.3.5 Reduction of phytic acids or anti-nutritional factors in food grains

Another aspect relevant to biofortification strategies is the bioavailability of micronutrients in cereal and legume grains, which is often low because it is affected by anti-nutritional factors such as phytic acid (Liang et al. 2008). Phytic acid forms chelation complexes with metals (Cu, Fe, Mn, Zn, etc.) and decreases the bioavailability of these micronutrients in dietary food, thus acting as an anti-nutritional factor (Hunt 2003; Kumssa et al. 2015). Vaid et al. (2014) reported that the inoculation of *Burkholderia* sp. SG1 + *Acinetobacter* sp. SG3 led to a reduction in phytate:Zn ratio in the grains of rice.

In our recent report, inoculation of the promising two Zn-solubilizing (*Bacillus subtilis* DS-178 and *Arthrobacter* sp. DS-179) and two siderophore-producing endophytes

Table 2 Iron transporters identified in various plants

Plant	Transporter	Function	References
<i>Arabidopsis thaliana</i>	<i>AtIRT1, AtIRT2, AtIRT3</i>	Increased accumulation of Zn in shoots and Fe in roots, translocate Fe and Zn in plant	Lin et al. (2009), Varotto et al. (2002), Vert et al. (2002, 2009), Zheng et al. (2018)
	<i>AtNRAMP1</i>	Transport Fe, Zn, and Cd	Curie et al. (2000), Thomine et al. (2000), Zheng et al. (2018)
	<i>AtNRAMP3</i>	Transport Fe, Mn, and Cd; mobilization of vacuolar Fe stores; export of vacuolar Mn into photosynthetic tissues of adult plants	Curie et al. (2000), Lanquar et al. (2010), Thomine et al. (2000)
	<i>AtNRAMP4</i>	Mobilization of vacuolar Fe stores, export of vacuolar Mn into photosynthetic tissues of adult plants	Lanquar et al. (2005, 2010)
	<i>AtATM3</i>	Export of Fe-S from mitochondria	Bernard et al. (2009), Chen et al. (2007)
	<i>AtNAP14</i>	Iron influx into plastids	Shimoni-Shor et al. (2010)
	<i>AtFPN1</i>	Iron efflux across plasma membrane; loading of Fe into xylem	Morrissey et al. (2009)
<i>Oryza sativa</i>	<i>AtFPN2 (AtIREG2)</i>	Influx of transition metals into vacuole; sequestration of toxic metals during Fe deficiency	Morrissey et al. (2009), Schaaf et al. (2006)
	<i>OsIRT1/OsIRT2</i>	Fe and Zn transportation	Ishimaru et al. (2006), Zheng et al. (2018)
	<i>OsNRAMP5</i>	Uptake and transport Mn, Fe, and Cd	Ishimaru et al. (2012)
	<i>OsYSL2, OsYSL9, OsYSL13, OsYSL18</i>	Translocation of Fe from root to shoot; loading of Fe in seeds	Aoyama et al. (2009), Ishimaru et al. (2010), Koike et al. (2004), Senoura et al. (2017), Zhang et al. (2018)
	<i>AtYSL1/AtYSL2/AtYSL3</i>	Influx of Fe (II)-NA complexes; remobilization of transition metals during senescence and seed set; iron uptake from xylem	Chu et al. (2010), Di Donato et al. (2004), Waters et al. (2006)
	<i>OsVIT1/OsVIT2</i>	<i>OsVIT1</i> and <i>OsVIT2</i> are localized to the vacuolar membrane. <i>OsVIT1</i> and <i>OsVIT2</i> modulate iron translocation between flag leaves and seeds in rice.	Zhang et al. (2012a, b)
	<i>ZmYS1</i>	Influx of Fe (III)-phytosiderophore complexes; primary iron uptake from soil	Curie et al. (2001), Inoue et al. (2009), Schaaf et al. (2004)
<i>Arachis hypogaea</i>	<i>AhNRAMP1</i>	Fe, Zn, and Mn transporter and responsible for Fe, Zn, and Mn acquisition and distribution	Wang et al. (2019), Xiong et al. (2012)
<i>Hordeum vulgare</i>	<i>ZmYS1</i>	Influx of Fe (III)-phytosiderophore complexes; primary iron uptake from soil	Curie et al. (2001), Inoue et al. (2009), Schaaf et al. (2004)
<i>Zea mays</i>	<i>ZmYS1</i>	Influx of Fe (III)-phytosiderophore complexes; primary iron uptake from soil	Curie et al. (2001), Inoue et al. (2009), Schaaf et al. (2004)
<i>Malus xiaojinensis</i>	<i>MxIRT1</i>	Ferrous transporter	Li et al. (2006)
<i>Solanum lycopersicum</i>	<i>LeNRRAPM1</i>	Distribution of Fe in the vascular parenchyma upon Fe deficiency	Bereczky et al. (2003)
<i>Malus baccata</i>	<i>MbNRAMP1</i>	Fe, Mn, and Cd trafficking	Xiao et al. (2008)
<i>Triticum aestivum</i>	<i>TaVIT2</i>	Transports Fe and Mn	Connorton et al. (2017)

(*Arthrobacter sulfonivorans* DS-68 and *Enterococcus hirae* DS-163) brought about significant enhancement in wheat plant growth, biomass, yield, and micronutrient uptake. Interestingly, endophyte inoculation decreased phytic acid concentration in wheat grains by approximately 26% over the RDF. This reduction of phytic acid concentration in grains may be correlated with increasing Fe or Zn concentration in grains ($r = -0.825$ for phytic acid vs Fe content in grains; $r = -0.660$ between phytic acid and Zn content in grains), as depicted by the positive and significant correlations between phytic acid

content in wheat grains of genotypes classified as low/high accumulators (Singh et al. 2018). However, more research needs to be undertaken to decipher the exact mechanisms involved.

6.3.6 Stimulation of secretion of phenolics like reducing substances

In nongraminaceous monocots and dicots (strategy I plants), phenolic compounds are the most frequently reported as a component of the root exudates produced in response to Fe

Table 3 Zinc transporters identified in various plants

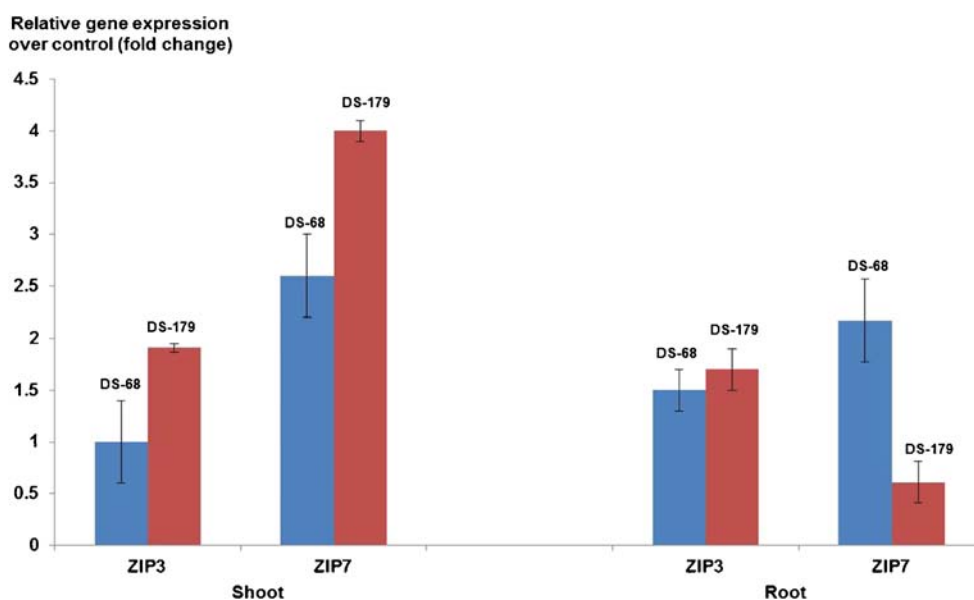
Plant	Transporter	Function	References
<i>Arabidopsis thaliana</i>	<i>At ZIP1–2, At ZIP1–12</i>	Zinc transporter in <i>Arabidopsis</i>	Grotz et al. (1998), Ivanov and Bauer (2017), Krämer et al. (2007), Milner et al. (2013), Zheng et al. (2018)
	<i>AtHMA2, AtHMA3, and AtHMA4</i>	Zn uptake from the soil	Axelsen and Palmgren (2001)
	<i>AtMTP1</i>	Stores Zn in the vacuole of predominantly leaf tissue	Desbrosses-Fonrouge et al. (2005), Kobae et al. (2004)
<i>Oryza sativa</i>	<i>OsZIP4</i>	Zn ²⁺ -HCO ₃ co-transporter	Ishimaru et al. (2005)
	<i>OsZIP1, OsZIP3, OsZIP1–10</i>	Functional Zn transporters	Ivanov and Bauer (2017), Ramesh et al. (2003), Zheng et al. (2018)
<i>Hordeum vulgare</i>	<i>HvZIPs</i>	Zn uptake	Tiong et al. (2015)
<i>Zea mays</i>	<i>ZmZIP1–8</i>	Functional Fe or Zn transporter	Li et al. (2013)
	<i>ZmZLP1</i>	May be responsible for transport of Zn from the ER to the cytoplasm	Xu et al. (2010)
<i>Triticum aestivum</i>	<i>TdZIP1, TaZIPs (TaZIP1–14)</i>	Transport of Zn in wheat	Durmaz et al. (2011), Evens et al. (2017)
<i>Glycine max</i>	<i>GmZIP1</i>	Highly selective for Zn and might play a role in the symbiotic relationship between soybean and <i>Bradyrhizobium japonicum</i>	Moreau et al. (2002)

deficiency (Curie and Briat 2003; Römheld and Marschner 1986; Susin et al. 1996). Compared to other compounds in the root exudates, phenolics are particularly interesting because of their multiple chemical and biological functions, such as chelating, reducing, radical scavenging, antimicrobial activity, and serving as a carbon source for microbial growth (Blum et al. 2000; Cao et al. 1997; Jin et al. 2007; Rice-Evans and Miller 1996). It has been suggested that the released phenolics function to enhance Fe availability in the rhizosphere soil, as an alternative or supplement to the plasma membrane-bound ferric reductase, through chelating and

reducing insoluble Fe (Dakora and Phillips 2002). Recently, it has been reported that the removal of the secreted phenolics from a hydroponic culture solution significantly enhances Fe accumulation and Fe deficiency responses in roots; this is attributed to the inhibition of solubilization and utilization of apoplasmic Fe (Jin et al. 2007). Moreover, phenolics such as protocatechuic acid (PCA) are reported to chelate Fe (III) and solubilize and reduce it to Fe (II) in vitro (Yoshino and Murakami 1998).

Moreover, many rhizosphere beneficial microbes that elicit the induced systemic resistance (ISR) improve Fe and perhaps

Fig. 4 Relative changes in TaZIP3 and TaZIP7 gene expression levels (expressed in fold increase) after 30 days of sowing, in low Fe and Zn accumulating wheat genotype-4HPYT-414, due to endophyte inoculation (*Arthrobacter sulfonivorans* DS-68 or *Arthrobacter* sp. DS-179), over control. Data represents the average of three replicates; error bars depict standard deviation (SD)



Zn acquisition in strategy I plants (in strategy II plants, this has been less studied), through the induction of Fe deficiency responses (Romera et al. 2019; Verbon et al. 2017). The ISR and the Fe uptake signaling pathways interact in plant roots via the transcription factor *MYB72*, which controls the biosynthesis of Fe-mobilizing phenolics. *MYB72*-dependent *BGLU42* activity is required for the secretion of Fe-mobilizing phenolics into the rhizosphere and the onset of ISR, as outlined by Verbon et al. (2017). They illustrated that the colonization of *Arabidopsis* plant roots (strategy I plants) by ISR eliciting beneficial microbes, e.g., *Pseudomonas* spp. and *Trichoderma* spp., activates the *FIT* (Fer-like Fe-deficiency-induced transcription factor) regulated transcription factor gene *MYB72* and the Fe uptake genes *FRO2* (Ferric reduction oxidase 2) and *IRT1* (Iron-regulated transporter 1). Volatile organic compounds secreted by ISR inducing microbes coordinate *MYB72* expression in *Arabidopsis* roots during the onset of induced systemic resistance and Fe deficiency responses through the activation of the *FIT* transcription factor gene (Zamioudis et al. 2015). Transcription factor *MYB72* controls the biosynthesis of phenolic compounds and the expression of the glucose hydrolase gene *BGLU42* (β -glucosidase 42) and the ABC (ATP-binding cassette) transporter gene *PDR9* (Pleiotropic Drug Resistance transporter 9). Glucose hydrolase activity of *BGLU42* (β -glucosidase 42) is involved in the processing of phenolic compounds to enable their secretion into the rhizosphere. Induced ABC (ATP-binding cassette) transporter gene *PDR9* (Pleiotropic Drug Resistance 9) is involved in the secretion of processed phenolic compounds from plant roots to the rhizosphere, and the phenolic compounds chelate and mobilize Fe^{3+} , making it available for the reduction by *FRO2* and *IRT1* genes and uptake by the roots. The antimicrobial activity of some phenolic compounds may play a role in shaping the rhizosphere microbial community. *BGLU42* is required for rhizobacteria-mediated ISR and, when overexpressed, confers resistance against a broad spectrum of plant pathogens (Zamioudis et al. 2014).

Neotyphodium coenophialum can stimulate the exudation of phenolic compounds in the rhizosphere of continental tall fescue (*Lolium arundinaceum*) with chelating characteristics; this was implicated in directly improving Fe uptake (Malinowski et al. 2004; Malinowski and Belesky 2000).

6.3.7 Secretion of phytohormones like signaling molecules

Several phytohormones, such as gibberellic acid and cytokinins, are key players in metal stress mitigation (Al-Hakimi 2007; Gangwar et al. 2010; Masood et al. 2016; Zhu et al. 2012). There are several reports on the effect of various phytohormones on Fe uptake gene expression—*IRT1* (Iron-regulated transporter 1) and *FRO2* (Ferric reduction oxidase 2). Auxin is known to act positively in *FRO2* induction under

Fe deficiency (Chen et al. 2010); ethylene is also a positive regulator of *IRT1* and *FRO2* in *Arabidopsis* and cucumber plants (Lucena et al. 2006).

Enhancing Fe-deficiency-inducible responses can facilitate an increase in the plant acquisition of Fe from Fe-limited soils. Xie et al. (2009) reported that the soil bacterium *Bacillus subtilis* GB03 could enhance Fe acquisition of *Arabidopsis* plants by activating the Fe-deficiency-inducible responses, suggesting that soil microorganisms could regulate plant Fe acquisition via signaling processes. In the last decade, plant physiologists have made efforts to uncover the signals responsible for triggering Fe deficiency responses in plant roots, and several hormonal compounds have been identified as signaling elements (Hindt and Gueriot 2012; Ivanov et al. 2012; Kobayashi and Nishizawa 2012). These include auxins (Chen et al. 2010), nitric oxide (NO) (Graziano and Lamattina 2007), ethylene (García et al. 2011), cytokinin (Seguela et al. 2008), and brassinosteroids (Wang et al. 2012). Among these, auxins, NO, and ethylene are particularly interesting, as several soil microorganisms can produce these compounds. This helps to emphasize the significant and potential interactions between soil microorganisms and Fe uptake of plants. Auxins have been demonstrated to be an important chemical signal, enhancing Fe-deficiency-inducible responses. Exogenous addition of synthetic auxin, either IAA or α -naphthaleneacetic acid, enhances Fe-deficiency-induced reduction of ferric Fe, expression of *FRO2* and *IRT1*, and development of root hairs and lateral roots to increase the surface area for Fe uptake (Chen et al. 2010; Wu et al. 2012). Production of auxin-like compounds by soil microorganisms can play a similar role and prove beneficial for plant Fe uptake under Fe-limited conditions. In support of this interaction, auxins produced by a microbe, isolated from soil mixed with phenolics, and secreted from Fe-deficient red clover plants markedly enhanced the activity of ferric chelate reductase in roots of Fe-deficient plants (Jin et al. 2006).

7 Conclusions and future outlook

The availability of low amounts of micronutrients is generally known as “hidden hunger” and draws less consideration than the conspicuous starvation of individuals. As an example, micronutrient deficiency refers to a situation in which a family can just earn enough to eat rice but not any of the natural products, including vegetables and meat that would make a nutritious diet. There is a need to understand, as biologists, that there is an intricate networking between soil, plants, and microbiomes of soil and plants that is responsible for crop productivity and soil fertility. Hence, along with plant breeding and agronomic fortification, significant efforts need to be undertaken to include microbes as partners in such

approaches. Therefore, focused research needs to be undertaken toward the following:

- Priming seeds with microbes or their products to improve bioavailability of micronutrients or reduce phytic acid in grains
- Understanding the interactions of the microbiome of plants and gut microflora for improving absorption, including prebiotics and Fe absorption in the human gut
- Conserving and exploring our native germplasm of wild cereals to identify the novel plant–microbiome combinations responsible for micronutrient enrichment
- Development of food grain mixes, with probiotic or prebiotic supplements

Future challenges include a synergism of technologies toward providing nutritious food for the growing populations, using sustainable and environment-friendly technologies.

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Author contributions Devendra Singh collected the information, wrote the first draft, and prepared the figures and tables. Both the authors conceptualized the topic and its subdivisions. Radha Prasanna edited the draft and revised versions and provided inputs for the improvement of figures and tables.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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