bacteria

MDPI

Communication

Enhancing Manganese Availability for Plants through Microbial Potential: A Sustainable Approach for Improving Soil Health and Food Security

Bahman Khoshru [1,*], Debasis Mitra [2], Alireza Fallah Nosratabad [1], Adel Reyhanitabar [3], Labani Mandal [4], Beatrice Farda [5], Rihab Djebaili [5], Marika Pellegrini [5], Beatriz Elena Guerra-Sierra [6], Ansuman Senapati [7], Periyasamy Panneerselvam [7,*] and Pradeep Kumar Das Mohapatra [2,*]

1 Soil and Water Research Institute (SWRI), Agricultural Research, Education and Extension Organization (AREEO), Karaj 31785-311, Iran; rezafayah@yahoo.com
2 Department of Microbiology, Raiganj University, Raiganj 733134, West Bengal, India; debasismitra3@raiganjuniversity.ac.in
3 Department of Soil Science, Faculty of Agriculture, University of Tabriz, Tabriz 51664, Iran; areyhani@tabrizu.ac.ir
4 Department of Agriculture (Plant Breeding and Genetics), Midnapore City College, Midnapore 721129, West Bengal, India; labaniruna@gmail.com
5 Department of Life, Health and Environmental Sciences, University of L'Aquila, 67100 L'Aquila, Italy; beatrice.farda@graduated.univaq.it (B.F.); rihab.djebaili@guest.univaq.it (R.D.); marika.pellegrini@univaq.it (M.P.)
6 Grupo Microbiota, Facultad de Ciencias Naturales, Universidad de Santander, Bucaramanga 680002, Colombia; bguerra@udes.edu.co
7 Crop Production Division, Indian Council of Agricultural Research—National Rice Research Institute, Cuttack 753006, Odisha, India; asenapati89@gmail.com
* Correspondence: bahmankhoshru@yahoo.com (B.K.); panneerselvam.p@icar.gov.in (P.P.); pkdmvu@gmail.com (P.K.D.M.)

Abstract: Manganese (Mn) is essential for plant growth, as it serves as a cofactor for enzymes involved in photosynthesis, antioxidant synthesis, and defense against pathogens. It also plays a role in nutrient uptake, root growth, and soil microbial communities. However, the availability of Mn in the soil can be limited due to factors like soil pH, redox potential, organic matter content, and mineralogy. The excessive use of chemical fertilizers containing Mn can lead to negative consequences for soil and environmental health, such as soil and water pollution. Recent research highlights the significance of microbial interactions in enhancing Mn uptake in plants, offering a more environmentally friendly approach to address Mn deficiencies. Microbes employ various strategies, including pH reduction, organic acid production, and the promotion of root growth, to increase Mn bioavailability. They also produce siderophores, anti-pathogenic compounds, and form symbiotic relationships with plants, thereby facilitating Mn uptake, transport, and stimulating plant growth, while minimizing negative environmental impacts. This review explores the factors impacting the mobility of Mn in soil and plants, and highlights the problems caused by the scarcity of Mn in the soil and the use of chemical fertilizers, including the consequences. Furthermore, it investigates the potential of different soil microbes in addressing these challenges using environmentally friendly methods. This review suggests that microbial interactions could be a promising strategy for improving Mn uptake in plants, resulting in enhanced agricultural productivity and environmental sustainability. However, further research is needed to fully understand these interactions' mechanisms and optimize their use in agricultural practices.

Keywords: manganese (Mn); microbial interactions; soil health; sustainable agriculture; plant growth promotion

Citation: Khoshru, B.; Mitra, D.; Nosratabad, A.F.; Reyhanitabar, A.; Mandal, L.; Farda, B.; Djebaili, R.; Pellegrini, M.; Guerra-Sierra, B.E.; Senapati, A.; et al. Enhancing Manganese Availability for Plants through Microbial Potential: A Sustainable Approach for Improving Soil Health and Food Security. *Bacteria* **2023**, *2*, 129–141. https://doi.org/10.3390/bacteria2030010

Academic Editor: Bart C. Weimer

Received: 6 June 2023
Revised: 23 July 2023
Accepted: 4 August 2023
Published: 6 August 2023

1. Introduction

Manganese (Mn) is an essential micronutrient for plants, playing a crucial role in soil–plant–microbial interactions. It is involved in various physiological and biochemical processes, making it indispensable for plant growth and development [1,2]. It is required in relatively small amounts compared to macronutrients like nitrogen, phosphorus, and potassium, but its availability is still vital for optimal plant growth and development. Mn acts as a cofactor for several enzymes involved in essential plant processes [3]. For example, it is required for the activation of enzymes involved in photosynthesis, respiration, and nitrogen metabolism. Mn is a cofactor for the enzyme superoxide dismutase, which protects plants from oxidative stress caused by reactive oxygen species. Mn plays a critical role in the water-splitting complex of photosystem II (PSII) in chloroplasts. It participates in the oxidation of water molecules during the light-dependent reactions in photosynthesis, contributing to the production of oxygen and energy-rich molecules like ATP [4,5]. Mn is involved in the synthesis and activation of antioxidants, such as ascorbate peroxidase and catalase, which help plants combat oxidative stress. These enzymes scavenge harmful reactive oxygen species generated during various metabolic processes [6,7]. Mn is essential for the uptake and transport of other nutrients within plants [1]. It is involved in the conversion of nitrate (NO_{3^-}) to ammonia (NH_3) during nitrogen assimilation. Mn also influences the uptake and utilization of iron (Fe), calcium (Ca), and magnesium (Mg) by plants. It influences cell division and elongation, thereby affecting root architecture and nutrient acquisition efficiency [8]. Mn deficiency can lead to stunted root growth and reduced nutrient uptake [9]. Mn plays a role in the plant's defense against pathogens [10,11]. It contributes to the synthesis of lignin, a structural component of cell walls that acts as a physical barrier against invading pathogens. Mn also enhances the activity of defense-related enzymes, such as peroxidases, which participate in the plant's immune response. Mn availability in soil affects microbial communities and their activities [12]. Some soil bacteria and fungi are capable of solubilizing and mobilizing Mn, making it more accessible to plants [13]. Conversely, Mn availability can influence microbial growth and metabolic processes, indirectly affecting nutrient cycling and soil health. It is worth noting that while Mn is essential for plant growth, excessive levels can be toxic [14]. High Mn concentrations in soil can inhibit nutrient uptake and cause physiological disorders in plants [14,15]. Therefore, maintaining an optimal Mn balance is crucial for achieving healthy soil–plant–microbial interactions. Mn toxicity can occur in acidic soils or as a result of the over application of Mn-containing fertilizers [8,16–18]. Soil testing and proper nutrient management practices can help maintain the right Mn levels for healthy plant growth and sustainable management of agricultural crop production.

This review highlights the crucial role of Mn as an essential element for plant growth and development, along with its various oxidation states in soil. This article explores the factors affecting Mn cycling in soil, such as the climatic conditions, pH, organic matter content, and the type and quantity of the microorganisms present. It also discusses the different types of microorganisms involved in the Mn cycle, including Mn-oxidizing/reducing bacteria, fungi, and archaea, and provides a visual representation of their contributions to the Mn cycle. This article emphasizes the importance of understanding the Mn cycle in soil and the role of microorganisms in maintaining soil health and nutrient cycling.

2. Manganese

2.1. Chemistry

Manganese is a transition metal, with atomic number 25 and the symbol Mn in the periodic table. It is a silvery-gray metal found in nature as a free element or in combination with other elements, such as oxygen, sulfur, and silicon [19,20]. Mn is the twelfth most abundant element in the Earth's crust and is widely distributed in rocks, soil, water, and air [21]. Mn has a wide range of oxidation states from −3 to +7, but the most common oxidation states are +2, +3, +4, +6, and +7 [19]. Mn is a relatively reactive metal that readily forms compounds with other elements. It reacts with oxygen in the air to form

Mn oxide (MnO) or Mn dioxide (MnO_2), depending on the oxidation state of the Mn. Mn also reacts with halogens, sulfur, and nitrogen to form various compounds such as Mn chloride ($MnCl_2$), Mn sulfide (MnS), and Mn nitride (Mn_3N_2) [19]. Mn compounds exhibit a wide range of colors, depending on the oxidation state and coordination geometry of the Mn [14]. For example, Mn^{2+} compounds are usually pale pink or lavender, while Mn(III) compounds are usually brown or black. Mn(IV) compounds are usually dark brown or black, and Mn(VII) compounds are usually purple or pink [11]. Mn also forms complexes with various ligands, such as water, ammonia, and organic molecules, which can affect its chemical and physical properties [19]. In aqueous solutions, Mn can exist in various forms, such as Mn^{2+}, Mn^{3+}, Mn^{4+}, Mn^{6+}, and Mn^{7+}, depending on the pH and redox potential of the solution [22]. Mn^{2+} is the most stable and soluble form of Mn in aqueous solutions and is the predominant form in most natural waters [21]. Mn^{3+} and Mn^{4+} are less stable and more insoluble than Mn^{2+} and are usually found in soils and sediments [10]. Mn^{7+} is a highly reactive and unstable form of Mn that is rarely found in nature [19]. Mn compounds are used in various industrial applications, including the production of steel, batteries, ceramics, and fertilizers. Mn is also used as a catalyst in chemical reactions and as a pigment in paints and dyes. Moreover, Mn has potential applications in medicine, as it has antioxidant and anti-inflammatory properties [19].

2.2. Mobility in the Soil

Biological activity, including microbial activity and plant root exudates, can play an important role in the mobility and transformation of Mn in soil [1,12]. As mentioned earlier, microbes can solubilize insoluble Mn and make it more available for plants through mechanisms such as the production of organic acids and the release of protons and, ultimately, reducing the pH [12,13]. They can also contribute to the solubilization and mobilization of Mn by reducing Mn to Mn^{2+} [13]. Some microbes also reduce the mobility of Mn in the soil by oxidizing it [13]. In similar conditions, some plants can also increase the solubility of manganese by reducing the pH and can also absorb Mn from the soil and transfer it to different parts of the plant, which can lead to a change in the distribution of Mn in the soil and rhizosphere [1].

Environmental factors, such as the weather, precipitation, soil moisture, temperature, and wind intensity, can also play a role in the mobility and transformation of Mn in soil [21]. Precipitation and soil moisture can affect Mn mobility by increasing the availability of Mn in soil solutions. During wet periods, Mn can dissolve in soil water and become more mobile, which can lead to leaching and loss from the soil. Conversely, during dry periods, Mn can become immobilized in soil minerals, reducing its availability for plant uptake [20]. Temperature can also affect Mn mobility in soil. At higher temperatures, microbial activity can increase, leading to more Mn reduction and increased solubility. However, high temperatures can also cause Mn oxide minerals formation, which can immobilize Mn in soil [19]. Wind intensity can affect Mn mobility by causing erosion and soil movement, which can lead to the redistribution of Mn in soil. Erosion can also lead to the loss of Mn from soil and its deposition in other areas [21].

Soil properties, including the soil pH, redox potential, organic matter content, iron and aluminum content, and soil cation exchange capacity (CEC), can play a role in the mobility and transformation of Mn in soil [20–22]. Soil pH can affect Mn availability by changing the speciation of Mn in soil. At low pH, Mn is more soluble and available for plant uptake, while at high pH, Mn can form insoluble precipitates and become less available [22]. Redox potential can also affect Mn availability by controlling the oxidation state of Mn in soil. Under reducing conditions, Mn^{3+} and Mn^{4+} can be reduced to Mn^{2+}, which is more soluble and available for plant uptake. Under oxidizing conditions, Mn^{2+} can be oxidized to Mn^{3+} and Mn^{4+}, which are less soluble and less available [21]. The content of organic matter can affect the availability of Mn by increasing its solubility in the soil. Organic matter can act as an electron donor and create negative redox potential, and then Mn is converted into a reduced form and its solubility increases [20]. On the other hand, in the process of decomposition of organic matter, some of the complexed Mn could be released [20]. Iron (Fe), aluminum (Al), Copper (Cu), and Cobalt (Co) content can also affect Mn availability for plants. Fe and Cu can compete with Mn for adsorption sites on soil particles and oxidize Mn^{2+} to Mn^{3+} and Mn^{4+}, which are less available for plant uptake. Co can affect Mn behavior in soil by influencing microbial activity [16,19–22]. Soil CEC can affect Mn availability by controlling the adsorption and desorption of Mn in soil. Soil with high CEC can absorb more Mn and make it less available for plant uptake [20,22]. Crop type can affect Mn availability in the soil through differences in root exudates and nutrient uptake patterns [16]. Soil and water management practices, and the use of fertilizers and chemicals can also affect Mn mobility in the soil [21,22].

Manganese extraction as a human activity and its side effects, including air and water pollution and the entry of waste materials into the soil, could have significant effects on the mobility and state of Mn in the soil. Mn extraction activities can lead to the release of Mn in the environment and increase its concentration in the soil and the environment [23–29]. Some factors affecting the mobility of Mn in soil are presented in Figure 1.

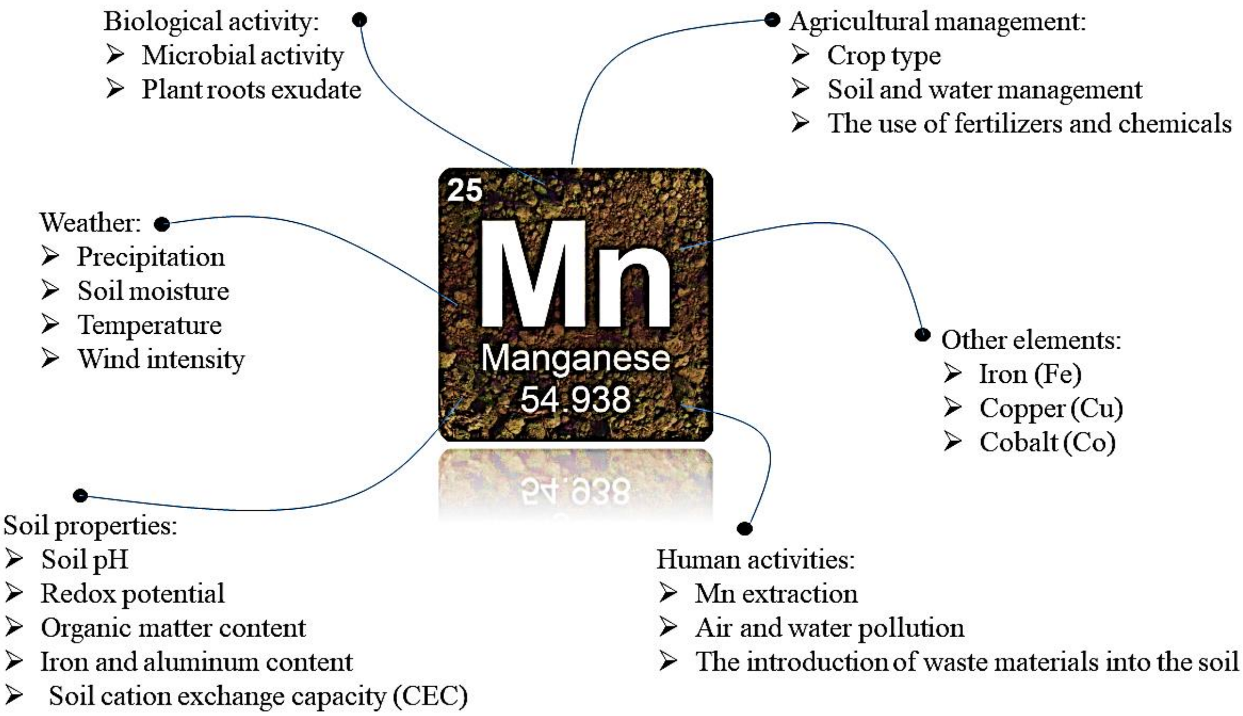

Figure 1. The factors affecting the mobility of Mn in soil [19–22,29].

2.3. Sources and Environmental Impact

The widespread use of Mn in various industrial applications, such as the production of steel, batteries, ceramics, and fertilizers, is mainly derived from deep-sea Mn ore clusters, rock crust, soil, and freshwater, with reserves concentrated in developing countries, such as Australia, Russia, India, Brazil, and South Africa [12], and it exists in both organic and inorganic forms in rocks, soil, water, and air, with the concentration varying widely depending on the geology and hydrology of the region; however, the extraction, processing, and disposal of Mn ore and products can have negative environmental effects, such as soil degradation, air and water pollution, including Mn pollution of the ecological system due to the formation of rock storage yards from the production of waste rocks during continuous mining in the Mn ore area, with Mn-containing leachate migrating into the soil, surface, and underground water in the mining area through rainfall leaching and infiltration [15,21].

2.4. Fertilizers

Chemical fertilizers containing Mn are commonly used to supplement the soil with this essential micronutrient. Table 1 shows different sources of Mn (including manganese sulfate, manganese chloride, manganese carbonate, manganese oxide, manganese oxide, manganese chelate, and manganese ferrite), their chemical formulas and the percentage of Mn content. Mn sulfate is the most commonly used form of Mn fertilizer due to its high solubility and availability to plants [22]. The primary source of Mn for fertilizer production is oxide manganese (MnO) ores of sedimentary origin, which are categorized into three types based on their iron and basic substance content. Manganese ores contain 40% Mn and less than 10% iron, ferromanganese ores contain 5–40% Mn and 10–35% iron, and Mn iron ores contain less than 5% Mn [19]. In oxide ores, manganese compounds are poorly soluble in acids, making the use of carbonate manganese ores and industrial waste more effective for fertilizer production [22]. Industrial waste must undergo a reduction roasting stage and contain manganese in the form of MnO; typically waste products from manganese ore enterprises contain 10–18% Mn [22].

Table 1. Different sources of chemical fertilizers and their manganese content.

Formula	Source	Mn Content (%)
$MnSO_4\ 3H_2O$	Manganese Sulfate	26–28
$MnCl_2$	Manganese Chloride	17
$MnCO_3$	Manganese Carbonate	31
MnO_2	Manganese Oxide	63
MnO	Manganese Oxide	41–68
MnEDTA	Manganese Chelate	12
-	Manganese Frits	10–25

Fertilization with Mn salts at the soil surface is often not effective because soluble Mn^{2+} is rapidly converted to plant-unavailable Mn oxides, especially in sandy alkaline soils. However, it has been argued that the use of Mn fertilizers in the soil can be an effective way to reduce Mn deficiency, but only if the soil pH is also corrected [15]. Foliar application of Mn can provide enough Mn to overcome Mn deficiency, but this strategy is expensive and often impractical for farmers on marginal lands. In addition, Mn foliar application is only effective for a limited period of time, because Mn has very little mobility in the plant and is not transferred from older leaves to Mn-deficient young leaves [19]. On the other hand, Mn toxicity can occur in poorly drained and highly acidic soils, where it is usually associated with other acidity-related soil fertility problems, such as aluminum toxicity and deficiencies of calcium (Ca), magnesium (Mg), and molybdenum (Mo) [21]. While manganese chemical fertilizers can be effective in correcting manganese deficiency in plants, their excessive use can lead to pollution and environmental hazards. Excessive use of manganese fertilizers can lead to soil contamination, which can affect soil quality and reduce plant growth. Manganese can penetrate groundwater and surface water, and lead to water pollution and impact on aquatic ecosystems [23]. In order to avoid the adverse effects of manganese chemical fertilizers on the environment, it is necessary to use them wisely and follow the recommended dosage. In addition, it is recommended that other environmentally friendly sources are used, such as organic products, including compost, animal manure, and microbial fertilizers, etc., which can increase soil fertility and improve plant growth [12,13,20].

2.5. The Biological Role

Manganese as an essential element in almost all living organisms performs two different functions: as an enzyme cofactor or as a metal with catalytic activity in biological clusters [1,12,25–27]. In humans, Mn acts as a cofactor for a variety of enzymes, including arginase, glutamine synthetase, pyruvate carboxylase, and manganese superoxide dismutase (Mn-SOD) [27]. However, Mn deficiency in humans is rare compared to other essential micronutrients, such as iron (Fe) and zinc (Zn) [27].

Manganese is included in most broad-spectrum plant fertilizers due to its role in diverse processes in a plant's life cycle, such as photosynthesis, respiration, scavenging of ROS, reactive oxygen species, pathogen defense, and hormone signaling, and its importance in photosynthetic oxygen evolution in chloroplasts, where the oxygen-evolving complex (OEC) in photosystem II contains four atoms of Mn and is responsible for the terminal photooxidation of water during the light reactions in photosynthesis [1,2,23]. Although Mn is an essential element for plant growth, excessive Mn poses a major abiotic stress in plant agriculture worldwide. It decreases the photosynthetic rate, which regulates the biosynthesis of photosynthetic pigments and regulates the stomatal conductance and transpiration rate, leading to a decline in crop production and quality. Moreover, Mn in excess can poison plants by generating ROS and triggering oxidative stress, which could cause lipid peroxidation and damage photosynthetic pigments if the ROS are not well scavenged [8,14,17].

Manganese superoxide dismutase (Mn-SOD) is the type of SOD present in eukaryotic mitochondria, and is also in most bacteria [6,7]. The Mn-SOD enzyme is probably one of the most ancient, because nearly all organisms living in the presence of oxygen use it to deal with the toxic effects of superoxide (O_{2^-}), formed from the 1-electron reduction of dioxygen [7]. The exceptions include *Lactobacillus plantarum* and related *lactobacilli*, which use a different nonenzymatic mechanism with Mn^{2+} ions complexed with polyphosphate, suggesting a path of evolution for this function in aerobic life [7,12]. A high amount of Mn could affect microorganisms by influencing their function, principal component, variation in the typical variables, stability, and diversity [12]. Studies show that Mn-contaminated soil has significantly different microbial communities than normal soil, with increased variation and decreased stability in the microbial community when the soil Mn^{2+} concentration exceeds 300 mg/kg [12]. Many enzymatic systems need Mn to function, but in high levels, Mn can become toxic. Mn can affect the renewal of immunocytes and their functionality, such as phagocytosis and the activation of pro-phenoloxidase, suppressing the organisms' immune systems. This causes the organisms to be more susceptible to infections [18].

2.6. Manganese in Plants

Manganese plays a vital role in various physiological and biochemical processes, such as chlorophyll synthesis, photosynthesis, cellular respiration, the activation of enzymes involved in carbohydrate metabolism, nitrogen metabolism, and the detoxification of superoxide radicals [12]. Mn deficiency in plants can lead to reduced growth, chlorosis, necrosis of the leaves, and reduced resistance to diseases and pests [29]. Mn-deficient plants show chlorosis in the interveinal areas of young leaves due to impaired chlorophyll synthesis and photosynthesis. In addition, Mn deficiency can also lead to weakened stems and reduced plant stability [23]. On the other hand, excessive amounts of Mn can be toxic to plants and cause oxidative stress and damage to cell membranes and photosynthetic pigments [24]. Also, Mn toxicity in plants can lead to reduced growth, chlorosis, and necrosis of the leaves, as well as reduced root growth and absorption of nutrients. The symptoms of Mn toxicity vary depending on the plant species and the level of Mn in the soil. For example, in rice plants, Mn toxicity can cause leaf browning, while in soybean, it can lead to leaf necrosis and reduced nodulation [30].

3. Impacts of Different Microbes on the Mn Cycle in Soil

Soil is a complex ecosystem that includes various types of living microorganisms, including bacteria, fungi, and archaea. These organisms play crucial roles in nutrient cycling and soil health [31–34]. One of the essential elements in the soil is Mn, which is highly important for plant growth and development. The Mn cycle is a complex process that involves various chemical and biological reactions [35].

As mentioned in the previous sections, Mn exists in soil in four oxidation states, Mn^{2+}, Mn^{3+}, Mn^{4+}, Mn^{6+}, and Mn^{7+} and microbes are able to convert manganese from one oxidation state to another through oxidation and reduction reactions [36]. Bacteria that are involved in Mn oxidation are known as Mn-oxidizing bacteria (MOB). These bacteria oxidize Mn from the Mn^{2+} state to Mn^{3+}, Mn^{4+} or Mn^{6+}, which can lead to the formation of Mn oxides, such as birnessite and cryptomelane [37]. In addition, there are Mn-reducing bacteria that convert Mn from the oxidized state to the reduced state, Mn^{2+} [38]. In addition, fungi and archaea also play a role in the cycle of Mn in the soil. Some fungi can oxidize Mn^{2+} to Mn^{3+} or Mn^{4+}, and also help in the formation of Mn oxides, such as birnessite and birovite [39].

Manganese in the oxidation state can be converted to Mn^{2+} through chemical or biological processes that involve protons and electron-carrying reducing agents produced by microorganisms, plant roots, or the decomposition of organic matter [40,41]. Several microorganisms capable of reducing Mn have been identified, including *Arthrobacter*, *Acinetobacter*, *Achromobacter*, *Aspergillus*, *Bacillus*, *Clostridium*, *Enterobacter*, *Lysinibacillus*, *Micrococcus*, *Pseudomonas*, and *Staphylococcus* [30,32,40–51]. Inoculation with Mn-reducing microorganisms, particularly bacteria, has been shown to enhance Mn uptake and plant growth in Mn-deficient soil [38]. Mn-reducing bacteria are also known as Mn-solubilizing bacteria (MSB), which promote Mn dissolution by protonating metal anions and producing organic acids that form a soluble complex of Mn ligands [38]. Recently, it was reported that inoculation with Mn-resistant *Bacillus cereus* WSE01 resulted in plant growth promotion and Mn accumulation in *Myriophyllum verticillatum* [40].

Various factors can affect the Mn cycle in soil, including the climatic conditions, pH, organic matter content, and the type and quantity of the bacteria and fungi [51–57]. For example, the soil temperature and moisture can directly affect the rate of chemical and biological reactions in the Mn cycle. In hot and dry weather conditions, the rate of Mn oxidation and reduction reactions decreases, while in moist and cool conditions, the rate increases [36]. Moreover, the soil pH can also have an impact on the Mn cycle in soil. In acidic pH, Mn reduces to the Mn^{2+} state, while in basic pH, it can be oxidized to the Mn^{4+} state [35]. Additionally, the presence of organic matter in soil can affect the Mn cycle. The presence of organic matter increases the activity of bacteria and fungi, which can lead to an increase in the rate of Mn oxidation and reduction reactions [39]. Finally, the type and quantity of bacteria and fungi can also affect the Mn cycle in soil (Table 2). Some bacteria and fungi are capable of oxidizing Mn, while others can reduce it (Figure 2).

Table 2. Mechanism of microbes to increase Mn motility.

Microbe Type	Microbe Name	Mechanism Effect on Mn	References
Bacteria	*Rhizobium* sp.	Organic acid production	[41,45]
Bacteria	*Azospirillum* sp.	Production of organic acid	[46]
Fungi	*Aspergillus niger*	Organic acid production	[17,40]
Fungi	*Penicillium* sp.	Organic acid production	[47]
Fungi	*Rhizopus* sp.	Production of organic acid	[48]
Bacteria	*Bacillus* sp.	Altering soil pH	[49]
Fungi	*Trichoderma* sp.	Enzymatic breakdown of organic matter	[50]
Bacteria	*Pseudomonas* sp.	Various	[51,52]
Bacteria	*Streptomyces* sp.	Root association for increased uptake	[53]
Fungi	*Glomus* sp.	Root association for increased uptake	[54]
Bacteria	*Bradyrhizobium* sp.	Symbiotic relationship with leguminous plants	[41,55]
Fungi	*Laccaria* sp.	Symbiotic relationship with plants	[40,56]

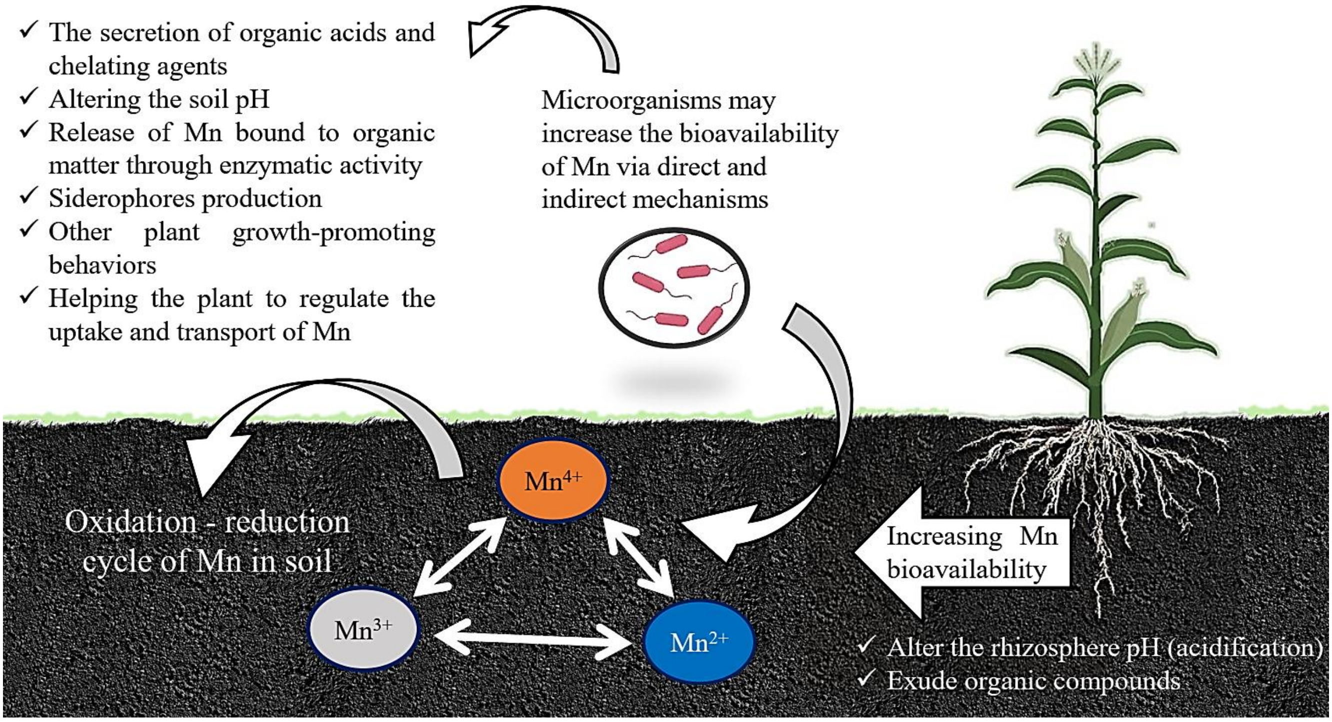

Figure 2. Effect of microbes on Mn cycle in soil and plant [57–60].

Mechanism of Microbes to Increase Mn Bioavailability for Plants

Mn is often present in the soil in an insoluble form, which makes it difficult for plants to absorb. In this regard, microbes play a crucial role in increasing the bioavailability of Mn for plants (Table 2, Figure 2). Some bacteria and fungi use the secretion of organic acids, chelating agents, and ligands to solubilize insoluble manganese compounds. These organic acids and chelating agents form complexes with Mn, which makes it more soluble and available for plants. For example, some fungi such as *Aspergillus* niger, *Penicillium* sp., and *Rhizopus* sp., are known to produce organic acids, such as citric, oxalic, formic, pyruvic, salicylic, and gluconic acid that cause a significant reduction in soil pH, which plays an important role in the conversion of MnO_2 into the plant-available Mn^{2+} form [40–45,61–67]. Sometimes the solubilization of insoluble sources containing elements such as phosphorus, potassium, iron, and zinc by MSB strains through the production of organic acids, such as 2-ketogluconic, acetic, citric, and gluconic, etc., is also the reason for the solubilization of Mn [32,39,41,45]. Such organic acid production by various types of bacteria is autonomous of their genetic relatedness, and each strain has its specific capability for producing organic acids during the solubilization of inorganic minerals [43,44,60–62].

Enzymatic reduction of Mn^{4+} oxidized Mn^{2+} serves as a terminal electron acceptor for aerobic and facultative anaerobic bacteria in the form of respiration and reduced Mn^{2+} concentration to satisfy their nutritional needs [38]. The extracellular heme or flavin enzyme called cellobiose dehydrogenase plays a role in the redox cycling of Mn in nature and can reduce insoluble MnO_2 into soluble Mn^{2+} [38,47]. The production of inorganic compounds, including ferrous iron (Fe^{2+}) and sulfide (S^{2-}), during anaerobic respiration, or the production of H_2O_2, during aerobic respiration, also causes a reduction in Mn^{4+} [38]. Additionally, some microbes can produce enzymes that breakdown complex organic matter in the soil, releasing Mn that is bound to organic matter [40]. Moreover, some microbes can also produce siderophores, which are iron-chelating compounds that can also chelate Mn, making it more available for plants [34,40]. Furthermore, some bacteria and fungi have been found to form symbiotic relationships with plants, which further enhances the bioavailability of Mn for plants [33,44]. In addition to increasing the bioavailability of Mn for plants, microbes also play a role in regulating the uptake and transport of Mn by plants.

Also, some microbes can produce compounds such as phytohormones that stimulate the growth of plants, which can enhance the uptake of Mn by the plant roots [40,42].

4. Biofertilizers with Mn

Mn is an essential micronutrient required by plants for numerous physiological processes. However, its availability to plants is often limited in soil due to its insolubility under normal soil pH conditions. This has led to the development of various strategies to improve Mn availability to plants, one of which is the use of biofertilizers [32,60].

Biofertilizers contain beneficial microorganisms, such as plant growth promoting rhizobacteria (PGPR), and arbuscular mycorrhizal fungi (AMF), which are added to the soil to promote plant growth and improve soil fertility [30–41,60–71], Table 3. These microorganisms can increase the growth and development of plant roots and increase the solubilization and absorption of insoluble Mn compounds by plants through various mechanisms, including by increasing the bioavailability of certain elements (such as nitrogen fixation, phosphate solubilization, etc.), the production of phytohormones, the secretion of organic acids, and the production of siderophore, hydrogen cyanide, and anti-pathogenic compounds [32,60–67]. Several studies have reported the effectiveness of biofertilizers in improving Mn availability for plants. For instance, Prasad et al. [41] reported that PGPB can enhance Mn uptake by plants through various mechanisms, including organic acid secretion, siderophore production, and root association. Similarly, Maldonado-Mendoza et al. [53] reported that AMF and associated bacteria can enhance Mn uptake and translocation in contaminated soil. In addition, Mukherjee et al. [42] reported that PSMs can solubilize insoluble Mn compounds, thereby enhancing their availability to plants. Moreover, biofertilizers can also indirectly alter the physicochemical properties of soil, leading to improved Mn availability [65–71]. For instance, *Bacillus* sp. has been reported to alter soil pH, leading to increased Mn availability to plants [40,49,57]. Similarly, *Trichoderma* sp. has been reported to enzymatically breakdown organic matter, leading to improved soil structure and increased Mn availability [50,62,65]. *Bradyrhizobium* sp. has been reported to have a symbiotic relationship with leguminous plants, leading to improved Mn uptake [66].

Table 3. The effect of microbes on increasing plant Mn absorption and their mechanisms.

Microbe Name	Effect on Plant Growth	Mechanism of Action	References
Bacillus subtilis	Increased root length and biomass	Production of indole acetic acid	[40,49]
Pseudomonas fluorescens	Increased plant growth and yield	Induced systemic resistance	[64]
Trichoderma harzianum	Increased root length and biomass	Production of enzymes and secondary metabolites	[65]
Azospirillum brasilense	Increased root length and biomass	Production of phytohormones	[46,66]
Rhizobium leguminosarum	Increased nitrogen fixation and plant growth	Symbiotic relationship with legumes	[45,66]
Frankia spp.	Increased nitrogen fixation and plant growth	Symbiotic relationship with actinorhizal plants	[68]
Glomus intraradices	Increased nutrient uptake and plant growth	Mycorrhizal association with plant roots	[54,69]
Streptomyces spp.	Increased plant growth and disease resistance	Production of antibiotics and enzymes	[52,67]
Cyanobacteria spp.	Increased plant growth and tolerance to abiotic stress	Production of phytohormones and antioxidants	[70]
Bacillus amyloliquefaciens	Increased plant growth and disease resistance	Production of antibiotics and enzymes	[71]

5. Conclusions

Mn is an essential micronutrient for plant growth and development, and its availability in the soil is crucial for maintaining plant health. Mn deficiency can lead to significant reductions in crop yields and overall plant health. Microbes can play a significant role in increasing the bioavailability of Mn in the soil by solubilizing it and making it easier for plants to absorb. The use of microbial-based fertilizers can also help improve Mn uptake by plants. The potential of microbes to enhance the bioavailability of Mn in soils and increase plant uptake holds promise for sustainable agriculture and the development of more effective and eco-friendly fertilizers.

Further research is necessary to explore alternative options for manganese chemical fertilizers in order to reduce their consumption and mitigate soil and water pollution. By investigating the effects of biological and microbial fertilizers and evaluating the resulting agricultural product quality, we can find improved approaches. It is important to note that the effectiveness of Mn biofertilizers may vary depending on the soil conditions, crop type, and other factors. Enhancing our understanding of the relationship between plants, microbes, and the manganese cycle will enable us to develop more effective biofertilizers that contain manganese-related microbes. Consequently, conducting additional research, experiments, and tests in this area can facilitate the development of optimal and environmentally friendly strategies for enhancing agricultural conditions, food security, and preserving the environment.

Author Contributions: Conceptualization, B.K. and D.M.; data curation, B.K., A.F.N. and A.R.; writing—original draft preparation, B.K., D.M., A.F.N., A.R., L.M., A.S., B.F., R.D. and M.P.; writing—review and editing, B.K., D.M., B.E.G.-S., M.P., P.P. and P.K.D.M.; visualization, B.K.; supervision, P.P. and P.K.D.M.; project administration, B.K. and D.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors are thankful to Soil and Water Research Institute (SWRI), Agricultural Research, Education and Extension Organization (AREEO), Karaj, Iran; University of Tabriz, Tabriz, Iran; Raiganj University, India; University of L'Aquila, 67100 L'Aquila, Italy and Universidad de Santander, Colombia.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Alejandro, S.; Höller, S.; Meier, B.; Peiter, E. Manganese in plants: From acquisition to subcellular allocation. *Front. Plant Sci.* **2020**, *11*, 300. [CrossRef] [PubMed]
2. Schmidt, S.B.; Husted, S. The biochemical properties of manganese in plants. *Plants* **2019**, *8*, 381. [CrossRef] [PubMed]
3. Thomine, S.; Merlot, S. Manganese matters: Feeding manganese into the secretory system for cell wall synthesis. *New Phytol.* **2021**, *231*, 2107–2109. [CrossRef] [PubMed]
4. Najafpour, M.M.; Isaloo, M.A.; Eaton-Rye, J.J.; Tomo, T.; Nishihara, H.; Satoh, K.; Carpentier, R.; Shen, J.R.; Allakhverdiev, S.I. Water exchange in manganese-based water-oxidizing catalysts in photosynthetic systems: from the water-oxidizing complex in photosystem II to nano-sized manganese oxides. *Biochim. Biophys. Acta (BBA)-Bioenerg.* **2014**, *1837*, 1395–1410. [CrossRef]
5. Farzadfar, S.; Zarinkamar, F.; Hojati, M. Magnesium and manganese affect photosynthesis, essential oil composition and phenolic compounds of *Tanacetum parthenium*. *Plant Physiol. Biochem.* **2017**, *112*, 207–217. [CrossRef]
6. Li, L.; Yang, X. The essential element manganese, oxidative stress, and metabolic diseases: Links and interactions. *Oxid. Med. Cell. Longev.* **2018**, *2018*, 7580707. [CrossRef]
7. Li, C.; Zhou, H.M. The role of manganese superoxide dismutase in inflammation defense. *Enzyme Res.* **2011**, *2011*, 387176. [CrossRef]
8. Millaleo, R.; Reyes-Díaz, M.; Ivanov, A.G.; Mora, M.L.; Alberdi, M. Manganese as essential and toxic element for plants: Transport, accumulation and resistance mechanisms. *J. Soil Sci. Plant Nutr.* **2010**, *10*, 470–481. [CrossRef]

9. Chen, A.; Husted, S.; Salt, D.E.; Schjoerring, J.K.; Persson, D.P. The intensity of manganese deficiency strongly affects root endodermal suberization and ion homeostasis. *Plant Physiol.* **2019**, *181*, 729–742. [CrossRef]
10. Huber, D.M.; Graham, R.D. The role of nutrition in crop resistance and tolerance to disease. In *Mineral Nutrition of Crops Fundamental Mechanisms and Implications*; Rengel, Z., Ed.; Food Product Press: New York, NY, USA, 1999; pp. 205–226.
11. Tripathi, R.; Tewari, R.; Singh, K.P.; Keswani, C.; Minkina, T.; Srivastava, A.K.; De Corato, U.; Sansinenea, E. Plant mineral nutrition and disease resistance: A significant linkage for sustainable crop protection. *Front. Plant Sci.* **2022**, *13*, 3116. [CrossRef]
12. Marschner, P.; Fu, Q.; Rengel, Z. Manganese availability and microbial populations in the rhizosphere of wheat genotypes differing in tolerance to Mn deficiency. *J. Plant Nutr. Soil Sci.* **2003**, *166*, 712–718. [CrossRef]
13. Ijaz, A.; Mumtaz, M.Z.; Wang, X.; Ahmad, M.; Saqib, M.; Maqbool, H.; Zaheer, A.; Wang, W.; Mustafa, A. Insights into manganese solubilizing *Bacillus* spp. for improving plant growth and manganese uptake in maize. *Front. Plant Sci.* **2021**, *12*, 2456. [CrossRef] [PubMed]
14. Li, J.; Jia, Y.; Dong, R.; Huang, R.; Liu, P.; Li, X.; Wang, Z.; Liu, G.; Chen, Z. Advances in the mechanisms of plant tolerance to manganese toxicity. *Int. J. Mol. Sci.* **2019**, *20*, 5096. [CrossRef] [PubMed]
15. Rashed, M.H.; Hoque, T.S.; Jahangir, M.M.R.; Hashem, M.A. Manganese as a micronutrient in agriculture: Crop requirement and management. *J. Environ. Sci. Nat. Resour.* **2019**, *12*, 225–242. [CrossRef]
16. Montgomery, A.R. Manganese Geochemistry and Plant Availability in Response to Agricultural Practices. Master's Thesis, University of Tennessee, Knoxville, TN, USA, 2022. Available online: https://trace.tennessee.edu/utk_gradthes/6458 (accessed on 1 August 2022).
17. Huang, Y.L.; Yang, S.; Long, G.X.; Zhao, Z.K.; Li, X.F.; Gu, M.H. Manganese toxicity in sugarcane plantlets grown on acidic soils of southern China. *PLoS ONE* **2016**, *11*, e0148956. [CrossRef]
18. Fernando, D.R.; Lynch, J.P. Manganese phytotoxicity: New light on an old problem. *Ann. Bot.* **2015**, *116*, 313–319. [CrossRef]
19. Gilkes, R.J.; Mc Kenzie, R.M. Geochemistry and mineralogy of manganese in soils. In *Manganese in Soils and Plants: Proceedings of the International Symposium on 'Manganese in Soils and Plants' Held at the Waite Agricultural Research Institute, The University of Adelaide, Glen Osmond, South Australia, as an Australian Bicentennial Event*; Springer: Dordrecht, Netherlands, 1988; pp. 23–35. [CrossRef]
20. Meek, B.D.; MacKenzie, A.J.; Grass, L.B. Effects of organic matter, flooding time, and temperature on the dissolution of iron and manganese from soil in situ. *Soil Sci. Soc. Am. J.* **1968**, *32*, 634–638. [CrossRef]
21. Trebien, D.O.P.; Bortolon, L.; Tedesco, M.J.; Bissani, C.A.; Camargo, F.A.O. Environmental factors affecting chromium-manganese oxidation-reduction reactions in soil. *Pedosphere* **2011**, *21*, 84–89. [CrossRef]
22. Walter, K.H. Manganese fertilizers. In *Manganese in Soils and Plants: Proceedings of the International Symposium on 'Manganese in Soils and Plants' Held at the Waite Agricultural Research Institute, The University of Adelaide, Glen Osmond, South Australia, August 22–26, 1988 as an Australian Bicentennial Event*; Springer: Dordrecht, Netherlands, 1988; pp. 225–241. [CrossRef]
23. Fageria, N.K.; Baligar, V.C.; Li, Y.C. Manganese in Crop Production. In *Handbook of Plant Nutrition*; CRC Press: Boca Raton, FL, USA, 2014.
24. Gupta, U.C.; Gupta, S.C. Trace Element Toxicity Relationships to Crop Production and Livestock and Human Health: Implications for Management. *Commun. Soil Sci. Plant Anal.* **1998**, *29*, 1491–1522. [CrossRef]
25. Atajan, F.A.; Mozafari, V.; Abbaszadeh-Dahaji, P.; Hamidpour, M. Fractionation and speciation of manganese in rhizosphere soils of *Pseudomonas* sp. rhizobacteria inoculated Pistachio (*Pistacia vera* L.) seedlings under salinity stress. *Commun. Soil Sci. Plant Anal.* **2019**, *50*, 894–908. [CrossRef]
26. Kaur, P.; Kaur, R.; Kaur, S. Role of manganese in plant growth, development and stress tolerance: A review. *Plant Cell Rep.* **2021**, *40*, 717–731.
27. Raghunath, A.; Tripathi, R.M. Manganese metabolism in humans. *Indian J. Med. Res.* **2009**, *130*, 634–641.
28. Zlokolica-Mandić, M.; Mandić, M.; Kostić, D.; Ristić, M. Manganese toxicity in plants: A review. *Arch. Biol. Sci.* **2019**, *71*, 117–130.
29. Broadley, M.R.; White, P.J.; Hammond, J.P.; Zelko, I.; Lux, A. Manganese in Plants and Soil: Integrating Environment and Physiology. *Plant Soil* **2012**, *335*, 1–4.
30. Ghosh, S.; Mohanty, S.; Nayak, S.; Sukla, L.B.; Das, A.P. Molecular identification of indigenous manganese solubilising bacterial biodiversity from manganese mining deposits. *J. Basic Microbiol.* **2016**, *56*, 254–262. [CrossRef] [PubMed]
31. Baveye, P.C.; Baveye, J.; Gowdy, J. Soil "ecosystem" services and natural capital: Critical appraisal of research on uncertain ground. *Front. Environ. Sci.* **2018**, *6*, 77. [CrossRef]
32. Khoshru, B.; Mitra, D.; Khoshmanzar, E.; Myo, E.M.; Uniyal, N.; Mahakur, B.; Das Mohapatra, P.K.; Panneerselvam, P.; Boutaj, H.; Alizadeh, M.; et al. Current scenario and future prospects of plant growth-promoting rhizobacteria: An economic valuable resource for the agriculture revival under stressful conditions. *J. Plant Nutr.* **2020**, *43*, 3062–3092. [CrossRef]
33. Khoshru, B.; Sarikhani, M.R.; Reyhanitabar, A.; Oustan, S.; Malboobi, M.A. Evaluation of the ability of rhizobacterial isolates to solubilize sparingly soluble iron under in-vitro conditions. *Geomicrobiol. J.* **2022**, *39*, 804–815. [CrossRef]
34. Khoshru, B.; Mitra, D.; Joshi, K.; Adhikari, P.; Rion, S.I.; Fadiji, A.E.; Alizadeh, M.; Priyadarshini, A.; Senapati, A.; Sarikhani, M.R.; et al. Decrypting the multifunctional biological activators and inducers of defense responses against biotic stresses in plants. *Heliyon* **2023**, *9*, e13825. [CrossRef]
35. Baglin, E.; Noble, E.; Lamsphire, D.; Eisele, J.A. Solubilization of manganese from ores by heterotrophic micro-organisms. *Hydrometallurgy* **1992**, *29*, 131–144. [CrossRef]

36. Gupta, S.; Kaushal, R.; Sood, G. Impact of plant growth–promoting rhizobacteria on vegetable crop production. *Int. J. Veg. Sci.* **2018**, *24*, 289–300. [CrossRef]
37. Das, A.P.; Sukla, L.B.; Pradhan, N. Microbial recovery of manganese using *Staphylococcus epidermidis*. *Int. J. Nonferrous Metallurgy* **2012**, *1*, 9–12. [CrossRef]
38. Liu, J.; Li, X.; Su, J.; Zhang, W.; Liang, X. Microbial manganese reduction by bacteria and fungi: A review. *Bull. En-Viron. Contam. Toxicol.* **2018**, *101*, 139–144.
39. Gadd, G.M. Metals, minerals and microbes: Geomicrobiology and bioremediation. *Microbiology* **2010**, *156*, 609–643. [CrossRef] [PubMed]
40. Tang, Y.; Kang, H.; Qin, Z.; Zhang, K.; Zhong, Y.; Li, H. Significance of manganese resistant bacillus cereus strain WSE01 as a bioinoculant for promotion of plant growth and manganese accumulation in *myriophyllum verticillatum*. *Sci. Total Environ.* **2020**, *707*, 135867. [CrossRef] [PubMed]
41. Prasad, M.; Srinivasan, R.; Chaudhary, M.; Choudhary, M.; Jat, L.K. Plant growth promoting rhizobacteria (PGPR) for sustainable agriculture: Perspectives and challenges. *PGPR Amelior. Sustain. Agric.* **2019**, 129–157. [CrossRef]
42. Mukherjee, A.; Roy, P.; Mitra, A.; Kundu, M. Microbial siderophores and their potential applications: A review. *Environ. Sci. Pollut. Res.* **2019**, *26*, 34682–34699.
43. Khoshru, B.; Moharramnejad, S.; Gharajeh, N.H.; Asgari Lajayer, B.; Ghorbanpour, M. Plant microbiome and its important in stressful agriculture. *Plant Microbiome Paradig.* **2020**, 13–48. [CrossRef]
44. Khoshru, B.; Sarikhani, M.R.; Reyhanitabar, A.; Oustan, S.; Malboobi, M.A. Evaluation of the Potential of Rhizobacteria in Supplying Nutrients of *Zea mays* L. Plant with a Focus on Zinc. *J. Soil Sci. Plant Nutr.* **2023**, *23*, 1816–1829. [CrossRef]
45. Kumar, S.; Verma, R.; Singh, J. Rhizobium and phosphate solubilizing bacteria mediated manganese solubilization and its uptake by wheat plants. *J. Plant Nutr.* **2020**, *43*, 1281–1293.
46. Chen, Y.; Liu, Y.; Li, H.; Li, Y.; Zhou, J. Biocontrol and plant growth-promoting activity of *Azospirillum* sp. in tomato. *Arch. Microbiol.* **2021**, *203*, 1441–1453.
47. Tahir, H.A.S.; Gu, Q.; Wu, H.; Raza, W.; Hanif, M.K. *Penicillium janthinellum* enhances manganese solubilization and uptake by *Brassica napus* L. in manganese-deficient soil. *J. Plant Nutr.* **2020**, *43*, 508–521.
48. Dua, M.; Joshi, S.; Yadav, A.; Kumar, V. Role of *Rhizopus* spp. in the solubilization of insoluble manganese in soil. *Int. J. Curr. Microbiol. Appl. Sci.* **2020**, *9*, 1188–1197.
49. Zhang, Z.; Li, Z.; Chen, Y.; Li, Y. *Bacillus* sp. N1-1 promotes plant growth and improves manganese stress tolerance in soybean via regulation of root architecture and antioxidant defense. *J. Plant Growth Regul.* **2021**, *40*, 836–849.
50. Tariq, M.; Hameed, A.; Yasmin, S.; Shahzad, S. *Trichoderma harzianum* enhances plant growth and manganese uptake in maize grown on manganese-deficient soil. *J. Plant Nutr.* **2020**, *43*, 689–700.
51. Khoshru, B.; Nosratabad, A.F.; Mitra, D.; Chaithra, M.; Danesh, Y.R.; Boyno, G.; Chattaraj, S.; Priyadarshini, A.; Anđelković, S.; Pellegrini, M.; et al. Rock Phosphate Solubilizing Potential of Soil Microorganisms: Advances in Sustainable Crop Production. *Bacteria* **2023**, *2*, 98–115. [CrossRef]
52. Barka, E.A.; Vatsa, P.; Sanchez, L.; Gavriel, S.; Jacquard, C.; Klenk, H.P.; Clément, C.; Ongena, M. Taxonomy, physiology, and natural products of Actinobacteria. *Microbiol. Mol. Biol. Rev.* **2016**, *80*, 1–43. [CrossRef]
53. Maldonado-Mendoza, I.E.; Dewbre, G.R.; Harrison, M.J. Rhizobia and arbuscular mycorrhizae enhance manganese accumulation and root-to-shoot translocation in soybean. *Mycorrhiza* **2021**, *31*, 51–60.
54. Lazzari, A.; Dufresne, A.; Redecker, D. *Glomus intraradices* and *Claroideoglomus etunicatum* differentially affect manganese uptake and its translocation to shoots in *Medicago truncatula*. *Mycorrhiza* **2020**, *30*, 355–362.
55. Li, L.; Shi, Q.; Li, Z.; Gao, J. Genome-wide identification and functional characterization of manganese (Mn) transporter genes in soybean. *BMC Plant Biol.* **2021**, *21*, 266. [CrossRef]
56. Uroz, S.; Ioannidis, P.; Lengelle, J.; Cébron, A.; Morin, E.; Buée, M. Laccaria bicolor, a key player in soil functioning: From saprotrophic abilities to bioremediation potential. *Microorganisms* **2021**, *9*, 2116.
57. Chen, X.; Koumoutsi, A.; Scholz, R.; Eisenreich, A.; Schneider, K.; Heinemeyer, I.; Morgenstern, B.; Voss, B.; Hess, W.R.; Reva, O.; et al. Comparative analysis of the complete genome sequence of the plant growth-promoting bacterium *Bacillus amyloliquefaciens* FZB42. *Nat. Biotechnol.* **2018**, *25*, 1007–1014. [CrossRef]
58. Riaz, U.M.; Ghulam, A.; Wajiha, S.; Tayyaba, S.; Muhammad, M.; Nazir, M. Zulqernain. Plant growth-promoting rhizobacteria (PGPR) as biofertilizers and biopesticides. In *Microbiota and Biofertilizers*; Spinger: Berlin/Heidelberg, Germany, 2021; pp. 181–196. [CrossRef]
59. Tchameni, N.S.; Chérif, H.; Hafidi, M.; Verdin, A. Effect of phosphate-solubilizing bacteria on manganese solubilization and plant growth promotion in tomato (*Solanum lycopersicum*). *J. Plant Nutr.* **2020**, *43*, 1028–1041.
60. Sarikhani, M.R.; Aliasgharzad, N.; Khoshru, B. P solubilizing potential of some plant growth promoting bacteria used as ingredient in phosphatic biofertilizers with emphasis on growth promotion of *Zea mays* L. *Geomicrobiol. J.* **2020**, *37*, 327–335. [CrossRef]
61. Sarikhani, M.R.; Khoshru, B.; Greiner, R. Isolation and identification of temperature tolerant phosphate solubilizing bacteria as a potential microbial fertilizer. *World J. Microbiol. Biotechnol.* **2019**, *35*, 1–10. [CrossRef] [PubMed]

62. Khoshmanzar, E.; Aliasgharzad, N.; Neyshabouri, M.R.; Khoshru, B.; Arzanlou, M.; Asgari Lajayer, B. Effects of *Trichoderma* isolates on tomato growth and inducing its tolerance to water-deficit stress. *Int. J. Environ. Sci. Technol.* **2020**, *17*, 869–878. [CrossRef]
63. Bashan, Y.; Kamnev, A.A.; de-Bashan, L.E. Tricalcium phosphate is inappropriate as a universal selection factor for isolating and testing phosphate-solubilizing bacteria that enhance plant growth: A proposal for an alternative procedure. *Biol. Fertil. Soils* **2014**, *50*, 1087–1093. [CrossRef]
64. Raj, S.N.; Saritha, K.; Sreenivasa, M.Y. *Pseudomonas fluorescens* mediated systemic resistance in tomato against early and late blight diseases. *Biol. Control.* **2014**, *75*, 64–72.
65. Vinale, F.; Sivasithamparam, K.; Ghisalberti, E.L.; Marra, R.; Barbetti, M.J.; Li, H.; Woo, S.L.; Lorito, M. A novel role for *Trichoderma* secondary metabolites in the interactions with plants. *Physiol. Mol. Plant Pathol.* **2008**, *72*, 80–86. [CrossRef]
66. Cassán, F.; Perrig, D.; Sgroy, V.; Masciarelli, O.; Penna, C.; Luna, V. *Azospirillum brasilense* Az39 and *Bradyrhizobium japonicum* E109, inoculated singly or in combination, promote seed germination and early seedling growth in corn (*Zea mays* L.) and soybean (*Glycine max* L.). *Eur. J. Soil Biol.* **2014**, *60*, 53–60. [CrossRef]
67. Gopalakrishnan, S.; Srinivas, V.; Alekhya, G.; Prakash, B.; Kudapa, H.; Rathore, A.; Varshney, R.K. The extent of grain yield and plant growth enhancement by plant growth-promoting broad-spectrum *Streptomyces* sp. in chickpea. *Springer Plus* **2015**, *4*, 31. [CrossRef] [PubMed]
68. Benson, D.R.; Silvester, W.B. Biology of Frankia strains, actinomycete symbionts of actinorhizal plants. *Microbiol. Rev.* **1993**, *57*, 293–319. [CrossRef]
69. Smith, S.E.; Read, D.J. *Mycorrhizal Symbiosis*, 3rd ed.; Academic Press: Cambridge, MA, USA, 2008.
70. Singh, S.; Bala, A.; Singh, S.K. Soil microbial community structure and function: A review. *J. Environ. Manag.* **2022**, *302*, 114029.
71. Zhou, J.; Li, L.; Li, N. Plant growth-promoting bacteria in agriculture: Mechanisms and applications. *Sci. Agric. Sin.* **2021**, *54*, 1733–1743.