Uptake of Micro-Nutrients by Plants through Microbial Channels: A Review

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Abstract

In natural ecosystems, most of the micronutrients are present in forms that are inaccessible to plants or bound in organic molecules. The assimilation of nutrients by plants is assisted by millions of soil microbes that possess the ability to depolymerize or mineralize nutrients into an available form to plants. A deficiency in micronutrients can disrupt the morphological and physiological growth of plants. Accessibility to both micro and macro nutrients by utilizing microorganisms has emerged as an excellent strategy in sustainable agriculture. Microbes found in the soil-root interface have the potential to solubilize the trace element. The abundant proliferation of Plant Growth-Promoting Microorganisms (PGPMs) in the *rhizosphere* is advantageous for plants, as these microorganisms are widely acknowledged for their growth-promoting activities. Nevertheless, there is still a considerable amount to discover regarding the physiology and mechanisms governing the absorption, translocation, and deposition of plant micronutrients facilitated by *rhizobacteria*. Microbes enhance plant growth by altering hormonal signaling, inhibiting pathogens, or increasing nutrient bioavailability. Application of microbial inoculants to plants at an early stage of development enhances their performances even under stress conditions. PGPM has come up as a reliable alternative to replace the chemicals in agricultural sectors as an environment cleanup strategy. This review highlights the role of soil microbes and their mechanisms they adopt in plant nutrient mobilization and uptake.

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Abbreviations

PGPR   Plant Growth-Promoting *Rhizobacteria*
PGPM   Plant Growth-Promoting Microorganisms
ACC   (1-aminocyclopropane-1-carboyclic acid)
ROS   Reactive Oxygen Species
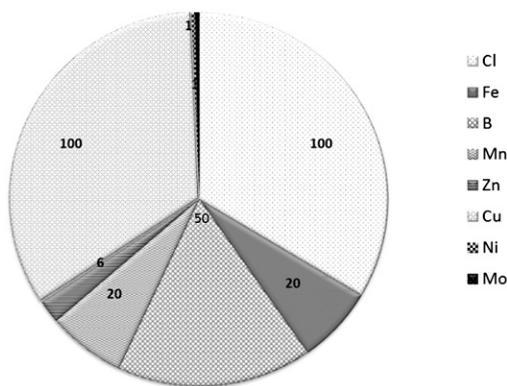SOD   Superoxide Dismutase

Introduction

Plants require a diverse array of important nutrient elements for the fulfillment of their life cycle. The 17 vital nutrients required are categorized into macro and micro-nutrients based on their concentrations in plant tissue, essential for promoting robust plant growth.[1] The macro-nutrients form structural components of molecules and are required up to 10 mmol/kg dry weight. The nine macro-elements required are Carbon (C), Hydrogen (H), Oxygen(O), Nitrogen(N), Potassium (K), Magnesium (Mg), Calcium (Ca), Sulfur (S) and Phosphorus (P). Some macro elements like Ca and Mg serve regulatory roles in addition to their structural role.[1] Certain micronutrients, though required in minute amount (less than 10 mmol/kg of dry weight) are vital for supporting growth, development, and metabolic processes of plants.[2] These micronutrients required in minute quantity perform crucial catalytic and regulatory functions, often acting as enzyme activators and include Chlorine (Cl), Boron (B), Iron (Fe), Manganese (Mn), Zinc (Zn), Copper (Cu), Nickel (Ni), and Molybdenum (Mo) as depicted in Fig 1. Sodium, Cobalt, Silicon, Selenium are the elements that play role in plant growth and development. These are known as Trace elements as they are present in very minute amount in plants. Despite being present in smaller quantities, micro-nutrients play a vital role in plant development by influencing the levels of phenolics and lignin, and also by contributing to the stability of the plasma membrane.[3] Plants exist within a rich ecosystem teeming with diverse microbes in the *rhizospheric* region surrounding their roots. These microbes are incredibly important for plant health, going beyond simply helping with nutrient uptake. In natural ecosystems, most nutrients are present in the form of complex organic molecules or rocks which make them less bioavailable to plants. PGPRs show various enzymatic activities that break down and convert organic and inorganic nutrient, thereby increase their availability to plants. Besides, they also aid in breaking down recalcitrant nutrients into usable forms and producing organic acids and siderophores that increase the availability of specific nutrients. Many microbes also form symbiotic relationships with plants, like mycorrhizae, which extend their hyphae far beyond the root area, significantly enhancing the plant's ability to absorb nutrients and water. Mycorrhizal fungi also enhance nutrient transport into plant cells by stimulating the genes associated with nutrient uptake. Similarly, nitrogen-fixing bacteria, provide a readily available source of nitrogen to the plant by forming symbiotic relationships. Analyzing root released—compounds by plant roots can help us to understand the complex communication between plants and microbes. The enormous potential of these microbial communities to replace current fertilization practices could be realized once their specific mechanisms are fully understood.

Factors such as soil pH, climate change, and lack of farmer awareness contribute to poor micronutrient availability, particularly of iron, zinc, and boron. This not only lowers crop yield and quality but also results in micronutrient-deficient food, contributing to "hidden hunger" in humans, particularly in developing regions that rely heavily on plant-based diets. Iron and zinc deficiencies are linked to anemia, impaired immunity, and stunted growth. Addressing these issues require sustainable strategies like improved soil management, biofortification, microbial interventions, and supportive policies to enhance crop nutrient density and protect global food and nutrition security.[4] The strategic utilization of microbial strains through intellectual applications can lead to the production of nutrient-rich grains, addressing global under-nourishment and benefiting populations in need. The biofortification of nutrients in crops through effective PGPM is a novel, eco-friendly technique in addressing the problem of malnutrition. The *rhizospheric* niche showing an enormous diversity of microbial taxa[5] as revealed through sequencing studies has become an exploring area in the plant-microbe interactions for beneficial purposes. There is a need for further research focused on exploring

and documenting the diversity and complexity of the root microbiome through metagenomic approaches. With changing global climatic conditions, interest has also shifted more towards designing synthetic communities. These communities consist of strains representing the predominant *rhizospheric* taxa, aiming to replicate beneficial microbial functions by harnessing efficient microbes in controlled experimental settings.[6] This review focuses on the microbes assisting in micro-nutrient mobilization and uptake by plants to sustain healthy growth.

Fig 1: Required micronutrients for plant growth (µg/g).[7]

Rhizospheric Niche

The *rhizosphere* constitutes an exceptionally intricate environment housing billions of microbes, predominantly bacteria and fungi. These microorganisms play a pivotal role in enhancing plant growth, with a particular emphasis on maintaining root health, thereby ensuring a sufficient supply of nutrients for overall plant development. Robust plants, in return, activate the soil microbial community by releasing root exudates and leaving behind organic residues. A plant's root modifies the *rhizospheric* environment by exuding large amounts of carbon. The carbon exuded by the root leads to a huge increase in the *rhizospheric* microorganisms living both inside and outside the root system. These root exudates consist of complex mixtures of low-molecular-weight organic compounds such as organic acids, amino acids, sugars, and phenolics along with enzymes for the *rhizosphere* organisms. In some plants through roots, 30 to 50% of the photosynthetically assimilated carbon goes to the soil.[8] The *rhizospheric* zone serves as a focal point for intricate biological interactions between plants and microbes. The wide range of interactions can be competitive, mutualistic, exploitative, commensal, or neutral. Previous studies on plant-microbe interactions have demonstrated the crucial role of *rhizospheric* microbes in alleviating the impacts of pathogens, herbivory[9,10] and various abiotic stresses.[11,12] Further research is crucial to unveil the mechanisms of micro-nutrient uptake, given their vital role in influencing plant growth. The three major ways by which the microbes influence plant growth are depicted in Fig 2.
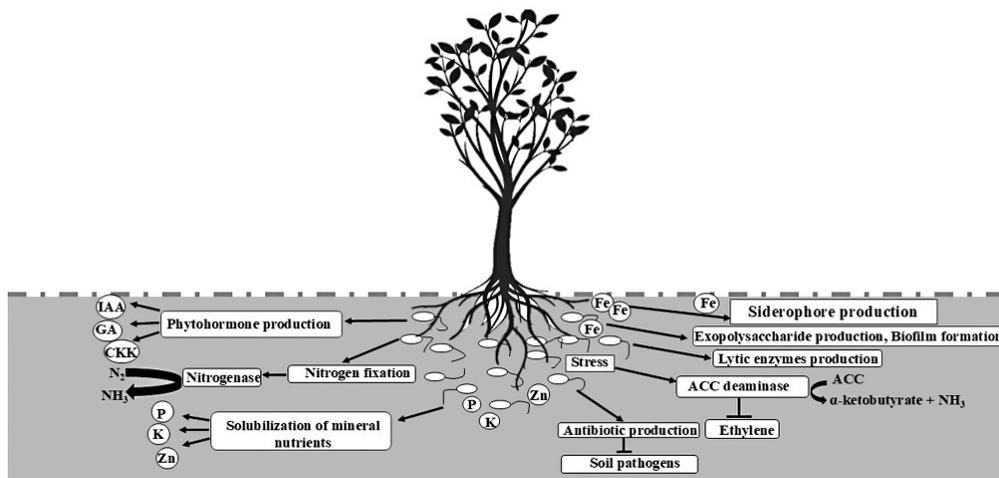
Fig 2: Various microbial influences on plant growth

Mobilization of Nutrients by Microbes

Ecosystem productivity is mainly governed by the nutrient transformation ability of the microbes present in the soil.[13] Metabolic processes within soil microbes enable the depolymerization and mineralization of nutrients bound in organic molecules, resulting in their release into the soil. The microbial cell contents are subsequently exudated into the soil through processes such as turnover, protozoic predation, or cell lysis.[14,15] Increasing crop productivity by the addition of chemical fertilizers and fungicides for meeting the goals of food security has adversely affected the microbial flora, which is the key governing component in ecosystem productivity and stability.

Addition of biostimulators or inhibitors along with traditional practices like tillage, manuring, residue placement, irrigation has influence on vital microbial processes. Chemical fertilizers and fungicides can be substituted by the growth-promoting *rhizospheric* microbes which get associated with roots of plants and stimulate plant productivity by uptake of nutrients in a soluble form. Microbial mediated soil transformation takes place through various mechanisms like extracellular enzyme activity, acidic dissolution, altering the oxidation state of ions, siderophore production, chelation, mineralization, etc., which make nutrients available to plants (Table 1).

Table 1: Microbes associated in uptake of micronutrient and their role plant growth.

S. No	Nutrient	Uptake form	Plant requir -ements	Deficiency symptoms	Soil system deficient	Microbe in nutrient uptake and solubilization
1	Manganese	Mn^{2+}	Photosynthesis, N-metabolism	Interveinal chlorosis, brown necrotic spots, premature leaf drop, delay anther maturity	Organic soil, high pH soil, sandy soil low organic matter, over-limed soils	*Glomus diaphanum, G. aggregatum, Bacillus megaterium, Penicillium citrinum*
2	Molybdenum	MoO_4^{-2}	N & S-metabolism,protein synthesis, pollen formation	Irregular leaf blade, inter-veinalmottling, marginal chlorosis	Acid, sandy soils in humid regions	*Pseudomonas, Bacillus leptothrix, Citrobacter, Acetobacter, Nitrospira fermicutes*
3	Zinc	Zn^{2+}	Protein synthesis, growth regulation	Short internodes, decreased leaf size	Sandy soil, organic soil	*Klebsiella spp, Serratia marcescense, Azotobacter, Azospirillum, Burkholderia Enterobacter, Anabaena, Calothrix, P. fluorescens, P. pudida, Bacillus aryabhattai, Pseudomonas*
4	Chloride	Cl-	Stomatal opening, photosynthetic reactions	Wilting, branched root	sandy, inland soil	*Bacillus megaterium, Hafnia alvei, Pantoea agglomerans.*
5	Boron	Bo_3^{-3}	Cell wall formation, sugar transport, flowering,	Rosetting, barren ears, hollow stem and fruit, discolored	Acidic sandy soil in regions of high rain fall	*G. intraradices, Arthrobacter, Rhodococcus, Gracibacillu, Lysinibacillus,*

			pollen formation and germination	leaves, loss of fruiting bodies		Algoriphagus, *Enterococcus*
6	Copper	Cu$^+$, Cu^{2+}	Carbohydrate and nitrogen metabolism, lignin synthesis, Vitamin A synthesis	Stem and twig dieback, leaf yellowing, stunted development, and pale green foliage.	Sandy soil low in organic matter	*G. mosseae, Burkholderia* sp. GL12, *Bacillus megaterium* JL35
7	Iron	Fe^{2+}	Production of chlorophyll, lignin formation, nitrogen reduction and fixation	Interveinal chlorolysis, Necrosis	Sandy soil, high pH soil	*P. fluorescens, P aeruginosa, Thiobacillus ferrooxidans, Bacillus megaterium*
8	Nickel	Ni^{2+}	N-metabolism, seed germination,	Hindered embryo growth, decreased leaf size, leaf tip necrosis	High pH soils	*Sphingomonas macrogoltabidus, Microbacterium liquefaciens, Microbacterium, arabinogalactanolyticum*

Microbes release extracellular enzymes and organic compounds with the specific purpose of solubilizing plant-available nutrients from sources such as soil organic matter, crop and animal residues, or manures. Soil microbes produce organic acid and extracellular enzymes which help in solubilizing the nutrients fixed in organic material and soil minerals thereby speeding up the nutrient cycle. Microbes can enhance the solubility of nutrients like iron by deriving energy from oxidation and reduction reactions. The increased nutrient content in plants after application of PGPR is primarily attributed to their influence on the growth and development of roots. This, in turn, leads to enhanced nutrient uptake by the plants.[16] Much work has been done to understand the role of microbes in N$_2$ fixation and P-solubilization compared to other minerals. Certain specialized symbiotic bacteria like *Rhizobium* and *Bradyrhizobium* can fix atmospheric N$_2$ into ammonium-based compounds for plant nutrition. There are also symbiotic N$_2$-fixing bacteria like *Frankia* that associate with woody shrubs. *Azospirillum*, an asymbiotic bacterium, provides additional N by getting inoculated with roots of grasses of economic importance like sugarcane. N$_2$ fixation is estimated to provide 10 to 20% of the N requirement in the case of cultivated crops and accounts for approximately 25 to 40% of the global annual demand for reactive nitrogen. The significance of mycorrhizal fungi and nodulated legumes were well realized long back from the second half of 19th century.[17] By the 1950s, efforts to improve crop yield by coating seeds with PGPR cultures like *Azotobacter chroococcum* or *Bacillus megaterium* known as seed priming came into practice.[18] By the 1980s many different *rhizobacteria* strains, with promising growth-promoting activities like *Pseudomonas*, and *Azospirillum*, were described as plant growth-promoting bacteria and since then many bacterial strains have been added to the list like *Klebsiella aerogenes*, *Serratia marcescens, Enterobacter cloaceae.*[19]

PGPRs have been extensively researched for their role in promoting plant growth through multiple mechanisms, including phytohormone production, nitrogen fixation, improvement of soil structure, decomposition of organic matter, recycling of vital nutrients, and solubilization of minerals such as phosphorus, potassium, and zinc. These activities significantly enhance crop growth, yield, and seed

size, while also supporting soil fertility and overall soil health.[20,21] PGPR produces high molecular weight carbohydrates known as exopolysaccharides which help in maintaining soil moisture under drought conditions.[22] Inoculation of seedlings with high exopolysaccharide producing bacteria shows enhanced soil aggregation capability and the roots of such plants adhere to more soil and show higher relative water content in their leaves.[23] Application of PGPR increases the antioxidant enzyme level in plants under severe water stress conditions and hence can be used as inoculants to reduce the oxidative damage elicited by water stress.[24] Plants that have been inoculated with PGPR possessing ACC (1-aminocyclopropane-1-carboyclic acid) deaminase activity exhibits a comparatively higher tolerance to environmental stress.[25] ACC serves as the precursor in ethylene production in plants. Bacteria that produce ACC deaminase can reduce ethylene levels by breaking down ACC into α-ketoglutarate and ammonia. This enzymatic action promotes root growth, as it lowers endogenous ethylene levels.[26] The application of PGPR in the form of eco-friendly fertilizer has become a sustainable agricultural approach, providing an effective substitute for harmful chemical fertilizers. The application of mineral fertilizers, containing concentrated soluble nutrients affects the adjacent microbial niche. An osmotic stress on adjacent microbial environment is generated due to the presence of salt in higher concentration around a fertilizer granule until the diffusion of nutrients into the soil. Likewise, high pH around the microbial niche due to anhydrous ammonia temporarily hinders its activity. In contrast, the use of PGPR biofertilizers mitigates these concerns and promotes sustainable agricultural practices. A better perception of the contribution of PGPM in micronutrient uptake is required. This approach can aid in the effective management of microbial inoculums by pairing them with compatible host crops under optimized soil conditions. This includes ensuring sufficient soluble phosphorus (P) and molybdenum (Mo) levels, as well as adjusting soil pH, to enhance the overall efficacy of microbes in various cropping systems. The *rhizospheric* soil harbor essential soil enzymes and microorganisms which coordinate in the breakdown of organic matter, mineralization and nutrient cycling thereby enhancing nutrient availability for plant uptake. Addition of at least 10% of *rhizospheric* soil

was found to promote vegetation reconstruction.[27] The biosynthesis pathways of phytohormones generated or regulated by PGPMs have been better understood through developments in genomics, proteomics, and metabolomics. This has also highlighted the potentials of PGPMs in controlling vital physiological processes in plants. As microbes also secrete various toxins, antibiotics and enzymes which influence plant biochemistry, physiology, and secondary metabolisms, their application is a new and eco-friendly approach to control the proliferation of plant pathogens.[28,29]

Boron
Boron (B) is an essential micronutrient necessary for the growth and development of organisms ranging from diatoms to vascular plants. However, fungi, bacteria, green algae, and animals do not require B.[30] Boron deficiency is a common global agricultural problem as 11.26 % of it in earth is in the form of borax. Plant uptake of B occurs passively when B availability is high, while under low B supply, the uptake becomes facilitated (with boric acid) or active (with borate). Boron deficiency in plants affects some of the critical physiological processes such as cell wall synthesis, sugar transport, lignin deposition, cell wall structure,[31] metabolism of carbohydrates, RNA integrity, respiration, indole acetic acid secretion, phenol secretion, and membrane integrity. Recent studies have revealed that deficiency in vitamin B can potentially disrupt the metabolism of ascorbate metabolism[32] as well. Adequate B in plants has been shown to minimize the chances of attack on crop plants by pathogenic fungi like *Plasmodiophora brassicae* infecting crucifers, *Fusarium solani* infecting beans, *Verticillium albo-atrum* infecting tomato and cotton, and many viruses like tomato yellow leaf curl virus in tomato, tobacco mosaic virus in bean, *Gaeumannomyces graminis* (Sacc.)[33] and *Blumeria graminis* in wheat. Boron acquisition occurs easily in low pH soils as compared to high pH soils as the mannitol–B complex is stable in alkaline environment and checks its entry into plant cells. Few species of mycorrhiza like *Glomus intraradices*, *G. etunicatum*, and *G. diaphanum* irrespective of soil pH conditions, when inoculated in maize plants have been documented to enhance B transport to shoots and enhance the yield two folds as compared to uninoculated maize crops.[34] Inoculation of Glomus fasciculatum in lemon (*Citrus jambhiri* Lush)

plants grown in soil amended with B enhanced B accumulation from 11-18% in leaves, simultaneously enhancing the secretion of amino acids and root sugars, as compared to control plants.[35] *Bacillus boroniphylus* a novel PGPR found in boron-rich soil promotes plant growth by producing organic acid which helps in solubilizing boron. *B. boroniphylus* is also recorded to protect plants from various stress factors.[36] Boron is tightly held in organic matter and can be released into the soil solution after the breakdown of organic matter facilitated by *Gypsophila, Bacillus*, and Microbacter which sequester B by forming unreactive precipitate mineral form with Fe, Ca, or PO_4, at pH 8-9. A few bacteria like *Rhodococcus*, *Lysinibacillus*, *Gracibacillus*, *Arthrobacter,* and *Algoriphagus* are much being worked out as efficient B solubilizers.[37]

Iron

Iron (Fe) is an important micro-nutrient that functions as a cofactor for numerous enzymes involved in key physiological processes like photosynthesis, respiration, and nitrogen fixation; therefore, its deficiency leads to significant metabolic disruptions. Iron primarily exists in its oxidized form (Fe^{3+}), which leads to the formation of oxides and hydroxides that are insoluble, making them unavailable to plants and soil microorganisms. Plants can avail iron by two basic methods. The first method involves the chelation of iron through the release of organic compounds. This increases iron solubility further allowing it to diffuse toward the plant. Subsequently, it undergoes reduction and is absorbed by the plant through a membrane-associated enzymatic system. The second method involves the absorption of a reduced form of iron inside the plant by forming the complex formed between Fe^{+3} and organic compound.[38] Some PGPRs are capable of releasing iron-chelating molecules called siderophore which attracts iron towards the *rhizospheric* part and makes them easily available for plant.[39] Siderophores, the low-weight organic compounds of nearly less than 1kDa containing functional groups like hydroximates and catechols reversibly bind to iron. Estimated siderophore content in soil is around 10−30M. PGPRs such *Pseudomonas aeruginosa* and *Pseudomonas fluorescens* secretes pyoverdine and pyochelin type of siderophores.[40] With more studies being carried out in this area the siderophore-producing bacteria enlisted has increased. *Rhizobacteria Aeromonas*, *Arthrobacter, Bacillus*, and *Streptomyces* produce Fe-chelating compounds or siderophores like hydroxate, catechol, and pyoverdins, which sequester Fe from soils. The stability of siderophores is highly pH dependent, (for example hydroxamate siderophores are stable at pH 3-4, while catechol is stable at pH 7.5-10).[41] PGPRs can increase their competitive potential, in the *rhizosphere* as these compounds also have an antimicrobial activity besides improving iron nutrition in plants.[42] *Bacillus megaterium* strain, showed 60-80% manganese and iron mobilization by its bio-solubilization capacity that were checked on polluted soil, whereas zinc was mobilized only by 20%.[43] Results reveal that *Azospirillum* bacteria were capable of significantly increasing the Cu, Fe, Mn, and Zn content in maize leaves.[44] Co-inoculation of *Enterobacter*, *Serratia marcescens,* and *Microbacterium arborescens* increased the micronutrient contents, including copper (Cu), zinc (Zn), manganese (Mn), and iron (Fe), in wheat grain under both pot and field experiments as compared to control.[45]

Manganese

In plants, manganese (Mn) functions as a cofactor, playing a role in the activation of around 35 different enzymes. The majority of these enzymes are involved in catalyzing decarboxylation, oxidation-reduction and hydrolytic reactions. Mn plays a structural role in enzymes, including the Mn-protein of Photosystem II and the Mn-dependent superoxide dismutase.[46] As the oxidized forms of manganese are insoluble, plants can absorb it only in its reduced form, such as Mn^{2+}. The oxidation-reduction state of manganese is influenced by soil pH. Soil having pH less than 6 reduction state exists and more than 6.5 Mn exists in its oxidation state. It was found that yield of wheat, oats, barley, sorghum, rice, and legumes were equally affected by both deficient and excessive levels of soil Mn. Manganese is the most well-known micronutrient for its ability of enhancing plant resistance to various root and foliar diseases such as blast of rice, wilt of tomato, common scab of potato, downy mildew, powdery mildew and all disease of wheat.[47,48] Mn plays an important role in photosynthesis, secondary metabolite synthesis like lignin, phenolic compounds, and some other physiological mechanisms in plants[49] that develops resistance against diseases.

Rhizospheric microbes by their redox activity considerably affect the Mn availability in soil. Some studies have shown that under Mn deficiency P. *fluorescens* and *B. subtilis* when inoculated in crops have been reported for increasing Mn uptake in crops which results in improving lignin production and defense mechanism of crops against some phytopathogens.[50] Some more studies reveal that *Bacillus* cereus improves the yield parameters of wheat like seed size, biomass, and nutrient value of seed by enhancing the availability of Mn.[51] Certain actinomycetes, along with species from the *Streptomyces, Pseudomonas,* and *Bacillus* genera, have also been found to enhance manganese availability in crops.[52] Glomus diaphanum, G. *aggregatum, Bacillus megaterium,*[53] and *Penicillium citrinum*[54] play a significant role in enhancing manganese uptake by plants through their nutrient-solubilizing abilities.

Zinc

Zinc (Zn) is a vital micronutrient necessary for plant growth and reproduction. Insufficient levels of Zn can compromise membrane integrity, impede the production of carbohydrates, cytochromes, auxin, nucleotides, and chlorophyll, and make plants more susceptible to heat stress.[55] It is also responsible for suppressing male fertility in plants.[56] The available fraction of Zn in plants is very limited in soil due to its low persistency and high reactivity. In India, nearly 50% of soils are zinc-deficient, even though zinc is relatively abundant in the soils of the country's semi-arid tropical regions.[55]

Application of inorganic zinc is not an effective solution as up-to 96–99% of applied Zn within 7 days of application becomes insoluble due to soil types and physicochemical reactions[57] and thus becomes unavailable to plants. Excessive utilization of zinc containing fertilizers impairs the absorption of iron and copper. Zinc solubility is strongly influenced by soil pH and moisture levels, which makes the semi-arid areas often zinc-deficient. Soil pH plays a crucial role in determining the microelements availability and even a minor alteration in pH has a considerable effect, as lowering of pH influences Zn availability significantly in plants.[58] Therefore, lowering the soil pH can enhance the availability of zinc to plants. Microbes facilitate the solubilization of metal forms through protons, oxidoreductive

systems, and chelated ligands located on the surface of their cells. Organic acids released by *rhizobacteria* contain some protons which decreases the pH of *rhizospheric* soil[59,60] that facilitates the mobility of Zn. PGPR produces gluconate or some gluconic acid derivatives like 2-keto gluconic acid as reported for *Pseudomonas fluorescence,*[60] 5-keto gluconic acids,[61] and various organic acids[62] which solubilize insoluble zinc. *Bacillus* sp. AZ6 demonstrates the ability to solubilize insoluble forms of zinc by secreting organic acids such as caffeic acid, ferulic acid, cinnamic acid, gallic acid, chlorogenic acid, and syringic acid in a liquid medium.[63]

Rhizobacteria comprising *Rhizobium, Acinobacter, Pseudomonas, Bacillus,* etc. are also considered proficient Zn-solubilizers. *Bacillus* spp. solubilizes ZnO, ZnS and $ZnCO_3$[57] by altering the broth pH. Mostly wheat, rice, maize, oats, and cotton are affected by Zn deficiency.[64] Many genera of both bacteria and fungi are known to improve zinc availability for plants and increase zinc content in cereal crops.[65]

The bioavailability of Zn in the *rhizosphere* has also been reported to increase by microbes secreting Zn-chelating compounds.[66] Chelation has been demonstrated as the primary phenomenon to improve Zn availability in plant roots by *Microbacterium saperdae, Pseudomonas* monteilii and *Enterobacter cancerogenesis.*[67] *Pseudomonas* Sp. (K-1, 96-51), *Azospirillum lipoferum* (JCM-1270, ER-20) and *Azospirillum* sp. (Ca-18) have been documented to solubilize fixed zinc from soil and makes it available for rice for longer duration by secreting chelating substance like ethylene diamine tetra acetic acid (EDTA).[62] It has also been reported that Penicillium bilaji enhance Zn availability to plants through a chelation mechanism.[68] PGPR such as *Pseudomonas fluorescens, Klebsiella* spp., and Serratia marchesense found in soil, solubilizes insoluble form of Zn to soluble form *Pseudomonas.*[69,70] Treatment of seeds with some zinc solubilizing PGPR like *Azospirillum, Pseudomonas,* Burkholderia, *Azotobacter* and Acinetobacter strains have shown potential as plant growth promoters by enhancing attributes such as root volume, shoot height, leaf area, and dry biomass.[71] Some of the effective Zn-enhancing bacterial strains reported in maize are *Bacillus* species AZ6[72] *Pseudomonas,*[73] *Azotobacter* and *Azospirillum.*[44] *Bacillus aryabhattai*

strains MDSR7, MDSR11, and MDSR 14 have been shown to substantially mobilize Zn in soybean and wheat.[74] A few cyanobacteria like Anabaena sp cw1, Providecie sp pw5, Anabaena sp. Cw3 and Calothrix sp. Cw2 has been reported to improve the nutrient quality of wheat grain by improving micronutrients like Zn, Fe, Cu and Mn0.[75] Joshi *et al.*[76] have reported a positive relationship between microbial inoculations and grain yield. The use of microbial inoculants offers multiple advantages, including increased zinc content in the flag leaf and a 50% reduction in nitrogen fertilizer requirements, which helps lower cultivation costs. The study indicated that comparable yields of wheat and maize can be achieved even with a 50% reduction in nitrogen fertilizer application.

Arbuscular mycorrhizal fungi are also found to lower the pH of *rhizospheric* soil, which contributes to the release of zinc from mineral fraction.[77,65] Mycorrhizal fungi capable of solubilizing zinc prevent various fungal and bacterial diseases[64] by elevating the Zn level in plants. According to the findings of Imran *et al.*,[68] supplementing essential micronutrients—particularly zinc (Zn)—effectively mitigated growth inhibition and oxidative leaf damage in maize seedlings exposed to low root zone temperatures.[78] Inoculation with PGPM, such as cyanobacteria, bacterial strains, and biofilms, can significantly enhance the concentration of micronutrients in the *rhizosphere* of different maize hybrids.[79]

Zn application in soil minimizes the chances of infections caused by Fusarium graminearum and *Gaeumannomyces graminis* in wheat. Zn protects plants by detoxifying the superoxide radicals that cause oxidative damage to membranes.[80] Plants growing in calcareous and sodic soils contains large amount of insoluble $ZnCO_3$ (zinc carbonate) that reduces Zn availability for plants. So, the plants growing in these regions suffer more with Zn deficiency as compared to others.[81]

Copper
Copper (Cu) is required in lignin synthesis as well as carbohydrate and nitrogen metabolism. It is also essential in photosynthesis and plant respiration. Due to its necessity for maintaining cell wall strength and preventing wilting; therefore, its deficiency in plants leads to symptoms like stunted growth,

dieback of stems and twigs, and leaf yellowing, primarily due to impaired lignin production.

From a nutritional standpoint, mycorrhiza is the most prevalent and significant symbiotic association between roots and fungi residing in soil. Virtually all plants of economic importance form mycorrhizal association. This symbiotic relationship came into existence over 350 million years[82] ago and has played beneficial roles in the colonization of land plants. Usually, the intra-radical mycelium of AM fungi profusely grows in the cortical region of the host plant roots. Extra radical arbuscular mycorrhiza hypha multiplies in the soil around the root and easily absorbs micro and macro nutrients such as Nitrogen, phosphorus, zinc, and copper and transports them into the host plant.[83] Although well known for phosphorus uptake, the arbuscular mycorrhizal fungus also enhances the availability of other important micronutrients like Zn and Cu and macro element K.[84] About 30 to 150% increase in dry weight is observed in tree seeding infected with AM. Enrichment of nutrients in plants is of concern where either the soil's nutrient content is low or has heterogeneous distribution of nutrients.[85] AM fungi are among the few significant soil microbes recognized for their ability to absorb nutrients with limited mobility (e.g. P, Zn, NH_4+etc),[86] as the extra radical AM hyphae can provide the nutrients by exploring additional soil regions extending beyond the nutrient-depleted zone formed around the root. *Rhizobacteria* that are active in the supply of Cu are *Pseudomonas*, *Bacillus*, Sphingomonas, *Arthrobacter,* Stenotrophomonas, etc, but are mostly studied in natural phytoremediation perspective in polluted soils.[87] They help in maintaining homeostasis in the *rhizosphere*.

Molybdenum
In aqueous solution, Molybdenum (Mo) mainly occurs as molybdate ion MoO_4^{2-}. Among all identified micronutrients, Mo has the lowest requirement in plants, primarily associated with its function in nitrogen metabolism. The enzymes like dinitrogenase and nitrate reductase require molybdenum for their function. A plant's molybdenum requirement is therefore related to some degree to the form of nitrogen supply. The occurrence of molybdenum deficiency varies significantly among species, with a notable prevalence in legumes, Brassicaceae family

members, and maize. This deficiency is intensified in acidic soils with elevated iron precipitates, as these soils strongly absorb the molybdate ion. Bacterial genera like *Bacillus*, *pseudomonas*, *Citrobacter*, *Leptothrix*, *Acidobacter*, *Nitrospira* and *Firmicutes*, are known to make Mo available to plants by a similar mechanism as Fe, by producing Mo-binding siderophores, and therefore, facilitating towards the uptake under limiting conditions.[88] Limited information is accessible regarding molybdenum uptake in the cropping system.

Chlorine

Chloride ions (Cl⁻) are widely distributed and exhibit high solubility, making their deficiency a rare occasion. Manganese, in conjunction with chloride, is necessary for the oxygen-evolving process that takes place in photosynthesis. Chloride (Cl⁻) functions as an extremely mobile anion and serves as the primary counter-ion to diffusing cations, playing a crucial role in preserving electrochemical balance across cell membranes. It serves as the primary osmotically active solute within the vacuole and is essential for cell division. Research on the role of microbes in chloride uptake is limited as plants readily absorb chloride, and many accumulate chloride ions well beyond their minimal requirement. Chloride-deficient plants often show stunted growth, wilting at the tips of leaves, and *widespread chlorosis*.[89] *Bacillus megaterium* and *Pantoea agglomerans*[90] contribute to improved chloride uptake in plants by facilitating ion transport and enhancing root absorption efficiency.

Nickel

Nickel (Ni) is a plentiful metallic element that is readily absorbed by plant roots. Approximated 200ng of nickel is needed for a plant to go through its entire life cycle, a demand that is typically satisfied by the initial nickel content present in the seed.[91] While the precise role of Ni in plants remains somewhat unclear, it is potentially linked to the nitrogen requirement during the germination of seeds. It is known to be a component of two enzymes—urease and hydrogenase. A deficiency in nickel can result in reduced urease activity in plants. *Sphingomonas macrogoltabidus, Microbacterium liquefaciens,* and *Microbacterium arabinogalactanolyticum* enhance nickel uptake in plants by promoting metal solubilization.[92]

Trace Elements

Trace elements play an important role in plant nutrition. Despite being required by plants in minute quantities, elevated concentrations of these elements can be toxic to plants. Moreover, their lack and an excess both lead to severe disease symptom in plants. *Rhizospheric* microbes are mostly studied for land management in trace element contaminated soils. Trace elements like Selenium (Se), Sodium (Na), and Cobalt (Co) required by plants in trace amounts[93] are discussed below.

Sodium

Sodium (Na) stimulates cell expansion leading to growth, and can partially replace potassium as an osmotically active solute. The accumulation of solutes such as K^+ or Na^+ inside the cell reduces its water potential and increases its solute potential which leads to enter the water into the cell. This results in an increase in turgor pressure. This pressure drives cell growth by promoting cell expansion, thereby contributing to growth at both the tissue and whole-plant levels.[94] Mainly increase in sodium concentration is directly related to the salinity of soil.[95] Saline stress in plants adversely impacts fundamental processes including photosynthesis, protein synthesis, as well as energy and lipid metabolism.[96] White and Broadley[97] reported that the quantity of salt in a cell more than it's carrying capacity leads to cell dehydration and finally death.

Selenium

Selenium (Se) is a highly soluble and essential element for plants. At its low concentration, it shows free radicals scavenging activity by increasing antioxidant enzymes such as Superoxide Dismutase (SOD) activity. It contributes to the formation cell membrane and amending photosynthetic systems by improving the formation of chloroplast components. It also plays a role in mitigating abiotic stress factors such as cold,[98] drought,[99] temperature,[100] and heavy metal[101] in plants, although at high concentrations, it becomes toxic. It is reported that on application of Se (1 mg/L) pears and peaches, the quality of fruit was improved.[102] Additionally, Se concentration, extending up to 5 mg/L, have been found beneficial for certain Se-accumulating species, including *Spirulina platensis*, red seaweed, and *Pteris vittata*.[103] Thus, plants demonstrate a variation in its accumulation effects.

Cobalt

Cobalt (Co) is a component of various enzymes and proteins, plays an important role in plant metabolism. It is also an essential part of cobalamin (vitamin B12), which is necessary for the functioning of several enzymes involved in nitrogen (N_2) fixation.[104] Cobalt at its higher concentration interferes with the metabolism of plants. At its higher concentration, it inhibits seed germination, plant growth, and photosynthesis.[105] Cobalt is considered both a heavy metal and a micronutrient, and its precise regulation is important for normal plant growth and development.

Conclusion

Optimizing nutrient availability is crucial for maximizing crop yield and quality. While traditional fertilization methods aim to achieve this, their effectiveness can be limited, and their production and application often lead to significant environmental concerns. Fortunately, a vast array of soil microbes offers a more environment friendly pathways to fulfill plant nutritional needs. Microbe-dependent pathways for micronutrient uptake in plants involve enhanced solubilization of insoluble micronutrients via organic acid secretion, siderophore production for iron chelation, enzymatic release of bound nutrients, and stimulation of root growth through phytohormones. Additionally, nitrogen-fixing microbes also contribute to nutrient supply through asymbiotic/symbiotic nitrogen fixation. In contrast, microbe-independent pathways in plants while solely being depend on plant roots for absorbing nutrients from the soil solution, is often limited by soil nutrient solubility, availability and plant vigour. These pathways include direct ion uptake, root exudation of organic acids, and root morphological adaptations to improve nutrient acquisition. It is notable that the *rhizospheric* microbes not only help in plant nutrient uptake, particularly the recalcitrant nutrients but also influence the soil properties. Analyzing the root exudates can help decrypt the communication between plants and microbes. Plant's nutritional status actively influences its interactions with microbes, demonstrating the plant's role in initiating or deterring these associations. By unravelling the intricate signaling networks among microbes within the root microbiome, we can gain a deeper understanding of how microbial enhancements to plant nutrition function, especially when plants face various biotic and abiotic stresses. This knowledge will be key to developing more sustainable and effective agricultural practices. Many breakthroughs have been made in identifying the beneficial microbes but the complex plant-microbe interaction needs to be addressed more particularly by comparative genomic approaches to identify plant genes that shape the *rhizospheric* microbiome. Major gaps lie in understanding these signaling and the metabolic activities they share, which needs to be addressed to fully utilize their potential.

Conflict of Interest

The authors do not have any conflict of interest.

Data Availability Statement

All datasets generated or analyzed during this study are included in the manuscript.

Ethics Statement

This research did not involve human participants, animal subjects, or any material that requires ethical approval.

Informed Consent Statement

This study did not involve human participants, and therefore, informed consent was not required.

Permission to Reproduce Material from other Sources

Not Applicable

Author Contributions

- **Richa Raghuwanshi:** Conceptualization, Funding Acquisition, Resources, Supervision
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- **Jay Kishor Prasad:** Data Collection, Analysis,
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