Chapter 21
Solubilization of Micronutrients Using Indigenous Microorganisms

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Abstract Out of the 17 elements essential for plant growth and reproduction, 8 are micronutrients. The soil supplies relatively large amounts of nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur as macronutrients and relatively small amounts of iron, manganese, boron, molybdenum, copper, zinc, chlorine, and cobalt, as micronutrients. Both deficiency and excess of micronutrients negatively impact the growth and productivity of plants and therefore should be supplied in sufficient amounts in appropriate ratios. A number of biotic and abiotic factors and their relationships affect the appropriate balance of macro- and micronutrient pool in the soil. The focus on addressing micronutrient deficiencies in soil in relation to agriculture has not been adequate in comparison to that for macronutrients. However, with the recent recognition on their impact on crop productivity and the efficiency of NPK uptake by plants, much attention was drawn to regulating micronutrient content in soil with chemical supplements. Environmental concerns encountered with the use of chemical supplements have directed the world into eco-friendly and sustainable approaches in addressing issues in many fields including agriculture. The use of naturally inhabiting microorganisms, "indigenous microorganisms," has been one of such eco-friendly approaches in agriculture. This review discusses the approaches that have been researched and used with indigenous microorganisms having micronutrient solubilization ability to regulate micronutrient availability in soil and the potential of developing them to optimize the crop productivity while maintaining a sustainable environment.

Keywords Micronutrients · Solubilization · Bioavailability · Indigenous microorganisms

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21.1 Introduction

The nutrients which are required by organisms in comparatively small quantities are called micronutrients. They are required in plant tissues at concentrations of less than 100μ g^{-1} dry weight (Welch and Shuman 1995). The attention to micronutrients has increased in the recent past with the understanding of their important role in disease resistance in plants and stress resistance in roots especially in crop plants (Welch and Shuman 1995; Graham and Webb 1991; Miller et al. 1991; Van Campen 1991; Nielsen 1992). Micronutrients are as equally important as macronutrients for plant growth, yield, and quality (Maurya et al. 2018; Yadav et al. 2018). There are eight micronutrients which have currently been recognized to be essential for higher plants, namely, boron (B), iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), chlorine (Cl), molybdenum (Mo), and nickel (Ni) (Welch and Shuman 1995). However, an exact number of the micronutrients vital for higher plants cannot be strictly proposed since intense molecular and physiological studies are required for each and every nutrient before such conclusions and for elimination of controversies. One such example is Si where there are arguments whether it is to be categorized as an essential or a beneficial element (Maathuis 2013; Mengel et al. 2001; Barker and Pilbeam 2015). Micronutrients play a role in primary as well as in secondary metabolism, energy metabolism, cell defense, signal transduction, hormone perception, and gene regulation (Maathuis 2013; Barker and Pilbeam 2015; Maathuis and Diatloff 2013; Vatansever et al. 2017). They also enhance the chemical composition and the quality of plants including crops and are known to act as catalyst in various organic reactions in plants (Karthick et al. 2018). Since these play an important role in plant growth and development, the deficiencies result in several physiological disorders and diseases in plants that reduce the yield and quality of plant produce (Sharma 2006). It should be taken into account that a number of physiological events in relation to plant metabolism are directly or somewhat related to the mineral elements. Deficiencies of mineral elements or toxicities intensely affect the life cycle of plants, and their availability to plants especially crops should be closely looked at in order to address the food safety and food security issues that would upswing in the near future. With the United Nations sustainability goals to be met by 2030 with the already identified and not yet identified ecological, environmental, and health problems associated with chemical fertilization, eco-friendly alternatives for soil augmentation are being investigated from which mineral-solubilizing microorganism is one. Deficiencies in micronutrients in soil will ultimately be related to human and animal health risks by crops not having the required amount of micronutrients present in crop produce. This chapter will be focused on different mechanisms and methods by which soil indigenous microflora increases the micronutrient availability in soil, enhancing the soil fertility and crop production and thereby human health through a sustainable approach. When considering a sustainable environment, the role of microbes in other processes such as bioremediation and bioleaching in addition to biofortification and biofertilization should also be discussed. Therefore, the chapter will also discuss situations where indigenous microbes have been used in the above processes in relation to eight micronutrients.

21.2 Micronutrient Deficiencies

Deficiency of micronutrients in soil is a global issue with slight variations in particular to different micronutrients (Monreal et al. 2015; Voortman and Bindraban 2015; Dimkpa and Bindraban 2016). In addition, their low crop use efficiency (i.e., low crop response per unit of micronutrient, relative to no micronutrient application), typically $<10\%$ in comparison to 20% and 80% for N, P, and K (Baligar et al. 2001), has also contributed to their deficiency in global agro-ecosystems. Many arable lands are affected by deficiencies of more than one micronutrient (Monreal et al. 2015; Voortman and Bindraban 2015; Oliver and Gregory 2015). This issue has further been made complicated with extensive extraction by high yielded crops supplemented with NPK fertilizers in addition to inadequate micronutrient fertilization. Yield increments reported with the addition of micronutrient supplements in different crops both with and without NPK fertilizers (Dimkpa and Bindraban 2016; Katyal and Ponamperuma 1974; Kanwar and Youngdahl 1985; Rietra et al. 2015) suggest the importance of micronutrients in crop productivity and for effectiveness of NPK fertilization (Dimkpa and Bindraban 2016). An amount ranging from 0.01 to 4.9 kg ha^{-1} of micronutrients has been estimated to be collectively removed from the soil annually by different crops (Rietra et al. 2015) and the type of micronutrient (Mallarino et al. 2011; Marschner 2012). A normal growth of a plant requires an amount of each micronutrient ranging between 0.1 and 100 mg kg^{-1} with mean levels of 90 mg kg^{-1} present in DTPA-extractible form (Samourgiannidis and Matsi 2013; Sobral et al. 2013). Therefore, soils do not fulfill the micronutrient requirement of a normal healthy plant. These deficiencies in soil result in low crop productivity and nutritional quality which will ultimately affect human health (Marschner 2012; Alloway 2009; Itelima et al. 2018; Dhaliwal et al. 2019; Kaura et al. 2020).

Since human nutrition is directly or indirectly based on plants, any micronutrient deficiency in food crops could cause micronutrient deficiency in humans, referred to as “hidden hunger” (Oliver and Gregory 2015; Kaura et al. 2020; White and Broadley 2009; Joy et al. 2015; Riaz et al. 2020). For example, Zn deficiency in soil has been shown to cause Zn-deficient symptoms in humans, such as stunting and child death (Monreal et al. 2015; Cakmak 2008).

21.3 Micronutrients in Plants

The ability of a plant to obtain sufficient levels of vital minerals is also a function of specific characteristics in the plasma membranes of root cells such as the presence of relevant transport proteins and related acquisition mechanisms of ions (Vatansever et al. 2017; Dimkpa and Bindraban 2016; Kochian 1991). Modification of the rhizosphere by plant roots can also affect nutrient availability, through the release of protons, chelators, phytosiderophores, and/or chemical reductants and also by elaboration of extensive root systems (Dimkpa and Bindraban 2016; White et al. 2013; Keuskamp et al. 2015). Micronutrient availability for plants is not entirely dependent on the amount of mineral present in the soil matrix but also depends on the molar fraction existing in soil solution and on the variation of the ions of a particular mineral (Vatansever et al. 2017; Lindsay 1991). Speciation and solubility of a particular mineral are influenced by abiotic factors such as redox state, pH, and temperature as well as by biotic factors such as phenolic compounds and organic acids which are metabolically generated or released through degradation of soil organic matter by indigenous microorganisms. In the soil, some micronutrients react with compounds such as phosphates and carbonates, to form chemical precipitates or interact with clay particles and other mineral complexes, making them unavailable (Dimkpa and Bindraban 2016; Marschner 2012; Allen 2002).

Factors such as plant species, genotype, growth conditions, and different organs and tissues of the same plant species affect the micronutrient content of a plant. Genetic makeup together with physiological and environmental factors changes the concentrations of micronutrients inside the plants, deficiencies, or toxicities (Table 21.1). Environmental variables and differences between plant species, as well as genetic variation within a plant species, can affect micronutrient concentrations in higher plants (Luber and Taureau 1990; Benton-Jones 1991; Benton-Jones et al. 1992). Micronutrients play a significant role in both general and specific physiological processes in plants. Fe, Cu, Mn, and Cl are involved in different metabolic processes like photosynthesis acting as cofactors. Fe, Mn, Zn, Cu, Ni, Mo, and Cl contribute to the activity of different enzymes such as DNA/RNA polymerases, N-metabolizing enzymes, dismutases, catalases, superoxide, dehydrogenases, oxidases, ATPases, and enzymes involved in redox processes (Broadley et al. 2012). Zn specifically plays a role in the enzymatic biosynthesis of auxin (Hossain et al. 1997; Fageria 2002) which enhances root growth. Ni is involved in N metabolism of plants by transforming urea to ammonia (Polaccao et al. 1999; Sirko and Brodzik 2000). Mo is used by both symbiotic and free-living N-fixing bacteria for N fixation since it is a component of the nitrogenase enzyme system (Barron et al. 2009). The role of micronutrients as cofactors is crucial for enzyme and nonenzyme activities in plant metabolism depending on the environment especially in abiotic and biotic stress mitigation by plants. Zn is shown to modulate the activity of membrane-bound NADPH oxidase (Cakmak 2008) in homeostasis of reactive oxygen species which regulates defense and signaling by the host during drought or other abiotic stresses (Bagci et al. 2007; Golldack et al. 2014). Cu is an essential

Table 21.1 Summary of major functions, deficiency, and toxicity levels and symptoms of micronutrient defficiency and toxicity

Element	Major functions	Deficient concentration in plant	Deficiency symptoms	Toxic concentration in plants	Toxicity symptoms	References
Fe	Biological redox systems (i.e., electron transport chains in photosynthesis and respiration), enzyme activation, carrier in N fixation (i.e., leghemoglobin in bacteroids of legume roots)	Less than 50–100μg g^{-1}	Interveinal chlorosis in young leaves (caused by decreased chlorophyll synthesis), retarded/stunted growth and reduced activity of hill reaction	Above 50–100μg g^{-1}	Growth inhibition, reduced chlorophyll synthesis, inhibition of photosynthesis	Welch and Shuman (1995), Tripathi et al. (2015)
Mn	Enzyme activation, biological redox systems (e.g., electron transport reactions in photosynthesis), detoxification of oxygen free radicals, secondary plant metabolite synthesis, structural constituent of ribosomes, disease resistance	Less than 10–100μg g^{-1}	Interveinal chlorosis in young tissue, appearance of greenish-gray specks at the lower base of monocots, development of brown necrotic spots on the cotyledons of legume plants, premature leaf fall, white-gray spots of leaf and delayed maturity	Above 10–100μg g^{-1}	Interferes with absorption and utilization of other mineral elements, affects the energy metabolism, decreases photosynthetic rates, causes oxidative stress	Welch and Shuman (1995), Tripathi et al. (2015)
Zn	Membrane integrity, enzyme activation, gene expression and regulation, carbohydrate metabolism, anaerobic root respiration, protein synthesis, structural integrity of ribosomes, detoxification of	Below 15 mg Zn kg^{-1} dry weight	Impaired stem elongation in tomato, root apex necrosis ("dieback"), interveinal chlorosis ("mottled leaf"), development of reddish-brown or bronze "bronzing," internode shortening	Above 20 mg Zn kg^{-1} dry weight	Reduced yields and stunted growth. Leafy vegetable crops are sensitive to Zn toxicity. Soybean and rice have been recognized as Zn sensitivity crops in which Zn toxicity instigates genetic variation,	Welch and Shuman (1995), Tripathi et al. (2015)

(continued)

Table 21.1 (continued)

Element	Major functions	Deficient concentration in plant	Deficiency symptoms	Toxic concentration in plants	Toxicity symptoms	References
	superoxide radicals, phytohormone activity (e.g., IAA and gibberellic acid), gene structure (Zn finger motif), disease resistance		(“rosetting”), epinasty, inward curling of leaf lamina “goblet” leaves and reductions in leaf size (little leaf)		increased lipoxygenase activity and lipid peroxidation enhancing antioxidative activity in plants	
Cu	Physiological redox processes (e.g., photosynthetic electron transport, respiration), detoxification of superoxide radicals, lignification, disease resistance, pollen viability	Below 5µg g^{-1} dry weight	Improper growth rate and distortion or whitening (chlorosis) of young leaves, decrease in cell wall formation lignification in several tissues and curling of leaf margins, damages apical meristem, pollen development, the fruit and seed production, wood production	Above 20µg g^{-1} dry weight	Chlorosis and necrosis, stunting, and inhibition of root and shoot growth inhibit enzyme activity and protein function, which later produces highly toxic hydroxyl radicals leading to oxidative damage of plant cell	Welch and Shuman (1995), Tripathi et al. (2015)
Ni	Urea and ureide metabolism, iron absorption, seed viability, nitrogen fixation, reproductive growth	0.05–10 mg kg^{-1} of dry weight	Leaf tip necrosis (legumes), chlorosis and patchy necrosis (*Gramineae*)	>10 mg kg^{-1} dry weight (DW) in sensitive species like barley, water spinach, and wheat >50 mg kg^{-1} DW in moderately tolerant species and >1000 mg kg^{-1} DW in	Inhibition of mitotic activities, reductions in plant growth and adverse effects on fruit yield and quality. Extremely high soil Ni concentrations have left some farm land unsuitable for growing	Chen et al. (2009), Alloway (2008)

				Ni hyper-accumulator plants	crops, fruits, and vegetables	
Cl	Osmoregulation, charge compensation (i.e., counter ion in cation uptake), reactivity of enzymes, photosynthesis, disease resistance, stomatal regulation	Can vary from 0.1 to 6 mg g^{-1} (dry matter) or between 0.03 and 0.17 mmol L^{-1} of the plant tissue water content for different species	Wilting of leaves, especially at margins, shriveling and necrosis of leaves, frond fracture and stem cracking in coconut, sub-apical swelling in roots	Crops with high Cl endurance, such as corn, sugar beet, grain sorghum, cotton, and spinach, can endure the Cl of >600 mg kg^{-1} with no visible negative effects The crops with mid-Cl endurance, such as wheat, rice, cucumber, tomato, cabbage, peanut, and grape seedling, can endure the Cl of 300–600 mg kg^{-1} The crops with low Cl endurance, such as soybean, lettuce, sweet potato, strawberry, and apple seedling, can't endure the environmental Cl when it exceeds 300 mg kg^{-1}	Reduced yields	Chen et al. (2009), Alloway (2008)
B	Cell wall formation and stabilization, lignification, xylem differentiation, membrane	Less than 0.3 ppm and 0.14 mg kg^{-1} (generally required in greater amounts by	Stunted growth inhibition of cell expansion, cracking or rotting of fruits, wilted or curled	Above 0.3–1 ppm and 3–100μg g^{-1} dry weight	Yellowing of the leaf tips and distorted shoot growth, chlorotic and necrotic patches in the	Welch and Shuman (1995), Tripathi

(continued)

Table 21.1 (continued)

Element	Major functions	Deficient concentration in plant	Deficiency symptoms	Toxic concentration in plants	Toxicity symptoms	References
	integrity, carbohydrate utilization, pentose phosphate metabolism, phenol metabolism and auxin activity, pollen germination and growth, inhibition of callose formation, stomatal regulation	dicotyledonous plant species than by monocotyledons)	leaves, water-soaked petiole		margin/older leaves, spots on fruits	et al. (2015)
Mo	Electron transfer reactions, nitrate reduction, nitrogen fixation, ureide metabolism, sulfate oxidation, pollen formation, protein synthesis	0.2–2 ppm in forage legumes	Chlorosis of leaf margins, “whiptail” of leaves and distorted curding of cauliflower; “fired” margin and deformation of leaves due to NO3 excess and destruction of embryonic tissues	100–1000 mg kg^{-1}	Stunted growth with yellow-brown leaf discolorations	Maathuis (2013), Baligar et al. (2001)

element for lignin synthesis needed for cell wall strengthening (Yruela 2009; Ryan et al. 2013) which facilitates withstanding abiotic stresses such as wilting, wind, and rain. B facilitates cross-linking of pectic polysaccharides serving cell wall functioning and maintaining the structural support of the cytoskeleton (Miwa et al. 2008). Chloride plays a role in stomatal regulation and protects plants from wilting and death (Broadley et al. 2012).

When considering crop plants, the role of micronutrients in combating abiotic and biotic stresses, improving nutritional quality, increasing yield, and enhancing uptake of essential macronutrients, NPK, is substantial in addition to their physiological role. Micronutrients assist plants to mitigate biotic stresses by means of developing resistance to plant diseases either directly affecting the pathogens in the rhizosphere or inducing different types of physiological responses in the plant during pathogen attack through mechanisms such as siderophore production (Kloepper et al. 1980; Lim and Kim 1997; Fernandez et al. 2005; Vansuyt et al. 2007; Dimkpa et al. 2009, 2015a; Radzki et al. 2013), inducing cellular activity, disease resistance (Shirasu et al. 1999; Datnoff et al. 2007) and microbial biocontrol agents to produce antimicrobials (Dimkpa et al. 2012, 2015a; Duffy and Defago 1999) and acidification of soil (Dimkpa et al. 2013a, b). Zn and Mn were reported to suppress diseases (Huber and Wilhelm 1988), and Cu, Ni, Mn, Mo, and B have been reported through mechanisms such as inducing the production of antioxidants, strengthening cell walls through the production of lignin and suberin, and controlling N metabolism in the plant (Huber and Wilhelm 1988; Römheld and Marschner 1991; Boyd et al. 1994; Bai et al. 2006; Evans et al. 2007; Stangoulis and Graham 2007; Taran et al. 2014; Servin et al. 2015) which make the crop more resistant to diseases and drought conditions.

Even though there should be a remarkable contribution of micronutrients for the nutritional value of crop produce with a number of physiological roles governed by them in plants, their relationship has been inconsistent (Dimkpa and Bindraban 2016). Some studies demonstrated a positive outcome with the addition of micronutrients (Rietra et al. 2015; Dimkpa et al. 2015a, b; Kumar et al. 2009), especially through positively modulating the uptake of other micronutrients. Some studies reported that the levels of other micronutrients can be reduced by the addition of a specific micronutrient perhaps because of the competition for uptake among micronutrients (Dimkpa and Bindraban 2016). The positive effects of micronutrients in the yield, quality, earliness, fruit setting, postharvest life, and biotic and abiotic stresses in vegetable crops have been documented by Sidhu et al. (2019). In addition to crop nutritional quality, they have been reported to enhance seed vitality and thereby good seed emergence and vigorous seedling growth (Brodrick et al. 1995; Nestel et al. 2006; Eggert and von Wirén 2013; Velu et al. 2014). The role of micronutrients in improving the agronomic quality including yield has been overserved with the supplement of individual element (Dimkpa and Bindraban 2016) as well as in combined applications (Yaseen et al. 2013; Vanlauwe et al. 2014). The significance of fortification of micronutrients into the soil through different means in order to improve the quality and quantity of food crops, has been discussed only recently and its real value will be persuaded in the future.

21.4 Micronutrients, Ecosystems, and Environment

The major ecological role micronutrients play in soils is increasing the NPK fertilizer efficiency use by plants that would otherwise be lost via leaching, fixation, and/or volatilization. Additionally micronutrients in soils may improve water use efficiency of crops under water-deficient conditions (Movahhedy-Dehnavy et al. 2009; Molden et al. 2010; Ashraf et al. 2014), and when coupled with organic matter in soils, they have been observed to enhance the ion exchange capacity, soil structure, and water storage capacity, improve drainage and aeration, and decrease soil salinity (Dhaliwal et al. 2019). These benefits together with the suppression of plant diseases will enhance the sustainable agricultural production systems. However, most of the micronutrients are heavy metals; therefore, nonstrategic applications would exert ecological and environmental challenges. Further, contaminations with high levels of micronutrients can also occur through water irrigation, carrying pesticides and heavy metal-containing wastewaters, as biosolid accumulates in soil (Alloway and Jackson 1991; Wuana and Okieimen 2011) which ultimately can cause micronutrient toxicity to soil flora and fauna. Despite both beneficial and detrimental agronomical, environmental, ecological, and health effects of micronutrients to living beings, increasing their availability in soil strategically will offer great potential in mitigating some challenges related to food security and "hidden hunger" through enhancing the quality and quantity of food produce.

21.5 Addressing Micronutrient Deficiencies

Since micronutrient fertilization is not a prevailing cultural farming practice, mitigating their deficiencies in soil would require vigilant fortification intervened after prior evaluations of crop and soil conditions (Joy et al. 2014; Kumssa et al. 2015) with systematically determined nutrient ratios and antagonistic interactions among the micronutrients, as well as between micronutrients and macronutrients. This will lead to the need of vigorous experimentation on the micronutrient applications in combination with fertilizer regimes to ensure more plant-specific and balanced ratios of micronutrient in fertilizer formulations (Dimkpa and Bindraban 2016; Rietra et al. 2015; Kaura et al. 2020). Micronutrient can be fortified through a number of methods which have their own limitations. The most common and direct method is the agronomic fortification through soil applications (Cakmak 2008; Velu et al. 2014; Duffner et al. 2014), as foliar sprays or as seed treatments (Farooq et al. 2012; Mondal and Bose 2019) in which foliar sprays have been more effective in yield improvement and grain enrichment, but are restricted by high cost (Johnson et al. 2005). Soil application would require higher doses due to low nutrient-use efficiency since 60–90% of the total applied fertilizer is lost and only the remaining 10–40% is taken up by plants. Seed treatment with its easiness to apply would be a better option both economically and environmentally as less micronutrient is needed while improving seedling growth (Farooq et al. 2012; Mondal and Bose 2019; Singh et al. 2003). However, this is under thorough investigation in terms of optimization of formulation, application protocols, and storage methods (Farooq et al. 2012). As alternatives to agronomic fortification, methods such as plant breeding, genetic engineering (biofortification), and postharvest biofortification of food are used in different countries. These methods are usually time consuming, and several tedious optimization trials such as screening of germplasm, crossing between varieties, molecular marker-assisted selection, and new crop breed phenotyping and high technical skills are needed (Velu et al. 2014; Waters and Sankaran 2011). In addition, transformation of micronutrients to available forms through building up of soil organic matter content has gained attention recently (Dhaliwal et al. 2019); however, it is yet to be further investigated with field trials done in large scale and stimulation models to better understand the relationship and to formulate management strategies (Dhaliwal et al. 2019). With these practical issues encountered with other alternatives, soil applications as chemical fertilizers have been the most common method of micronutrient fortification; however, they would result in chemical residues in soil due to their low use efficiency which will lead to severe environmental problems and toxicities to plants if not duly addressed. Further, imbalanced application can enhance the micronutrient deficiency levels in soils (Dhaliwal et al. 2019). The use of chemical fertilizers causes soil acidification (Chun-Li et al. 2014) and groundwater and air pollution (Youssef and Eissa 2014). More importantly, concerns over the contribution of chemical fertilizer for global warming and climate change have led the world toward sustainable fortification strategies in the recent past. Using indigenous microorganisms which are capable of promoting growth (plant growth-promoting rhizosphere microorganisms, PGPMs) and disease resistance (biocontrol agents) in crops through different mechanisms including converting nutritionally significant elements from unavailable to available form (mineralization/solubilization) has gained attention in the recent past as a substitute to chemical fertilizer in sustainable farming (Kaura et al. 2020; White and Broadley 2009; Bhardwaj et al. 2014; Fomina et al. 2005b). It has also been identified as an eco-friendly and cheaper approach in maintaining a sustainable environment with their potential to conserve and increase the soil biodiversity (Vessey 2003; Raja 2013) and to reduce environmental pollution including heavy metal contamination. When considering a sustainable environment and increasing bioavailability of micronutrients, the role of indigenous microbes in bioleaching and bioremediation process should also be considered since they exist as ores mainly in insoluble forms, while some (Fe, Cu, Zn, Ni) are categorized as heavy metals. Therefore, there is a recent advancement of research on micronutrient-solubilizing indigenous microorganisms toward developing sustainable environments (Cai et al. 2013; Kumar and Gopal 2015).

21.6 Indigenous Microorganisms (IMOs)

Indigenous microorganisms refer to a group of beneficial microorganisms that are native to a given area which are different from effective microorganisms that are laboratory-cultured mixture of microorganisms (Kumar and Gopal 2015). Ideally indigenous microorganisms are a mixture of a variety of beneficial microorganisms yet can also be considered as organized microbial communities. Their ability of microbial biofilm formation and their microbiome networks in various activities in the soil have been discussed for the last few years (Mandakovic et al. 2018; Horton et al. 2019; Akkaya et al. 2020). Their potentiality in plant growth promotion through processes such as biodegradation, nitrogen fixation, soil fertility improvement, and mineral solubilization has been observed for decades (Umi and Sariah 2006). In addition, their role in bio-composting, biodegradation, bioremediation, bioleaching, and natural farming has gained attention in the recent past and has been the focus of many researchers (Dhaliwal et al. 2019; Kumar and Gopal 2015; Gadd 2010; Sangeetha et al. 2020; Saravanabhavan et al. 2020; Sarker and Rahman 2020; Sharma et al. 2020). These have made them potential tools in developing sustainable approaches in agriculture, environmental restoration, and safeguarding targets since they are composed of a natural microbiome (Kumar and Gopal 2015). Depending on the purpose, a variety of terms are being used to refer to indigenous microorganisms. In agriculture, they are mostly being termed as “biofertilizers” referring to the products containing a combination of different types of microorganisms which are applied to crops in order to increase their quality and quantity. In some other context, they are named as “plant growth-promoting microorganisms (PGPMs)” which inhabit in root rhizosphere and considered as bioprotectants of plants (Akkaya et al. 2020; Yang et al. 2009; Ahmad et al. 2018; Pitiwittayakul and Tanasupawat 2020). As biofertilizers and PGPMs, they lead to crop productivity through decomposition of organic matter, nutrient acquisition, absorption of water, nutrient recycling, weed control and bio-control of plant pathogens (Bhardwaj et al. 2014; Vessey 2003; Sangeetha et al. 2020; Ahmad et al. 2018; Berg et al. 2013) improving the soil structure and function. Mineralization and solubilization have been identified as two main methods by which IMOs increase the bioavailability of nutrients by increasing solubilization which ultimately promote growth and yield of plants (Vessey 2003). Further, the role of IMOs in bioremediation and bioleaching of metals has also been investigated and might have an impact on regulating nutrient contents in soil. Solubilization of nutrients, mainly NPK and to some extent other macro- and micronutrients, by solubilizing IMOs has widely been researched and reviewed recently (Djajadi and Hidayati 2020).

21.7 Nutrient-Solubilizing IMOs

Both macro- and micronutrients are originated from minerals deposited under the Earth's crust as ores. Many nutrients are metals from which some are considered as potentially hazardous metals or heavy metals when in high concentrations in soil, water, and biological tissues. The majority of metals exist as minerals in soil with a number of mineral forms for each metal element having varying distribution in the environment with different physicochemical properties (Gadd 2010; Ehrlich and Newman 2009). The minerals in soil are subjected to various geological processes such as chemical cycling of elements including mineral formation (mineralization), mineral deterioration, and chemical transformations of metals, metalloids, and radionuclides (solubilization/mobilization). Solubilization refers to "the preparation of a thermodynamically stable isotropic solution of a substance normally insoluble or very slightly soluble in a given solvent by the introduction of an additional amphiphilic component or components" (Yadav et al. 2018) so that its availability is increased. Mineralization refers to the conversion of organic compounds (metals) into inorganic compounds through various decomposition procedures. Microorganisms significantly contribute to all of these geological processes. Microbes are in continuous interaction with metals and minerals under natural and artificial environments. Their interactions alter the physical and chemical state of metals and minerals, while microbial growth, activity, and survival are in return affected by the characteristics of metals and minerals (Gadd 2010). As a result many minerals are biogenic in origin (biomineralization) and some make structural components for many organisms such as diatoms (Ehrlich 1996; Gadd and Raven 2010). Most biominerals are in the form of silicates, calcium carbonates, and iron oxides or sulfides (Baeuerlein 2000; Bazylinski 2001). All kinds of microbes (bacterial, fungi, protists) and their symbiotic associations such as lichens and mycorrhizae contribute actively to the above geological processes (Macalady and Banfield 2003; Bottjer 2005; Chorover et al. 2007; Konhauser 2007; Gleeson et al. 2007; Gadd 2008), especially metal and mineral transformations (Ehrlich 1996). Specific groups of microbes that are directly involved in geochemical transformations include both pro- and eukaryotes such as manganese-oxidizing and manganese-reducing bacteria, iron-oxidizing and iron-reducing bacteria, sulfate-reducing bacteria, and sulfur-oxidizing and sulfur-reducing bacteria that can form or degrade silicates, carbonates, phosphates, and other minerals (Gadd 2007, 2010; Ehrlich 1996; Kim and Gadd 2008). In addition, soil microorganisms, especially mycorrhizal fungi (Tao et al. 2008), are solely responsible for nutrient cycling through decomposition of soil organic matter and also by making chemically fixed nutrients such as phosphorus (P), zinc (Zn), potassium (K), and iron (Fe) available (Ahmad et al. 2018). In addition, early stages of soil formation are supported by the activity of microbes such as lichens through weathering process (Purvis and Pawlik-Skowronska 2008; Gilmour and Riedel 2009; Uroz et al. 2009). General metabolic activities of all microbes affect metal distribution and bioavailability through cellular accumulation, decomposition, or biodeterioration of organic and inorganic substrates (Gadd 2007;

Warren and Haack 2001; Huang et al. 2004). However, mineral and metal solubilization in other terms may have negative contribution when they are potentially hazardous/heavy metals in certain context such as contaminated soil including solid wastes (Sayer et al. 1999; Fomina et al. 2004, 2005a, b).

21.8 Role of Nutrients in Microorganisms

Microbial growth, metabolism and differentiation require nutrients (Gadd 1992). Microbes interact with minerals containing nutrients in several ways depending on the type of nutrient, organism, and environment. All microbes use nutrients for structural functions and/or catalytic functions (Ehrlich 1997). The structure and the function of microbes also affect metal speciation and thereby solubility, mobility, bioavailability, and toxicity of nutrients (Gadd 2010). When these elements are metals, they particularly interact with microbes in different ways. Firstly, microbes incorporate trace metals into metalloenzymes or utilize enzyme activation (Wackett et al. 1989) such as nitrogenase (Mo/Fe or sometimes V/Fe or Fe only), cytochromes (Fe) and cytochrome oxidase aa3 (Fe, Cu), superoxide dismutases (Fe, Mn, Cu, or Zn), bacteriochlorophyll (Mg), iron-sulfur proteins, CO dehydrogenase with Ni in anaerobic bacteria and Mo in aerobic bacteria, NADP-dependent formate dehydrogenase (W/Se/Fe), and formate dehydrogenase H (Mo/Se/Fe) (Wackett et al. 1989; Fridovich 1978; Yamamoto et al. 1983; Robson et al. 1986; Scheer 1991; Orme-Johnson 1992; Boyington et al. 1997). Some, especially by eubacteria and archaea, use certain metals/metalloids as electron donors or acceptors in energy metabolism (Ehrlich 1996). The entire energy demand of chemolithotrophs like eubacteria *Thiobacillus ferrooxidans* and *Leptospirillum ferrooxidans* and the archaea *Acidianus brierleyi* and *Sulfolobus acidocaldarius* can be satisfied by oxidizable metals or metalloids, particularly through oxidation (FeII) to Fe(III) (Ehrlich 1996, 1997). Thirdly, microbes can enzymatically detoxify harmful metals or metalloids by oxidation or reduction or, when cannot be detoxified, removed from cell interior using efflux systems (molecular pumps) (Gadd 2010). Anaerobes such as sulfate-reducing bacteria enzymatically catalyze biocorrosion through cathodic depolarization. Anaerobic biocorrosion is thought to be regulated by biofilms consisting of a consortium of a variety of bacteria, often including aerobic, facultative, and anaerobic bacteria, each with specific locations in the biofilm (Ehrlich 1997). Non-enzymatic usage of metals by microbes occurs with accumulating and even with dead cells, binding them as cations to the cell surface with a passive process (Gadd 1993).

Despite the positive interactions of microbes and nutrients, their toxicities for microorganisms can occur through natural geochemical events and anthropogenic contamination in aquatic and terrestrial ecosystems by domestic, agricultural, and industrial activities. However, many microbes grow and survive in locations polluted with metals by different mechanisms which contribute to resistance (Avery 2001; Holden and Adams 2003; Verma and Kuila 2019; Tarekegn et al. 2020).

Changes in metal speciation affect the survival of microbes. These changes can be redox transformations, efflux and intracellular compartmentalization with cell walls, production of metal-binding peptides and proteins (e.g., metallothioneins, phytochelatins), active transport, organic inorganic precipitation, and other constituents with metal-binding abilities (Gadd 2010). They also can convert the pollutants into metabolic intermediates and be utilized as primary substrates for cell growth (Verma and Kuila 2019). In addition, the presence of plasmids containing resistance genes (Rosen et al. 2005; Silver and Phung 1996) also affects the activity of bacteria and fungi toward certain nutrients (Van Ho et al. 2002). Many microbial processes such as energy generation, cell adhesion, biofilm formation, and nutrient acquisition (Hochella 2002; Brown et al. 2008) are influenced by minerals and nutrients. Further, some mineral surface properties such as surface composition, microtopography, surface charge, and hydrophobicity affect thigmotropism, microbial attachment and detachment, and thereby colonization and biofilm formation (Brown et al. 2008; Vaughan et al. 2002; Bowen et al. 2007; Gleeson et al. 2010). Oxides of some micronutrients such as Fe significantly influence microbial activity by altering soil behavior through soil physical, chemical, and biological processes (Huang et al. 2005).

21.9 Mechanisms of Solubilization/Mobilization Nutrients

Nutrient solubilization/mobilization from different substrates such as rocks, minerals, soil, and others can occur by different processes and can result in volatilization through protonolysis, complexation by excreted metabolites and Fe(III)-binding siderophores, chemical oxidation or reduction, indirect Fe(III) attack, and methylation (Gadd 2010). Other metabolites that are excreted with metal-complexing properties such as amino acids, phenolic compounds, and organic acids may also play a role. For example, oxalic acid can form soluble oxalate complexes with nutrients such as Al and Fe (Strasser et al. 1994). Microbes play a major role in all of these mechanisms which affect their bioavailability and toxicity. Extracellular compounds such as enzymes and other metabolic products such as gluconic acid and its derivatives (Gadd and Sayer 2000; Saravanan et al. 2007; Khan et al. 2013), H_2S, formate, or other secondary metabolites produced by microbes regulate redox processes (Fe) (Ehrlich and Newman 2009). Metal chelators of microbial origin related to Fe(III) solubilization include oxalate, citrate, humic acids, and tannins. Methylation is another mechanism by which some microbes such as methanogens, clostridia, and sulfate-reducing bacteria under anaerobic conditions and fungi (*Penicillium* and *Alternaria*), under aerobic conditions, solubilize nutrients (Gadd 2010). For example, the production of siderophores is the key mechanism by which Fe assimilation occurs in fungi and bacteria (Kalinowski et al. 2000; Glasauer et al. 2004). Since this chapter is focused on micronutrients, a detailed review of their importance to plants, deficiency and toxicity symptoms, availability, experimental records on solubilizing microorganisms, their role in microbial growth and function, and mechanisms of solubilization is presented in the following section and summarized in Tables 21.1 and 21.2.

21.10 Iron-Solubilizing IMOs

With a significant role in some life-sustaining processes of microbes and plants, iron is considered to be an essential, multifunctional micronutrient. It is required for the different physiochemical processes in plants and plays a vital role in the activation of chlorophyll, photosynthesis, structural component of the chloroplast membrane, respiration, and synthesis of many iron-sulfur (Fe-S) clusters and heme proteins as cofactors of proteins that function in the life of plants.

Iron mostly occurs in two oxidation states (+2 and +3) in nature. Plants absorb iron as Fe^{2+} and must be in the general range of >7.7-10 mol L^{-1} to avoid any deficiency (Lindsay and Schwab 1982). The functions of iron are mainly based on the reversible redox reaction of Fe^{2+} (ferrous) and Fe^{3+} (ferric) ions. The biosynthesis ALA, which is a precursor in the formation of chlorophyll, might need an intermediate that contains iron in the electron transfer chain, ferredoxin. This could control the reduction and activation of one or more enzymes responsible for ALA formation (Miller et al. 1984). Deficiency symptoms in plants include interveinal chlorosis in young leaves and stunted growth, while toxicity causes growth inhibition, reduced chlorophyll synthesis, and inhibition of photosynthesis (Table 21.1).

Iron is the fourth most prevailing element after O, Si, and Al in the crust and soils. The forms of Fe in the soil can be categorized into four types as Fe^{II} in primary minerals, Fe^{III} in secondary minerals, Fe crystalline minerals and poorly ordered crystalline (hydro) oxides, soluble and exchangeable Fe, and organic matter-bounded Fe in soluble or insoluble forms (Colombo et al. 2014).

Iron release by weathering of soil mineral deposits is a very slow process and it is regulated by pH value, O_2 concentration, and the dissolution-precipitation process of both crystalline and poorly ordered Fe-hydroxide minerals (Lindsay 1988). Once mobilized in weathering processes, occurrence of redox reaction and pH conditions of the soil environment affect the destiny of Fe^{II}. Although there is a more than enough iron (Fe) content in soils for plant requirement, especially in calcareous soils, bioavailability of Fe is often severely limited. Those types of soils are mainly found in dry areas of the earth. Plants grown in calcareous soils usually show iron deficiencies. These plant species have evolved various strategies to enhance their uptake of iron. However, usually these strategies are not sufficient to avoid Fe deficiency completely. Hence, soil microbial community plays a significant role in influencing plant Fe uptake.

The close relationship between microbes and oxides of Fe coexists in soils, and they provide adequate opportunities for mutual interactions. Primary minerals may provide Fe as well as many other important nutrients such as K, P, and S while accommodating microbes in mineral cycling (Lowenstam 1981; Lower et al.

Table 21.2 Summary of micronutrient-solubilizing microorganisms and the mechanisms of solubilization

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
Mo	*Escherichia coli*, *Enterobacter cloacae* strain, *Pseudomonas* sp., *Serratia* spp., *Enterobacter* sp., *Acinetobacter calcoaceticus*	Production of siderosphores	Halmi et al. (2013)
	Thiobacillus ferrooxidans (now *Acidithiobacillus ferrooxidans*)	Bioleaching by changing the soil pH	Frascoli and Hudson-Edwards (2018)
	Klebsiella, *Bacillus*, *Rhodobacter*	Possess NADH-dependent nitrate reductase caterlizers	Schaechter (2009)
	Azotobacter vinelandii	Siderophore production, protochelin and azotochelin	Hänsch and Mendel (2009)
	Rhizobium bacteria	Cofactor for the enzyme nitrate reductase which is involved in nitrogen assimilation	Hänsch and Mendel (2009)
	Rhodobacter capsulatus	Possess Mo and Fe nitrogenases. Mo-nitrogenases exhibit higher specific activities than the alternative nitrogenases	
Cu	*Aspergillus niger*	Production of organic acids such as oxalic, citric, malic, and tartaric acids	Mulligan et al. (2004)
	Pseudomonas lurida	Promote Cu uptake by roots and leaves in plants	Kumar et al. (2020)
	Bacillus toyonensis	Exhibited a considerable capacity for $Cu_2(OH)_2CO_3$ solubilization, increased the soluble Cu concentration in the soil	Sheng et al. (2012)
	Penicillium bilaji	Chelating mechanisms by lowering the solution/soil pH to 4.0	Asea et al. (1988)
	Herbaspirillum sp.	By metabolic products of the strain	Govarthanan et al. (2014)
	Phosphorus-solubilizing bacteria (PSB)	Production of low-molecular-weight organic acids	Li and Ramakrishna (2011)
	Mycorrhizal colonization	Redoxolysis, acidolysis, and complexolysis	Nouren et al. (2011)
	PGPR (plant growth-promoting bacteria)	Secreting siderophores and organic acid and by	Ke et al. (2020)

(continued)

Table 21.2 (continued)

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
		increasing soil organic carbon content	
Zn	*Aspergillus niger*, *A. oryzae*, *A. nomius*	Secretion of gluconic acid and its 2- and 2,5-keto-derivatives during growth via decreasing soil pH	White et al. (1997)
	Aspergillus niger	Production of citric and oxalic acid	White et al. (1997)
	Aspergillus terreus	Decrease in pH through the production of gluconic acid	Anitha et al. (2015)
	Trichoderma harzianum Rifai	Releasing Zn^{2+} ion via oxidative dissolution process	Altomare et al. (1999)
	Beauveria caledonica	Process of acidolysis, complex lysis, and metal accumulation	Fomina et al. (2004)
	Ericoid mycorrhizal fungus *Oidiodendron maius* Arbuscular mycorrhizae	Production of organic acids (solubilize ZnO and $Zn_3(PO_4)_2$)	Martino et al. (2003), Subramanian et al. (2009)
	Bacillus sp. alone or in combination *Bacillus pumilus* *Bacillus* sp. AZ6	Organic acid production Production of amino acids, plant hormones, chelating ligands, and organic acids via oxido-reductive systems and proton extrusion	Yadav et al. (2018), Monreal et al. (2015), Mahdi et al. (2010), Jha (2019), Hussain et al. (2015), Saravanan et al. (2004)
	Bacillus aryabhattai	Production of organic acids	Vidyashree et al. (2018)
	Pseudomonas sp. *Pseudomonas pseudoalcaligenes* *P. putida*	Organic compound production, keto-D-glutarate, propionic acid, formic acid, lactic acid, gluconic acid acetic acid, glycolic acid, citric acid, fumaric acid, succinic acid, malic acid, and oxalic acid. Auxin production Soluble carbohydrate production	Yadav et al. (2018), Jha (2019), Patten and Glick (2002), Vazquez et al. (2000)
	P. fragi	Production of siderophores	Kamran et al. (2017)
	Pseudomonas taiwanensis	Production of gluconic and 2-keto-gluconic acid	Fasim et al. (2002)
	Gluconacetobacter diazotrophicus	Solubilize insoluble zinc source especially ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$	Saravanan et al. (2007)
	Azotobacter, *Azospirillum*	Production of chelating agents	Biari et al. (2008)

(continued)

Table 21.2 (continued)

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
	Burkholderia, *Acinetobacter*	Production of organic acids	Vaid et al. (2014)
	Consortia of *Azospirillum lipoferum Pseudomonas* sp., *Agrobacterium sp.*	Production of organic acids	Mengel et al. (2001)
	Pantoea agglomerans	Auxin production Extracellular enzyme production	Kamran et al. (2017)
	Enterobacter cloacae	Extracellular enzyme production	Kamran et al. (2017)
	Providencia sp. *Anabaena* sp. *Calothrix* sp. *Anabaena* sp.		Rana et al. (2011)
Ni	*Sphingomonas macrogoltabidus* *Microbacterium liquefaciens* *Microbacterium arabinogalactanolyticum*	Those rhizobacteria are shown to play an important role in increasing the availability of Ni in soil, thus enhancing Ni accumulation by *Alyssum murale*	Abou-Shanab et al. (2003)
	PGPR (*Pseudomonas* sp.)	Siderophore production	Tank and Saraf (2009)
	Aspergillus niger, *Aspergillus fumigatus*, *Acidithiobacillus ferrooxidans*	Solubilize nickel at room temperature 30–37 °C, whereas organism unable to solubilize nickel at higher temperatures 45 °C	Mohapatra et al. (2007)
	Pseudomonas sp. SRI2, *Psychrobacter* sp. SRS8, *Bacillus* sp. SN9	Production of indole-3-acetic acid (IAA), siderophores, utilization of 1-aminocyclopropane-1-carboxylic acid (ACC)	Ma et al. (2009)
	Azotobacter chroococcum (N-fixing bacteria), *Bacillus megaterium* (P-solubilizer), *Bacillus mucilaginosus* (K-solubilizer), and *Bacillus sp.* RJ16	pH reduction by producing acids	Arunakumara et al. (2015)
Cl	No available records	Most of the micronutrients are present in the form of chloride complexes of their cationic forms. Most of the soil microorganisms produce acids and siderophores and release into the soil. These	

(continued)

Table 21.2 (continued)

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
		chemical components reduce the soil pH and cause the changes of the pH which facilitate the breaking down metal-Cl complexes and release of chloride in to the soil	
Fe	Fe-reducing bacteria *Gallionella* spp. *Leptothrix* spp. (microaerophilic bacteria) *Shewanella alga* *Shewanella putrefaciens*	Release of low-molecular-weight Fe-binding molecules – siderophores	Colombo et al. (2014)
	Fe-oxidizing bacteria *Acidithiobacillus ferrooxidans*	Fe-oxide formation onto extracellular polymers in order to enhance metabolic energy generation The oxidation of Fe (II) increases the pH gradient across the cell membrane, which in return increases the proton motive force and the energy-generating potential of the cells	Graham and Webb (1991), Alloway (2009)
	Leptospirillum ferrooxidans	Catalysis of sulfide oxidation by ferric iron at very low pH (0.7–1.0)	
	Pseudomonas and *Trichoderma* genera	By the synthesis and release of siderophores	Singh (2020)
Mn	Acidophilic Mn solubilizers *Enterobacter* sp. *Bacillus cereus* *Bacillus nealsonii* *Staphylococcus hominis*	Enzymatic conversion, metal effluxing, and reduction in sensitivity of cellular targets, intra- or extracellular sequestration, and permeability barrier exclusion Direct solubilization by utilization of MnO_2 as a final electron acceptor in the bacterial respiratory chain, instead of oxygen Indirect solubilization by the formation of metabolic reductive compounds Metal anion protonation, soluble Mn ligand complex formation, and production	Samourgiannidis and Matsi (2013)

(continued)

Table 21.2 (continued)

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
		of bio-generated organic acids	
	Mn oxidation *Leptothrix* sp. *Pedomicrobium* sp. *Hyphomicrobium*, *Caulobacter*, or common Gram-positive or Gram-negative bacteria, e.g., *Arthrobacter*, *Micrococcus*, *Bacillus*, *Chromobacterium*, *Pseudomonas*, *Vibrio*, *Oceanospirillum*	Indirect oxidation by the production of hydrogen peroxide, free radical, or oxidant Direct oxidation (an enzymatic reaction) catalyzed by Mn binding and oxidizing proteins found in crude or purified extracts	Gounot (1994)
	Mn reduction *Pseudomonas* spp. *Bacillus* spp. *Corynebacterium* *Acinetobacter johnsonii* *Pseudomonas fluorescens*	Mn oxide reduction through a drop of pH and/or redox potential due to bacterial metabolism Reduction through direct or indirect processes Mn (IV) be reduced by inorganically or organic reductants produced by microorganisms Enzymatic Mn (IV) reduction (e.g., *Acinetobacter calcoaceticus*)	Maathuis and Diatloff (2013)
	Bacillus polymyxa	By coupling of metal reduction with oxidation of a non-fermentative carbon source like lactate	Marschner (2012)
	Geobacter metallireducens, *Shewanella* (formerly *Alteromonas*) *putrefaciens*, a facultative anaerobe and obligate respire *Shewanella putrefaciens*		Lovley et al. (1993)
B	Boron-tolerant microorganisms *Lysinibacillus boronitolerans* *Chimaereicella boritolerans* *Gracilibacillus boraciitolerans*	High B efflux and exclusions which actively pump boric acid from the cells and are thus able to maintain a lower B concentration in the cell than in the external medium	Ahmed and Fujiwara (2010)

(continued)

Table 21.2 (continued)

Element	Solubilizing microorganism	Mechanism(s) of solubilization	References
	Bacillus boroniphilus *Arthrobacter* sp. *Rhodococcus* sp. *Lysinibacillus* sp. *Algoriphagus* sp.		
	Boron accumulators *Variovorax boronicumulans*		Miwa et al. (2008)
	Boron uptake promoters *Bacillus pumilus*		Masood et al. (2019)

2001). Microbes especially by bacteria like *Thiobacillium* and *Metallogenium* sp. dissolve primary minerals which contain iron through various processes which are termed as solubilization or chelation, sorption, accumulation, transformation, and precipitation (Colombo et al. 2014; Mengel 1994). These mechanisms are even more complex within the rhizosphere, due to the activity of the plants. The activity of plant roots can affect the abundance, diversity, and activity of microbes as well as Fe availability, and the interactions between Fe minerals and microbes (Colombo et al. 2014).

Iron solubilization mediated by PGPR was reported by Kloepper et al. (1980). Many microbes belonging to bacterial genus *Pseudomonas* and fungal genus *Trichoderma* are found to possess the ability to solubilize iron (Singh 2020). In line with Jin et al. (2010), an isolated *Pseudomonas* sp. could grow and produce siderosphores under Fe-deficient medium (Jin et al. 2010). Their work also showed that phenolic compounds exuded from plant (red clover) roots under Fe-deficient conditions favor the rhizosphere microbes to secrete more siderosphores which help to improve plant iron uptake.

Reduction or oxidation of iron minerals provides energy for anaerobic ferric-reducing and ferrous-oxidizing bacteria. This apparently plays an important role in catalyzing iron transformations in anoxic environments. Lithotrophic acidophilic and neutrophilic bacteria oxidize ferrous iron aerobically (Harrison Jr 1984). The acidophile, *Acidithiobacillus ferrooxidans*, is the most widely studied of all iron oxidizers. Phototrophic purple, non-sulfur bacteria were found capable of anaerobic ferrous iron oxidation by utilizing ferrous iron as electron donor in the light (Widdel et al. 1993). *Desulfuromusa kysingii*, *Geospirillum barnesii*, *Rhodobacter capsulatus*, *Desulfofrigus oceanense*, *Desulfotalea psychrophila*, *Geobacter metallireducens*, *G. sulfurreducens*, and *Shewanella putrefaciens* (now *S. oneidensis*) are some of the reported iron-reducing bacteria (Straub et al. 2001).

21.11 Mechanisms of Fe Metabolism

The most accepted mechanism for iron solubilization by microbes is by production of siderosphores under iron-deficient growth conditions. Siderophores are chelating agents that are secreted by bacteria and fungi with formation constants for ferric iron in the range of 10^{25} to 10^{35} and in exceptional cases as high as 10^{51} (Hider 1984). Iron availability in the surrounding environment highly regulates the siderophore production of microorganisms (Kalinowski et al. 2000). Siderosphores differ in structure and are low in molecular mass. The main groups of siderophores are catecholates, hydroxamates, and carboxylates. The catecholate is a main siderophore which is produced by bacteria, whereas fungi produce hydroxamate (Miethke and Marahiel 2007; Hider and Kong 2010). Stable soluble complex, made by iron with siderophore in soil solution and at the mineral surface, makes them available for uptake by the cell membrane of plant roots. The siderophore is either destroyed or recycled during this reduction in some cases.

There are three different mechanisms in transporting siderophore combined with Fe across the cell membranes in microorganisms. Membrane-spanning proteins may involve in binding these to the substrate which are transported into the cell after undergoing a conformational change. The location of Fe release mechanisms differs. Alternatively, Fe may also be removed by hydrolytic destruction of the chelate. The second mechanism is termed as the direct shuttle (Crowley et al. 1991). In that mechanism, ferric siderophore binds to a cell surface receptor where Fe is cleaved and simultaneously transported without concomitant transport of the desferri siderophore. In the third mechanism, an indirect shuttle (extracellular dissociation) acquires Fe in which Fe is removed through reduction at a site some distance to the carrier protein (Crowley et al. 1991).

21.12 Manganese-Solubilizing IMOs

Manganese is an essential plant trace element that plays a significant role in plant metabolism and development but could be toxic at high concentrations. Mn occurs in many oxidation states like II, III, and IV in approximately 35 enzymes of a plant cell (Hebbern et al. 2009). In plant proteins, manganese acts either as a catalytically active metal or as an activator of enzymes. Superoxide dismutase which contains manganese protects the cells from the damaging effect of free radicals, oxalate oxidase, and manganese-containing water splitting system of photosystem II. Manganese activates PEP carboxykinase, malic enzyme, isocitrate dehydrogenase, and phenylalanine ammonia-lyase enzymes (Hänsch and Mendel 2009). Mn plays an important role in the synthesis of lignin along with Cu and provides resistance in root tissues to pathogens. Symptoms of Mn deficiency in plants include chlorosis, premature leaf fall, and delayed maturity, while toxicity causes reduced yields and stunted growth (Table 21.1).

Manganese is the fifth most abundant metal found on the earth's surface. In the Earth's crust, Mn is mainly found as minor components of rock-forming silicate minerals such as olivine, pyroxenes, and amphiboles along with Fe. Manganese oxide (pyrolusite) and Mn carbonate (rhodochrosite) minerals are among the most important Mn ore resources in the world. Mn is extensively available in deposits of complex ores, nodules on ocean floors (Patrick 2010), wastewater sludge (Wang et al. 2011), and municipal solid wastes (Abdulsalam et al. 2011). Reduced soluble or adsorbed Mn (II) and insoluble Mn (III) and Mn (IV) oxides are the naturally found forms of Mn in soil. Solubility and availability of Mn in soil are increased with increasing state of reduction. Oxidation of Mn in soil is basically a biological process, while reduction of Mn may be either chemical or biological. Mn availability in the rhizosphere soil depends on the redox condition and the pH ranges (Gounot 1994).

Both oxidation and reduction of manganese in natural environments is dominantly promoted by microbial catalysis, but abiotic converters are often important too and it may compete with the biological processes (Gounot 1994). Oxidation of Mn has been reported by many types of microorganisms such as fungi, bacteria, and algae (Ghiorse 1984). Most of them are bacteria that belong to common Gram-positive or Gram-negative bacteria or group of sheathed bacteria, *Leptothrix*, and budding and appendaged bacteria: *Pedomicrobium*, *Hyphomicrobium*, and *Caulobacter* (Gounot 1994). The demosponge *Suberites domuncula* was found to have a Mn-oxidizing bacterium by Wang et al. (2011) which belongs to *Bacillus* strain BAC-SubDo-03. Most Mn-oxidizing bacteria are heterotrophic aerobic bacteria that use organic substances as the substrate. Some rhizosphere bacteria like *Bacillus*, *Pseudomonas*, and *Geobacter* can reduce oxidized Mn^{+4} into Mn^{+2} which is the plant metabolite form of Mn.

Effective rhizosphere Mn-reducing bacteria (*Pseudomonas* sp.) have been reported by Marschner and Dell (1994). Most of Mn-oxidizing bacteria are heterotrophic aerobic bacteria that grow on organic substances. The bacterial isolates *Bacillus anthracis*, *Acinetobacter* sp., *Lysinibacillus* sp., and *Bacillus* sp. are capable of solubilizing Mn in a range of pH (Ghosh et al. 2016). *Bacillus thuringiensis* has been found to have the capability to tolerate high concentrations as 4000 mg L^{-1} of Mn (II) and the highest removal rate of Mn (II). Hence, *Bacillus thuringiensis* plays a significant role in detoxifying and immobilizing excessive Mn in soil (Huang et al. 2020). Many fungi like *Acremonium* spp. can also take part in manganese oxidation (Miyata et al. 2004). The white rot fungus *Ganoderma lucidum* has possessed a good potential in solubilizing Mn under shaking and non-shaking conditions (Nouren et al. 2011). The soil fungi *Aspergillus niger* and *Serpula himantioides* have shown the ability to tolerate and solubilize manganese oxides (Wei et al. 2012).

21.13 Mechanisms of Mn Solubilization

The possible mechanisms of Mn oxidation by microorganisms can be described as direct or indirect. Production of hydrogen peroxide, free radical, or oxidant indicates the indirect oxidation of Mn which is due to the change of the surrounding environment. *Arthrobacter and Leptothrix* like bacterial groups are found to oxidize Mn by producing hydrogen peroxide as a mechanism of protecting the cells from the harmful effects of hydrogen. Direct oxidation is an enzymatic reaction which is facilitated through Mn binding and oxidizing enzymes which are found in crude or purified extracts. Examples can be found as a spore protein of *Bacillus* SG-1 (de Vrind et al. 1986) and an intracellular protein of a *Pseudomonas* sp. (Jung et al. 1998). *G. lucidum* was able to solubilize Mn by production of organic acids such as citric acid, tartaric acid, and oxalic acid (Nouren et al. 2011). In addition, roots and rhizosphere bacteria produce chelating agents like phenolic compounds and organic acids and other elements and hence avoid precipitation of Mn (Marschner and Dell 1994).

21.14 Zinc-Solubilizing IMOs

Zinc is another vital micronutrient for normal growth and development of plants. The normal concentration range for zinc in plant tissue is 15–60 ppm. Zinc requirement in plants is 30–100 mg kg^{-1}, below which would result in its deficiency. Plants require Zn for optimum fruit size, crop production, and yield. It is also used in the carbonic anhydrase activity involved in photosynthetic tissues for biosynthesis of chlorophyll (Xi-Wen et al. 2013). Further, Zn plays a key role in the synthesis of protein, activation of enzymes, RNA and DNA synthesis and regulations, and oxidation and metabolism of carbohydrates and prevents the peroxidation of lipids and proteins due to reactive oxygen species. Zinc is important for auxin production and for normal fruit and flower development. In plants, genes responsible for environmental stress tolerance are Zn dependent (Hafeez et al. 2013). Several studies reported that the use of zinc-containing fertilizers and micronutrients improves crop quality (Hussain et al. 2018).

Soil contains considerable amounts of Zn but in insoluble forms. Zinc is easily mobile in oxidizing acid soils, whereas it is immobile in poorly reducing neutral or alkaline soils. In the soil solution, Zn is a divalent cation or complexes with ligand via different transporter systems which is carried by mass flow, diffusion, and root extension in the direction of roots. A majority of the Zn absorption happens via active transport system, and it is transported from the root to the shoots via both xylem and phloem tissues. A little amount of Zn is retained at the basal node which governs the distribution of Zn in plants (White et al. 1997). The deficiency symptoms appear in the new leaves due to its immobility. Symptoms depend on the crop. Deficiency symptoms are expressed as preliminary in young leaves and could be visualized as patterns of chlorosis of the new leaves (often interveinal) and necrotic spots on the margins or leaf tips (Table 21.1). These affected leaves are smaller in size and form leaf rosette. The shortened internodes give the plant a rosette appearance and poor bud development which result in reduced branching and flowering. Crops with Zn deficiency may have susceptibility to injury or infection (Ghosh et al. 2014; Gandhi and Muralidharan 2016).

Several studies have found that inoculations of potent strain of Zn mobilizer rhizobacteria have been found to increase the yield of field crop such as rice wheat barley and maize (Hussain et al. 2018; Kutman et al. 2010; Tariq and Ashraf 2016). For example, Zn-mobilizing PGPR inoculation had a significant impact on root weight (74%), root length (54%), root area (75%), root volume (62%), shoot weight (23%), and panicle emergence index (96%) (Kutman et al. 2010) which exhibits potential in mitigating Zn deficiency in soils and crops.

The composition of Zn in polluted soils is dependent on both soil location and sources of pollution (Kabata-Pendias and Pendias 2001). Zinc distribution in agricultural soils ranges from 10 to 300 mg kg^{-2}. Under anaerobic conditions, higher concentration of iron reduces the zinc bioavailability in soil (Hussain et al. 2018). Geochemical composition and weathering of the parent rock will determine the Zn content in the developing soil. Environmental pollution or Zn-rich products can add up and alter the parent rock composition. Zn composition in the Earth's crust is 78 mg kg^{-1} which varies in different parent rocks. In soil, active Zn occurs either in the divalent form (Zn^{2+}) or in complex form like $ZnOH^+$, $ZnHCO_3^+$, $Zn(OH)_3^-$, and ZnO_2^-. Zinc exists in five different pools within the soil, namely, water-soluble, organically bound, exchangeable, chelated, and adsorbed. The strength of these forms will determine their ability to plant uptake and leaching.

The bioavailability of Zn to plants is influenced by total Zn contents in the soil, soil pH, elevated concentration of cations (Na, Ca, and Mg), phosphate soluble forms, anion bicarbonate, soil organic matter, and $CaCO_3$ content. Zn is strongly adsorbed on calcium carbonate ($CaCO_3$), magnesium carbonates ($MgCO_3$), iron oxide (FeO), or manganese oxide (MnO) (Alloway 2009). Chemical fertilizers indirectly affect the conversion of soluble Zn into different insoluble Zn fractions. Therefore, several studies have suggested the use of biofertilizers containing Zn-solubilizing microbes to increase the soluble Zn concentration in the soil (Kamran et al. 2017).

Several microorganisms play a significant role in solubilization and mobilization Zn (Kamran et al. 2017; Fasim et al. 2002; Javed et al. 2018). Several studies have reported the effectiveness of rhizospheric fungi in solubilizing insoluble Zn compounds both in vitro and in vivo. The production of organic acids by microorganisms has been found to increase solubilization and release of Zn compounds (Agusto da Costa and Duta 2001). Some filamentous non-mycorrhizal fungi, namely, *Aspergillus niger*, *A. oryzae*, and *A. nomius* isolated from a Zn mining site at Tak Province, Thailand, showed that the solubilization of insoluble Zn compounds ZnO, $Zn_3(PO_4)_2$, and $ZnCO_3$ occurs through the secretion of gluconic acid and its 2- and 2,5-keto-derivatives during growth (White et al. 1997). Release of Zn from organic complexes and calcium carbonate is facilitated by microbes through mineralization and solubilization, respectively. It has been reported that *Aspergillus niger* solubilizes insoluble ZnO, $Zn_3(PO_4)_2$, and $Ca_3(PO_4)_2$ to soluble form through the production of citric and oxalic acid (White et al. 1997). *Aspergillus terreus* (ZSF-9) isolated from Tiruppur District, India, was found to solubilize ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$ through the production of gluconic acid (Anitha et al. 2015). *Trichoderma harzianum Rifai* 1295-22 (T-22) converts insoluble Zn present in the soil into soluble form by releasing Zn^{2+} ion via oxidative dissolution process. During the process, fungus releases a complex compound which segregates Zn^{2+}, resulting in the enhancement of dissolution of metallic Zn in the soil. Fungus *Beauveria caledonica* converts insoluble $Zn_3(PO_4)_2$ into soluble Zn through the process of acidolysis, complex lysis, and metal accumulation (Fomina et al. 2004). Similarly, ZnO and $Zn_3(PO_4)_2$ can be solubilized by the ericoid mycorrhizal fungus *Oidiodendron maius* (Martino et al. 2003).

Bacterial species such as *Pseudomonas striata*, *Gluconacetobacter diazotrophicus*, *Thiobacillus thiooxidans*, *Burkholderia cenocepacia*, *Pseudomonas pseudoalcaligenes*, *P. fluorescens*, *P. japonica*, *P. fragi*, *Acinetobacter*, *Serratia marcescens*, *S. liquefaciens*, *Enterobacter cloacae*, and *Pantoea agglomerans* and several cyanobacterial species have been reported to solubilize insoluble Zn (Kamran et al. 2017; Zaheer et al. 2019; Altomare et al. 1999; Bapiri et al. 2012; Abaid-Ullah et al. 2015; Hussain et al. 2015). However, some *Bacillus* sp. (*Bacillus subtilis*, *Bacillus pumilus*, *Bacillus thuringiensis*, *Bacillus aryabhattai*) alone or in combination with cheaper insoluble Zn such as ZnO, $ZnCO_3$, and ZnS has been suggested as an effective alternative to costly $ZnSO_4$ and found to be more effective than other Zn solubilizers (Mahdi et al. 2010; Pawar et al. 2015; Mumtaz et al. 2017; Jha 2019; Zaheer et al. 2019).

21.15 Mechanisms of Zn Solubilization

Microorganisms can solubilize Zn by either a single mechanism or multiple mechanisms. As for other micronutrients, soil pH affects the availability of Zn where a 100 times increase in solubility can be achieved by decreasing one unit in pH (Mumtaz et al. 2017; Havlin et al. 2005). In addition, *Pseudomonas, Bacillus* spp. (Saravanan et al. 2004) and arbuscular mycorrhizae (Subramanian et al. 2009) were observed to reduce pH in the solubilization of ZnS, ZnO, and $ZnCO_3$. The main mechanism by which plant growth-promoting bacteria improve the Zn availability is by releasing organic acids like gluconate (Saravanan et al. 2011) or the derivatives of gluconic acids, e.g., 2-ketogluconic acid (Fasim et al. 2002), 5-ketogluconic acid (Saravanan et al. 2007), and various other organic acids (Tariq et al. 2007) and extrude protons (Fasim et al. 2002; Wu et al. 2006). *Bacillus* sp. AZ6 was found to secrete organic acids like cinnamic acid, ferulic acid, caffeic acid, chlorogenic acid, syringic acid, and gallic acid in a liquid medium (Hussain et al. 2004). Mycorrhizal fungi were also observed to secrete organic acids (Martino et al. 2003) to solubilize Zn from insoluble $Zn_3\ (PO_4)_2$ and ZnO. Organic acids produced by some *Bacillus* sp. and *Pseudomonas* sp. include keto-D-glutarate, propionic acid, formic acid, lactic acid, gluconic acid acetic acid, glycolic acid, citric acid, fumaric acid, succinic acid, malic acid, and oxalic acid. Three ZSB isolates were found to produce 11 organic acids against ZnO, $ZnCO_3$, and $Zn_3(PO_4)_2$ including lactic acid, malonic acid, malic acid, citric acid, and succinic acid being the major acids. *Bacillus aryabhattai* produced many organic acids during Zn solubilization process as compared to *Pseudomonas taiwanensis* and other *Bacillus* sp. Organic acid secretions by *Bacillus* and *Pseudomonas* were dependent on the substrate of Zn minerals (Vidyashree et al. 2018). Some *Bacillus* strains were found to produce some other compounds in relation to Zn solubilization such as amino acids and plant hormones (Saravanan et al. 2004) and glucose or sucrose (*Gluconacetobacter diazotrophicus*) (Saravanan et al. 2007). Enhancement of chlorophyll, carotenoid, and antioxidant enzymes catalase (CAT)- and peroxidase (PO)-related functions by *Bacillus pumilus* and *Pseudomonas pseudoalcaligenes* had been reported to protect plants from salinity injuries. Further plants inoculated with the above ZMB also accumulated soluble carbohydrates in leaves, helping plants to overcome osmotic stress under salinity. Further, both bacterial isolates were positive for auxin production, *P. pseudoalcaligenes* showing more than *B. pumilus* in the presence of Zn in the medium compared to the control (Jha 2019). Auxin production in response to Zn has also been observed by Patten and Glick (2002) in *P. putida* which increased the length of canola seedling roots.

Zn-chelating compounds released by plant roots facilitate Zn solubilization by microbes in the rhizosphere (Obrador et al. 2003; Velazquez et al. 2016). Bacterial metabolites reduce reaction of Zn in the soil by forming complexes with Zn^{2+} (Tarkalson et al. 1998). At the root surface, Zn chelates the ligand (Zn^{2+}). *Pseudomonas monteilii*, *Microbacterium saperdae*, and *Enterobacter cancerogenesis* are thought to manufacture Zn-chelating metallophores (Whiting et al. 2001). A biofertilizer containing *Pseudomonas* sp. (96-51), *Azospirillum lipoferum* (JCM-1270, ER-20), and *Agrobacterium* sp. (Ca-18) produces chelating agent ethylenediaminetetraacetic acid (Tariq et al. 2007), and *Penicillium bilaji* was reported to increase Zn bioavailability to plants through chelating mechanism (Kucey 1988).

Zinc bioavailability can also be increased by facilitating nutrient uptake from long distance through improving root growth and surface area. Mycorrhizal fungi can change the root architecture which enables plant to obtain Zn from a distance of 40 mm from the root surface (Burkert and Robson 1994). An increase in Zn concentration up to 4% in cereal grains and increased root length by mycorrhizal fungus were reported (Subramanian et al. 2009). Tariq et al. (2007) reported significant increase in weight, length, and volume of root with biofortification of rice with Zn-solubilizing bacteria.

21.16 Copper-Solubilizing IMOs

Copper is another micronutrient needed for the growth of plants. Among many roles, it involves several enzyme processes and is the key to the formation of chlorophyll. Its normal range in most tissues is between 3 and 10 ppm. Cu requirement in plants is 3–20 mg kg^{-1} and below this range would result in deficiency. Although copper deficiencies or toxicities rarely occur, deficiencies have been reported in several parts of the world and need to be addressed since either extremes can have a negative influence on crop growth and quality. Cu ions act as a cofactor in enzymes such as Cu/Zn-superoxide dismutase (Cu/ZnSOD), cytochrome oxidase, ascorbate oxidase, amino oxidase, laccase, plastocyanin, biogenesis of molybdenum cofactor, and polyphenol oxidase (Krämer and Clemens 2006). Cu plays a vital role in the signaling of the transcription protein trafficking machinery, cell wall metabolism, iron mobilization, and oxidative phosphorylation and oxidative stress protection at cellular level (Yruela 2009; Puig et al. 2007). Cu is also required in photosynthesis and plant respiration electron transport chains and plant metabolism of carbohydrates and proteins. Its ethylene-sensing ability supports to intensify flavor and color of vegetables and flowers. Copper also acts as a structural element in certain metalloproteins (Pilon et al. 2006).

The deficiency symptoms of copper occur in the newer leaves. Symptoms vary depending on the crop. The symptoms are slight chlorosis of either in the whole leaf or between the veins of the new leaves. Small necrotic spots may form within the chlorotic areas on the leaf margins. The newest leaves are smaller in size, lose their sheen, and ultimately may wilt. Necrosis occurs on the apical meristems, which leads to death, inhibiting the growth of lateral branches. Lighter colored flowers than normal are produced by the plant (Welch and Shuman 1995; Tripathi et al. 2015).

Copper stress condition of the plant can cause burning of the root tips and thereby causes excess lateral root growth (Franco et al. 2011). When the copper concentration is higher in the soil, iron and sometimes molybdenum or zinc nutrients have to compete with copper for micronutrient availability in the soil and plant uptake (Tyler and Olsson 2001). Affected plants can exhibit symptoms of iron deficiency or other micronutrient deficiencies. Copper toxicity ultimately can reduce branching. Legumes have a tendency to be the most sensitive plants to copper toxicity (Carruthers 2016a, b).

The composition of Cu in polluted soils is dependent on both sources of pollution and soil location. Cu level in the environment has been increased by the mining of Cu-containing ores and industrial activities (Engelhardt et al. 2020). In soil, active Cu occurs mostly in the divalent form (Cu^{2+}) or in complex form with soil organic matter. The largest portion of Cu is usually present in the crystal lattices of primary and secondary minerals. The Cu ion is adsorbed to organic and inorganic negatively charged groups and is dissolved as Cu^{2+} and organic Cu complexes in the soil solution. Also it is specifically adsorbed to soil organic matter, carbonates, phyllosilicates, and hydrous oxides of Fe, Mn, and Al. The strength of these forms will determine their ability to plant uptake and leaching (Engelhardt et al. 2020).

The bioavailability of Cu in soil is influenced by physical, chemical, and biological properties at soil-root interface in rhizosphere. It is affected by different properties such as organic matter, soil type, pH, soil moisture, clay particles, temperature, retention, permeability, and different metal ions and their oxides (Hinsinger et al. 2009). In general, the bioavailable form of Cu^{2+} in the soil solution is decreased dramatically with an increasing soil pH. However, organic Cu complexes may dissolve at higher pH (Kumar et al. 2020). Calcareous or alkaline soils can limit the phytoavailability of Cu. Hence, the ability of plants to efficiently uptake Cu from soil solution, and distribution of this among different organs and tissues can strongly affect the crop growth and yield under Cu-limiting conditions (Migocka and Malas 2018).

Some micronutrients including Cu have limited mobility in soils which are transported to roots by slow diffusion. Even though Cu is usually present in large quantities in the bulk soil, the plant-available fraction in the rhizopheric soil solution can be insufficient to satisfy plant requirements. Copper allocation in the soils was found to be in the order of strong organic > residual > water soluble > ion exchangeable > carbonate > reducible > weak organic fractions, indicating that Cu is more distributed in organic fraction (84.67%). High affinity of Cu to organic matters make organic bound Cu distributed in the soil in large quantities. Cu in the crystalline lattice of the residual fraction cannot be easily released (Govarthanan et al. 2014). As one of the strategies to overcome this problem, microorganisms have been investigated in many studies.

Both bacterial and fungi have shown Cu-solubilizing ability (Table 21.2). Some filamentous non-mycorrhizal fungi, namely, *Penicillium* and *Aspergillus*, have been the most active metal-leaching fungi (Burgstaller and Schinner 1993). Several studies have shown the potential of *Aspergillus niger* to generate organic acids such as oxalic, citric, malic, and tartaric acids which resulted in maximum solubilization of Cu, Zn, and Ni (Mulligan et al. 2004). Bioleaching of Cu from ores has been done with *Penicillium simplicissimum* (Sukla and Panchanadikar 1993).

Several studies have reported the effectiveness of rhizosphere microorganisms in solubilizing insoluble Cu compounds both in vitro and in vivo. They mobilize and degrade organic pollutants. Cu-resistant bacterium, *Pseudomonas* sp. *DGS6* isolated from a natural Cu-contaminated soil, stimulated root elongation of maize and sunflower (Yang et al. 2013). *Pseudomonas lurida* strain EOO26 was found to increase Cu uptake by 8.6-fold by roots and 1.9-fold by leaves in inoculated plants (Kumar et al. 2020). The bacteria isolated from the rhizosphere, *Elsholtzia splendens*, significantly increased the bioavailability of Cu while stimulating the other heavy metals like Zn in the soil (Chen et al. 2005). Increasing Cu bioavailability and bioaccumulation with inoculations was observed to be species-specific in certain cases. The influence of *Bacillus* spp. on Cu bioavailability and the bioaccumulation for ryegrass and fescue were different to each other (Ke et al. 2020). Similarly, Liu et al. (2014) found that inoculations of 11 PGPR strains increased the Cu concentration in *Oenothera erythrosepala* and *Medicago sativa*, but decreased that in *Pennisetum purpureum*, which suggests the complex interactions between plants, microbes, and the soil (Liu et al. 2014). The addition of

Bacillus toyonensis alone had the maximum effect on $Cu_2(OH)_2CO_3$ solubilization (Sheng et al. 2012). *Penicillium bilaji* was able to solubilize cuprous and cupric oxide, cupric carbonate. This is mainly by chelating mechanisms under a low pH value as 4.0 (Asea et al. 1988). This mechanism involves the use of organic acids which have been reported to have phosphorus-solubilizing abilities (Khan and Bhatnagar 1977). Another study reported Cu leaching ability of *Herbaspirillum* sp. from ion-exchangeable, reducible, strong organic, and residual fractions (Govarthanan et al. 2014). The maximum solubilization (40%) in strong organic fractions was suggested to be resulted by the metabolic products of the microbe (Deng et al. 2012). The metabolites of microorganisms can act as indirect reactive species and solubilize metal sulfides and oxides during the bioleaching process (Mishra et al. 2008).

21.17 Mechanisms of Cu Solubilization

There are no clear mechanisms defined for Cu solubilization by microbes. Most of the literature suggest that microorganisms release chemical compound siderosphores that have ability to oxidize Cu ore, making them available to plants. However, the principal mechanisms of bioleaching of metal by fungi are documented to be redoxolysis, acidolysis, and complexolysis. The fungi are also found to produce organic acids such as citric, oxalic, malic, and gluconic acids during bioleaching which might contribute to solubilization (Mulligan et al. 2004; Johnson 2006). In addition, siderophores, organic acids and soil organic carbon content increased by the activity of PGPR improve soil Cu bioavailability (Ke et al. 2020). Phosphorus-solubilizing bacteria (PSB) also enhance Cu availability (Li and Ramakrishna 2011) by secreting low-molecular-weight organic acids. Many organic acids such as malic, lactic, 2-ketogluconic, citric, oxalic, glycolic, malonic, valeric, piscidic, tartaric, formic, and succinic have been identified as chemical compounds secreted by PSB, which have chelating properties.

21.18 Nickel-Solubilizing IMOs

Nickel is considered as an essential micro-element for plant growth since the late 1980s (Brown et al. 1987). The usual range for nickel in most plant tissue is between 0.05 and 5 ppm (Chen et al. 2009). Nickel is required to the plant as a component of certain plant enzymes like urease, superoxide dismutase, and hydrogenase. Legume plants use nickel as a catalyst in nitrogen fixation enzymes (Ahmad et al. 2012). It is required for urease enzyme which metabolizes urea nitrogen into usable ammonia in the plant. It prevents the accumulation of toxic levels of urea in plant tissues forming necrotic legions on the leaf tips. Therefore, the deficiency of nickel in plant can cause urea toxicity (Krämer 2005), reduced leaf size, disruption of amino acid metabolism, and urea accumulation in leaf (Bai et al. 2006). Nickel provides tolerance to plant diseases; however, the mechanism is unclear.

Nickel deficiency is unusual and minor and is often difficult to identify due to less symptom development. In certain cases, it can reduce yield and growth of plants. As nickel is a mobile element, its deficiency symptoms first appear typically in the mature leaves of the plants (Chen et al. 2009). In legume plants, deficiency causes whole leaf chlorosis along with necrotic leaf tips due to the increased levels of urea. In woody ornamentals, deficiency causes shortened internodes and it gives a rosette appearance to the plant, weak shoot growth, death of terminal buds, and eventual death of shoots and branches. The symptoms in pecans include decreased expansion of the leaf blade and necrosis of the leaf tips (Bai et al. 2006). Nickel turns out to be less available for plant uptake at higher pH of the soil or in growing media. Some other micronutrients like magnesium, zinc, iron, copper, cobalt, or cadmium in high amounts in the growth medium can result in nickel deficiency to the plant. Legumes (beans and alfalfa), barley, pecans, peach, plum, wheat, citrus, and certain wetland plants are some plants which are most sensitive to nickel deficiency (Merlot 2020).

The Earth's crust composition is comprised of approximately 3% of Ni and it is the 24th most abundant element. Its concentration in plant leaves ranges from 0.05 to 5 mg kg^{-1}, which is equal to 0.05–5 ppm on a dry weight basis. The required content of Ni in vegetative tissues of plants is between 2 and 4 ng g^{-1} dry biomass (Dalton et al. 1988) and up to 90 ng g^{-1} dry biomass in barley. Nickel concentrations $\geq$10 ppm are generally considered to be toxic to sensitive species. Ni^{2+} is the available form of Ni for plant. Rapid oxidation of Ni ion (Ni^{2+}) to unavailable forms in the soil makes total Ni concentration not a useful measure for Ni bioavailability. Thus, plants grown in high pH soils are vulnerable to Ni deficiency (Brown et al. 1987). In soil, active Ni occurs almost exclusively in divalent form (Ni^{2+}) or in complex form with soil organic matter. High pH soils can cause Ni deficiency. Other than that, excessive use of Cu and Zn can result in Ni deficiency in soil because Ni, Cu, and Zn share a common nutrient uptake system in the plant.

Rhizosphere microorganisms play a major role in Ni solubilization. Three bacteria, *Sphingomonas macrogoltabidus*, *Microbacterium liquefaciens*, and *Microbacterium arabinogalactanolyticum*, isolated from the rhizosphere of *Alyssum murale*, were observed to increase Ni uptake into the shoot by 17%, 24%, and 32.4%, respectively, compared to the non-inoculated control (Abou-Shanab et al. 2003). Tank and Saraf (2009) suggested that PGPR (*Pseudomonas* sp.) positively influence the growth of plants and also facilitate plant growth in Ni-contaminated soils. Mohapatra et al. (2007) reported that *Aspergillus niger*, *Aspergillus fumigatus*, and *Acidithiobacillus ferroxidans* solubilized nickel at room temperature, 30–37 °C, whereas organisms were unable to solubilize nickel at higher temperatures as 45 °C. In a pot experiment, inoculation of plants (*Brassica juncea* and *B. oxyrrhina*) with Ni-mobilizing strains of *Pseudomonas* sp. SRI2, *Psychrobacter* sp. SRS8, and *Bacillus* sp. SN9 maximized the biomass of the plants. In addition, strain SN9 was observed to increase Ni concentration in the root and shoot tissues of *B. juncea* and *B. oxyrrhina* (Ma et al. 2009).

21.19 Mechanisms of Ni Solubilization

The possible mechanisms of Ni solubilization by microbes include pH changes in the soil, siderophore production, and phosphate solubilization (Burd et al. 2000). Siderophore production in relation to Ni has significantly increased the size and chlorophyll content of leaf (Tank and Saraf 2009). Bacteria such as *Azotobacter chroococcum* (N-fixing bacteria), *Bacillus megaterium* (P-solubilizer) and *Bacillus mucilaginosus* (K-solubilizer), and *Bacillus* sp. RJ16 were reported to decrease the pH by producing acids which enhance the bioavailability of Ni in the soil (Arunakumara et al. 2015). Zaidi et al. (2006) reported a reduction in pH from 7.5 to 4.8 with the solubilizing *Bacillus subtilis* SJ-101, resulting in increased Ni availability. In addition, acidic soil conditions created by phosphate solubilization have shown to increase Ni accumulation in the presence of some bacteria (Rajkumar et al. 2008). Ma et al. (2009) reported the production of indole-3-acetic acid (IAA) and siderophores and utilization of 1-aminocyclopropane-1-carboxylic acid (ACC) by Ni-mobilizing bacterial strains.

21.20 Chlorine-Solubilizing IMOs

Chlorine is another micronutrient which is needed for the proper growth and processes in plants including osmotic and stomatal regulation, evolution of oxygen in photosynthesis, and disease resistance. Plant uses the ion (Cl^-) rather than the gas (Cl_2). In chloroplast, chloride is a structural constitute of photosystem II in the oxygen-evolving complex which is one of the three important cofactors (Kusunoki 2007). Chloride stimulates the ATPase at the tonoplast. However, excess chloride is accumulated in certain tissues such as guard cells, and their opening and closing is regulated by the flux of potassium and anions such as malate and chloride and therefore important for plant photosynthesis. It also maintains the rigidity of leaves (Chen et al. 2010).

Reports of Cl deficiency are rare in agriculture (Dordas 2008). Fairly a larger amount of Cl application was reported to enhance disease resistance in plants. These amounts are much higher than those required as a micronutrient but far less than those required to induce toxicity (Mann et al. 2004). Cl has been shown to be effective on a number of diseases such as stalk rot in corn, stripe rust in wheat, take-all in wheat, northern corn leaf blight and downy mildew of millet, and septoria in wheat (Graham and Webb 1991; Mann et al. 2004). The mechanism by which Cl increases resistance is not well understood. However, it appears to be nontoxic in vitro and does not stimulate lignin synthesis in wounded wheat leaves. It was suggested that Cl can compete with NO^{-3} absorption and influences the rhizosphere pH by suppressing nitrification and increasing the availability of Mn mediating reduction of $Mn^{III,IV}$ oxides which increases tolerance to pathogens.

As a beneficial micronutrient, Cl^- regulates increased fresh and dry biomass, greater leaf expansion, elongation of leaf and root cells, improved water relations, higher mesophyll diffusion to CO_2, and better water- and nitrogen-use efficiency (Colmenero-Flores et al. 2019). In most cases, deficient leaves exhibit distinct characteristic and continuous boundaries between the affected and healthy tissue and appear as blotchy leaf chlorosis and necrosis. In such cases, Cl deficiency may result in wilting and bronzing of leaves. Chlorine toxicity can occur naturally in plants grown in coastal soils due to the excess Cl. Chlorine toxicity usually results in necrosis along the leaf margins. Leaves are smaller than usual. They may be yellow and drop early. The symptoms first appear on mature leaves. In some species, chlorosis may also occur. Chlorine toxicity can result from air pollution, in the form of chlorine gas, or from excess chloride in the soil (Table 21.1).

Generally, soil contains sufficient amount of chloride in the soil. The plant available form of chlorine is an anionic form which is chloride (Cl^-). Anionic form is the dominant form of chlorine in soils. Chloride is thought to pass through the root by a symplastic pathway and is mobile within the plant (White and Broadley 2001). The content of Cl^- fluctuates greatly in soils. Most soils contain sufficient levels of chlorine. However, Cl may become deficient in inland soil under frequent high rainfall and irrigation. Plants may be able to absorb some metal-Cl complex such as $CdCl^+$, but with a minimal percentage (Weggler et al. 2004). Negatively charged chloride ion tends to be repelled from the surfaces of soil particles, making it difficult to form complexes readily with negatively charged mineral soils. Therefore, chloride in the bulk solution contains a higher concentration than in the diffuse layers surrounding soil particles. Water fluxes, relationship between precipitation, and evapotranspiration determine the movement of chloride ion within the soil (Chen et al. 2010).

There is no available literature on Cl-solubilizing microorganisms in the soil. However, the soil microbes make changes in soil pHs which will ultimately release chloride into the soils in plant available forms.

21.21 Mechanisms of Cl Solubilization

Most of the micronutrients are present as forms of chloride complexes in their cationic forms. Soil microorganisms produce acids which reduce the soil pH. Reduced pHs facilitate breaking down of metal-Cl complexes making them available for plants.

21.22 Boron-Solubilizing IMOs

Boron is a non-metal micronutrient which essentially optimizes plant growth and development. The critical concentration of B in plant tissues is 20–25 mg kg^{-1} (usually 35 mg kg^{-1}) on a dry mass basis (Ahmad et al. 2012). It plays an important role in cell wall synthesis and structural integration as well as in protein and enzymatic functioning of the cell membrane, providing improved membrane integrity (Brown et al. 2002). B is cross-linked with pectin assembly, glycosylinositol phosphorylceramides (GIPCs), and rhamnogalacturonan-II (RG-II) that control the tensile strength and porosity of the cell wall (Shireen et al. 2018). Optimum B concentration in cells enhances the plasma membrane hyperpolarization, while its deficiency alters the membrane potential and reduces H^+-ATPase activity. In young growing tissues, B acts primarily in cell division and elongation, and starvation leads to the inhibition in root elongation with deformed flower and fruit formation. Boron is also involved in phenolic metabolism and nitrogen metabolism in plants. The role of B in rhizobial N fixation, actinomycete symbiosis, and cyanophyceae heterocyst formation in leguminous crops has been highlighted in previous studies. B deficiency is thought to affect photosynthesis indirectly by weakening the vascular tissues responsible for ion transport (Rasheed 2009).

Boron affects the availability and uptake of other plant nutrients from the soil. B application increased the uptake and translocation of P, N, K, Zn, Fe, and Cu in leaves, buds, and seeds of cotton (Ahmed and Fujiwara 2010). Boron deficiency has occurred in over 132 crops and 80 countries during last 60 years. After Zn, B is the second most deficient micronutrient severely affecting the growth of crops on global scale (Alloway 2008). Deficiency symptoms depend on the age of the plant and include stunted root growth, restricted apical meristem growth, stunted root growth, reduced chlorophyll content, brittle leaves, and photosynthetic activity, disruption in ion transport, increased phenolic and lignin contents, and reduced crop yield (Shireen et al. 2018).

In the soil, the presence of boron is common as boric acid or borate. Boron is percolated in the form of uncharged molecules rather than as ions. It is extremely deficient in soils which are developed from calcareous, loessial, or alluvial deposits and also in highly leached soils (Borkakati and Takkar 2000). There are various other factors, including sandy/coarse texture, drought, alkalinity, liming, and intensive cultivation with more nutrient uptake and less fertilizer application, which affect the availability of B to plants (Ahmad et al. 2012). In many regions of the world such as Brazil, the USA, China, Japan, and Korea, B availability is limited which is resulted by its high solubility and leaching off by irrigation water or rainfall in shallow or coarse-textured soils. In drought conditions and in soils with less organic matter, the availability of B is low due to alkalization and breakdown of organic matter (Shireen et al. 2018). Optimal B availability in soils can be achieved by using several beneficial and eco-friendly techniques.

Boric acid uptake is affected by the transpiration stream. Enhancement of transpiration-driven water flow can be affected by plant growth-promoting bacteria which can increase B accumulation in plant. This may also cause B toxicity. Inoculation of these bacteria under low pH into soil increased the growth of rapeseed. Further, addition of P enhanced the uptake of B by rapeseed, while *B. pumilus* inoculation inhibited the growth of rapeseed under B supply (Masood et al. 2019). There have not been many studies done on increasing the bioavailability of B especially with indigenous microorganisms despite it being the second most deficient micronutrient affecting crops worldwide, therefore warranting investigations.

21.23 Molybdenum-Solubilizing IMOs

Molybdenum is most common in agricultural soils which can exist in several oxidation states ranging from zero to VI (Kaiser et al. 2005). In a plant, Mo performs various physiological and metabolic functions. Despite its requirement in small amounts for normal plant development, it plays a critical role in the regulation of various plant functions. The required concentration range in plant tissue for its normal function is between 0.3 and 1.5 ppm. Mo has been utilized by specific plant enzymes to participate in reduction and oxidative reactions (Thomas et al. 2017).

Molybdenum is an essential component in nitrogenase enzyme used by symbiotic nitrogen-fixing bacteria in legumes to fix atmospheric nitrogen. Plants also use Mo to convert inorganic phosphorus into organic forms in the plant (Beevers and Hageman 1969). Molybdenum deficiency can affect nitrogen deficiency in plant, since it is closely linked to nitrogen fixation process. Molybdenum is the only mobile micronutrient in the plants. Therefore, older and middle leaves show Mo deficiency symptoms early, but it spreads up to the stem and affects the new leaves (Table 21.1). Some plants such as poinsettias show thin chlorotic, leaf margins around the leaf perimeter followed by necrosis (Carruthers 2016a), which restricts plant growth and flower formation. Molybdenum deficiency or toxicity is uncommon in many plants. However, crops that are most sensitive to molybdenum deficiency are crucifers (broccoli, cauliflower, cabbage), legumes (beans, peas, clovers), poinsettias, and primula (Carruthers 2016a). Research has shown that high sulfates can reduce plant uptake of molybdenum (Kaiser et al. 2005).

The average concentration of Mo in the lithosphere is 2–3 mg kg^{-1} but can increase to a concentration like 300 mg kg^{-1} with significant content of organic matter (Kaiser et al. 2005; Reddy et al. 1997; Fortescue 1992). Different environmental factors such as soil pH, extent of water drainage, concentration of adsorbing oxides (e.g., Fe oxides), and organic compounds found in the soil influence the availability of molybdenum for plant growth. Molybdenum becomes more soluble and is accessible to plants mainly in its anion form MoO_4^- in alkaline soils, while it decreases in acidic soils ($pH < 5.5$) (Reddy et al. 1997). In agricultural soils, the complex that molybdenum is present depends on the chemical speciation of the soil zone. Molybdenite (MoS_2), wulfenite ($PbMoO_4$), and ferrimolybdenite [$Fe_2(MoO_4)$]

are the mineral forms of molybdenum found in rocks (Kaiser et al. 2005). Weathering releases Mo from solid mineral forms (Kaiser et al. 2005). Molybdenum is typically added to the soil by fertilization or by the addition of other chemicals such as sodium or ammonium molybdate.

Molybdate reduction by microbes has been reported from 100 years ago and includes mainly bacteria (Table 21.2). Potential mechanisms of reduction of molybdenum were first reported in *Escherichia coli*, *Thiobacillus ferrooxidans* (now *Acidithiobacillus ferrooxidans*), *Enterobacter cloacae* strain, *Pseudomonas* sp., *Serratia* spp., *Enterobacter* sp., *Acinetobacter calcoaceticus*, and *Klebsiella* sp. (Halmi et al. 2013). Mo-reducing soil bacteria are reported from Pakistan, Sudan (*Enterobacter* sp. strain Zeid-6), Indonesia, and Antarctica (*Pseudomonas* sp. strain DRY1). Except *Bacillus* sp., molybdenum-reducing bacteria are gram negative (Frascoli and Hudson-Edwards 2018). Many Mo-reducing bacteria isolated from Pakistani soils were resistant to high Mo concentrations (up to 50 mM) (Khan et al. 2014). Some plants eliminate Mo from their roots and shoots (e.g., *Cistus*, *Quercus* species), while some take up Mo without any harmful effects (e.g., *Baccharis* species) (Frascoli and Hudson-Edwards 2018). Autotrophic bacteria *Acidithiobacillus ferrooxidans* and *Thiobacillus thiooxidans* isolated from drainage from Kennecott's open-pit mine in Bingham Canyon, Utah, USA, were capable of bioleaching molybdenite (Frascoli and Hudson-Edwards 2018; Bryner and Anderson 1957).

Molybdenum is an essential component in nitrogenase enzyme and thereby in nitrogen fixation process (Hänsch and Mendel 2009). Molybdenum is the cofactor for the enzyme nitrate reductase during nitrogen assimilation (Hänsch and Mendel 2009). Also Mo is the key regulatory component for nodule initialization and maintenance of nitrogen fixation in legumes (Franco and Munns 1981), and the enzyme activity was elevated with a high Mo content. Several microorganisms are associated with the biofertilization process and they enhanced the activity of the Mo in plant growth and development. *Bradyrhizobium* inoculation and Mo fertilization with at least 50 g ha^{-1} increased the yield of peanut pods and kernels (Crusciol et al. 2019). Chatterjee and Bandyopadhyay (2017) found that the application of biofertilizers together with boron and molybdenum enhanced the growth, nodulation, and pod yield of vegetable cowpea in acid soil of eastern Himalayan region.

21.24 Mechanisms of Mo Solubilization

Molybdenum seems to induce the production of iron-chelating compounds such as dihydroxybenzoic acid (DHBA) and tris(catechol) protochelin and bis(catechol) azotochelin. Protochelin and azotochelin production also increases at lower concentrations of Mo and vanadium (V). Protochelin and azotochelin act as strong complexing agents for Fe(III), molybdate, and vanadate. Azotochelin (LH5) reacts with molybdate to form a 1:1 complex with Mo (VI) ($LH_4^- + MoO_4^{2-} \rightarrow MoO_2L^{3-} + 2H_2O$). Essential metals (Fe, Mo, and V) are acquired by these compounds while excluding toxic ones (such as W). At low concentrations, these catechol compounds form siderophore complexes with essential metals (Fe, Mo, V) and are taken up by the bacteria through specialized transport systems (McRose et al. 2017).

Microorganisms, those who have a capability of fixing atmospheric nitrogen and form ammonia, have Mo-nitrogenase or three forms of nitrogenase enzymes. Diazotrophic organisms such as *Klebsiella* and *Rhizobium* have Mo-nitrogenase. Mo in nitrogenase enzyme can also be combined with other metals depending on the microbial species. For example, *Azotobacter chroococcum* possesses Mo and V nitrogenases, *Rhodobacter capsulatus* has Mo and Fe nitrogenases, and *Azotobacter vinelandii* contains the three enzymes. The most commonly occurring nitrogenases have Mo in their active center to form the iron-molybdenum cofactor. Mo-nitrogenases exhibit higher efficacy than the alternative nitrogenases with respect to N_2 reduction rates. The metal cluster called FeMoco, an abbreviation for the iron-molybdenum cofactor, is the site of conversion of N_2 into ammonia (Hänsch and Mendel 2009).

Assimilatory nitrate reductases (Nas) that catalyze the first reaction in nitrate assimilation are molybdoenzymes. Molybdenum acts as the cofactor in nitrate reductase. Nitrate reductase in higher plants is proposed to be a homodimer, with two identical subunits joined and held together by the Mo cofactor. In bacteria, there are two types of nitrate reductases, first the ferredoxin- or flavodoxin-dependent enzyme found in cyanobacteria, *Azotobacter*, and the archaeon *Haloferax mediterranei*, and second, the NADH-dependent enzyme present in heterotrophic bacteria and *R. capsulatus*. The cyanobacterial nitrate reductase enzyme is an 80 kDa monomer, encoded by narB. Electrons from ferredoxin or flavodoxin are transferred to the cluster and the Mo-bis-molybdopterin guanine dinucleotide (Mo-bis-MGD) cofactor, the nitrate reduction site. NADH-dependent nitrate reductase catalizers are present in *Klebsiella*, *Bacillus*, and *Rhodobacter*. In *Klebsiella*, a catalytic subunit and a small electron transfer subunit are present in the enzyme, while the large subunit (nasA gene product) binds to Mo-bis-MGD (Schaechter 2009).

21.25 Conclusions and Future Prospects

This review discusses the significance of micronutrients for plants with special focus on increasing the productivity of crop plants and the role of microorganisms in sustainable agriculture while maintaining a sustainable environment. Furthermore, it presents developments in research and their applications in agriculture and environmental management and highlights their potential applications in achieving sustainable environments by taking into account their dimensions mainly in processes such as bio-composting, biodegradation, and other processes such as bioremediation and bioleaching. This review also highlights the fact that research has not given enough attention to microbes in terms of micronutrient solubilization and when did, the focuse has mainly been on bacteria with fungi to some extent. Other groups of microorganisms such as cyanobacteria and algae have not been investigated much for micronutrient solubility. Research especially on field trials/application of micronutrient-solubilizing microbes are currently being restricted to certain regions of the world mainly to India, Pakistan, and Africa and therefore should be expanded. With already successful stories and extensive future research, biofortification/biofertilization of crops with micronutrient-solubilizing microorganisms will open up new avenues in addressing the "hidden hunger" in a sustainable environment in years to come while creating a clean and efficient environment for sustainable developmental goals to be achieved.

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