REVIEW

Soil microbes and the availability of soil nutrients

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Abstract It is likely to provide plants with their necessary nutrients using chemical and biological fertilization. Although chemical fertilization is a quick method, it is not recommendable economically and environmentally, especially if overused. Biological fertilization is the use of soil microbes including arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria to inoculate plants. It has been proved that biological fertilization is an efficient method to supply plants with their necessary nutrients. It is economically and environmentally recommendable, because it results in sustainability. In this article, some of the most important details including the mechanisms and processes regarding the effects of soil microbes on the availability and hence uptake of nutrients by plant are reviewed. Such details can be important for the selection and hence production of microbial inoculums, which are appropriate for biological fertilization.

Keywords Biological fertilization · Chemical fertilization · Environment · Mycorrhizal fungi · Microbial inoculums · Plant growth promoting rhizobacteria · Soil nutrients

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Introduction

Soil microbes are among the most important components of ecosystem enhancing soil efficiency and hence plant growth. There is a wide range of microbes in the soil, with beneficial, neutral or pathogenic effects. For example, soil fungi such as arbuscular mycorrhizal (AM) fungi and soil bacteria such as plant growth promoting rhizobacteria (PGPR) including the N-fixing bacteria, *rhizobium* spp., are among the beneficial microbes (Miransari and Smith 2007, 2009; Miransari 2010, 2011a, b).

Plants require at least 16 macro- and micro-nutrients for their growth and for yield production. The absence or deficiency of each nutrient in soil can adversely affect plant performance. Nutrient availability in the soil is a function of soil, climate and plant properties. It is among the most important factors affecting plant growth. The optimum level of soil nutrients supplied by soil microbes can enhance plant growth and yield production, while economically and environmentally advantageous (Marschner 1995; Richardson et al. 2009; Hirel et al. 2011).

Because of the necessity to increase food production for the world increasing population, use of different chemicals including fertilizers and herbicides is unavoidable. Accordingly, their excessive amounts have resulted in some unfavorable effects on the environment including the pollution of under ground water and degradation of soil (Miransari and Mackenzie 2011a, b). It is hence important to use methods, which supply the plants with their required nutrients and are healthy to the environment (Miransari 2011c).

Nutrients may be present in the soil; however, their chemical properties can make them unavailable for plant use. Hence, different methods have been tested and proved to be effective on the enhancement of soil nutrient

availability. Such effects can be of significance by keeping the environment clean and enhancing crop production. Biological methods and the use of organic matter are among the most important ones. The use of different microbes, which is usually through inoculation, and is called biofertilization, can efficiently affect the availability of soil nutrients and hence plant growth (Adesemoye and Kloepper 2009; Wang et al. 2010; Miransari 2011b, c).

Hence, with respect to the favorable effects of soil microbes on soil productivity and ecosystem health, they have been used worldwide to improve plant growth and yield production. The favorable activities of soil organisms including microbes are (1) mineralization of soil organic matter and hence nutrient cycling (Fang et al. 2005; Miransari 2011c), (2) improving the soil structure (Egamberdiyeva 2007), (3) interacting with other soil microbes (Artursson et al. 2006; Miransari 2011b), (4) production of different biochemicals such as plant hormones and enzymes (Compant et al. 2010), and (5) controlling pathogens (Mendes et al. 2011).

Soil microbes can affect the solubility and hence the availability of different micronutrients in the soil. There are different mechanisms, utilized by soil microbes to increase the solubility of soil micro-nutrients as indicated in the following (Jin et al. 2010; Marschner et al. 2011; Podile and Kishore 2006): (1) Affecting plant metabolism and hence alteration of root exudates by symbiotically or non-symbiotically association with their host plant, (2) affecting the solubility and hence the availability of soil nutrients, and (3) interacting with the other soil microbes (Adesemoye and Kloepper 2009; Fitter et al. 2011; Hodge 2010; Miransari 2011a, b).

There is another important aspect regarding soil micronutrients, especially at high amounts in the presence of soil microbes. It has been indicated that under high concentration of micronutrients, soil microbes are able to alleviate the unfavorable effects of soil micronutrients on plant growth and on the environment using different mechanisms (Zhuang et al. 2007). For example, soil microbes can affect the solubility of micronutrients in the soil and hence their uptake by plant. This can be due to the effects of soil microbes on plant morphological and physiological properties and the translocation of micronutrients to different plant tissues.

The important point about the use of soil microbes for biofertilization is selecting the right combination of microbes (the enhancing interactions between the microbial strains), determining their inoculating potential, their persistence in the soil, their survival under stress, etc. Different microbial species and strains may perform differently under different conditions, determining their efficiency and hence their related use. For example, the strains which are isolated under stressful conditions may perform more efficiently under stress, as compared with the non-tolerant strains (Adesemoye and Kloepper 2009; Miransari 2011b).

PGPR are the soil bacteria, which can favor plant growth and yield production by their activities, as previously mentioned, in the soil. The soil N-fixing bacteria, rhizobia spp., which can form symbiotic association with their specific host plant, are also considered PGPR. These bacteria can fix nutrients like N and influence their availability in the soil by producing a wide range of products including different enzymes and plant hormones such as phosphatases and auxins, respectively (Lugtenberg and Kamilova 2009; Podile and Kishore 2006; van Loon 2007).

There is a wide range of soil bacteria, acting as PGPR. In addition to the enhanced availability of different nutrients in the soil, PGPR can also affect plant growth by the following: (1) production of enzymes such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which are able to alleviate the effects of stress on plant growth, (2) production of different plant hormones, and (3) controlling the adverse effects of pathogens on plant growth by producing products such as HCN and rhizoxin (Abbas-Zadeh et al. 2010; Podile and Kishore 2006; Zhao et al. 2010). Soil microbes such as Pseudomonas spp. are able to affect the availability of soil micronutrients by the production of: (1) carboxylates, which can chelate micronutrients, and (2) humic substances, riboflavin, phenazines and quinines, which can dissolve mineral oxides (Hernandez et al. 2004; Johal and Huber 2009; Uroz et al. 2009).

There are also AM fungi in the soil, developing symbiotic association with most terrestrial plants. In this association, AM fungi can increase the uptake of water and nutrients by their host plant in the exchange for carbon. In the presence of the host plant, the fungal spore would germinate resulting in the production of fungal hyphae, which grow into the mycorrhizosphere (the space around the host plant roots, with mycorrhizal presence) and eventually into the root cortical cells. The fungal hypha produces some organelles called vesicles (storage organ) and arbuscules (hyphal branched structure as the interface for the exchange of nutrients with the host plant roots) (Smith and Read 2008).

Plants can also affect the availability of soil nutrients, especially by their root activities. Production of different compounds such as organic acids by plant roots influences the solubility and hence availability of nutrients. Such products can affect rhizosphere properties and hence soil nutrient availability by altering rhizosphere pH and the activity of microbes including PGPR (Table 1) (van der Heijden 2010; Hodge 2010; Johnson et al. 2010).

With respect to the above-mentioned details, it is important to supply the optimum amounts of nutrients to the plant, using the appropriate fertilization methods such

Table 1 Root exudates affecting the rhizosphere (Jones et al. 2004)

Product	Activity
Phenolics	Chelating nutrients with little solubility (e.g., Fe)
	Source of nutrients
	Increasing microbial growth
	Inducing or inhibiting rhizobial Nod genes
	Signals attracting microbes
	Controlling pathogens
Phytosiderophores and amino acids	Source of nutrients
	Chelating nutrients with little solubility (e.g., Fe)
	Signals attracting microbes
Organic acids	Source of nutrients
	Signals attracting microbes
	Chelating nutrients with little solubility (e.g., Fe)
	Inducing Nod genes
Purines	Source of nutrients
Vitamins	Increasing the growth of plants and microbes
	Source of nutrients
Enzymes	Enhancing P solubility from organic molecules
	Increasing the of mineralization rate of organic products
Sugars	Source of nutrients
	Increasing microbial growth
Root cells	Controlling cell cycling and gene expression by producing signals
	Enhancing microbial growth
	Producing chemoattractants
	Producing proteins and mucilage
	Production of molecules to increase the rhizosphere immunity

as biofertilization. Accordingly, in the following the effects of soil microbes on the availability of soil nutrients and hence their uptake by plant are reviewed.

Soil microbes and N uptake by plants

Soil microbes such as bacteria can increase plant N uptake by processes such as the symbiotic and non-symbiotic N fixation. The nitrogenase enzyme is able to reduce the atmospheric N into ammonium. The legume host plant provides the bacteria with its necessary carbohydrates in the exchange for the fixed N by the bacteria. The process of N fixation initiates with some biochemical communications between the two symbionts. Such products include flavonoids and lipochitooligosaccharides, produced by the host

plant and the bacteria, respectively. Such products determine the specificity of the process of N fixation (Miransari and Smith 2007, 2009; Ferguson et al. 2010; Van de Velde et al. 2010).

The rhizobium bacteria realize the presence of the host plant by the produced flavonoids, and hence make a chemotactic movement toward the plant roots. As a result, the activated bacterial *nod* genes produce products such as lipochitooligosaccharides, which are able to alter the morphology of plant roots, especially the root hairs. The bacteria can enter the root cells by the production of the infection thread. They eventually reside in the root cortical cells, which their subsequent division produces the nodules, the place of N fixation by the rhizobium (Miransari et al. 2006; Ferguson et al. 2010; Van de Velde et al. 2010).

Under optimum conditions, the bacteria are able to fix significant amounts of atmospheric N, which is of economical and ecological importance. It is because the process of N fixation can significantly decrease the amounts of chemicals for fertilization both under dry and humid conditions. Under humid conditions, N is more mobile and hence subjected to processes such as leaching and denitrification, decreasing N availability to the plant (Miransari and Mackenzie 2011a, b; Miransari and Smith 2007, 2008, 2009).

There are also soil bacteria such as *Azospirillum* spp., *Acetobacter diazotrophicus*, *Azotobacter* spp., *Azoarcus* spp., cyanobacteria, *Bacillus* spp., *Enterobacter* spp., *Xanthobacter* spp., *Gluconacetobacter diazotrophicus*, *Achromobacter* spp., *Arthrobacter* spp., *Azomonas* spp., *Clostridium* spp., *Beijerinckia* spp., *Corynebacterium* spp., *Rhodospirillum* spp., *Klebsiella*, spp., *Derxia*, spp., *Herbaspirillium* spp., *Pseudomonas* spp., *Rhodopseudomonas* spp., etc., which can fix atmospheric N in non-symbiotic association with their host plant (Saxena and Tilak 1998; Saharan and Nehra 2011). AM fungi can also increase the uptake of different nutrients by their host plant through their extensive hyphal network. Although there are some signs indicating that AM fungi can affect the process of N uptake by the host plant through their extensive hyphal network and production of different compounds, the greater details have yet to be further investigated (Podile and Kishore 2006; van Loon 2007; Miransari 2011b).

Soil microbes and P uptake by plants

Similar to N, P is also among the macronutrients, which are necessary for plant growth and crop production. However, in comparison with N, P is absorbed at much less amounts by plant, as it acts differently in the soil, which is due to its chemical properties. Accordingly, P is subjected to processes such as desolubilization and hence its availability to

plant would significantly decrease. For example, during the first year of P application, only 20 % of soil P is available for the use of plant and the remaining part would precipitate. Accordingly, different methods must be examined to increase the availability of soil P (Zabihi et al. 2011). There are the two main types of organic and mineral P in the soil. The availability of organic P in the soil is more than mineral P with less solubility. Organic P is subjected to different microbial activities determining its availability to the plant (Marschner 1995).

For example, at the time of using P fertilization in the field, P has to be applied around the plant roots, using P compounds, with the highest solubility such as triple super phosphate. In addition, the use of biological methods such as PGPR has also been indicated to be affective on the enhancement of P availability in the soil. For example, such bacteria are able to produce enzymes (phosphatases) (at less amounts compared with plants) and products such as organic products such as organic acids (carboxylic acids), protons, etc., which can increase P availability in the soil by affecting the mineral P sources such as rock phosphate. The source of P (organic or mineral), host plant, microbial combination, pH, anions and cations, etc. determine P solubility in the soil (Houser and Richardson 2010; Niu et al. 2010; Salimpour et al. 2010).

Enzymes such as ACC deaminase can affect plant root growth by degrading the precursor for the production of the stress hormone, ethylene. Increased level of ethylene production in plant can decrease root growth. As a consequence, the enzymes can also indirectly influence P effect on root growth as well as its uptake by plant, because ethylene can adjust root architectural response to P availability in the soil. Under stresses such as P deficiency, the increased production of stress can adversely affect plant response to P and decrease the number of root hairs (Borch et al. 1999).

Soil microbes and K uptake by plants

Potassium is soluble in the soil and hence is subjected to processes such as leaching. Accordingly, the amount of K in the soil is usually higher under arid and semi arid conditions, in comparison with humid areas. Similar to N, and as a macronutrient K is necessary for plant growth and crop production at high amounts. When K is deficient for plant use, it can be applied by the use of chemical and organic fertilization resulting in the production of K^+ for plant use. However, there are also PGPR, which can enhance K availability in soil by their activities (Adesemoye and Kloepper 2009; Blaise et al. 2005; Hu et al. 2006; Wu et al. 2005).

Biological activities in the soil can also affect K availability. For example, Hu et al. (2006) isolated the K solubilizing strain, *Paenibacillus mucilaginosus*. This bacteria has K solubilizing activities even higher than the inoculum strain, *Bacillus mucilaginosus* (Li et al. 2007), which is usually used with K fertilization. Using a range of different mechanisms including acidolysis, chelation and oxidoreduction, and production of different products such as oxalate, lactate, gluconate, citrate, catechol and pseudobactin, soil microbes can solubilize nutrients including potassium from minerals (Marschner and Rengel 2007; Uroz et al. 2009).

Liu et al. (2012) isolated a bacterial strain with K solubilizing bacteria from a Chinese soil. The gene sequence of the full length 16s-rRNA indicated a similarity of 95.2–96.7 % to the genus *Paenibacillus*. The results showed that the strain was able to release potassium from potassium-bearing rock. Such kind of bacteria can be used to supply plants with potassium. Zeng et al. (2012) isolated another K solubilizing bacterial strain from feldspar using staining, electron scanning and morphological and physiological tests. Accordingly, the bacteria were recognized as a *Bacillus circulans*, a Gram-positive and rod-shaped bacteria with the ability to form capsule and spore. Compared with control, the K solubilizing ability of the strain was 70 % higher than the control indicating its potential application for biofertilization.

Soil microbes and S uptake by plant

Sulfur is also a macronutrient, which is necessary for plant growth and yield production as it can regulate different plant functionings such as the production of proteins and amino acids. Similar to some other nutrients, S is also subjected to biological alterations in soil by the soil bacteria, such as *Thiobacillus* sp. Such bacteria are able to oxidize S to sulfate and decrease soil pH due to the production of hydrogen. This is particularly of significance in calcareous areas where it is necessary to decrease soil pH by adding elemental S to the soil. Usually, under such conditions, adding S with the use of *Thiobacillus* sp. is a safe method to decrease soil pH, affecting different soil properties including the availability of soil nutrients (Miransari and Smith 2007). The collection of sulfur oxidizing bacteria, which are able to oxidize thiosulfate to sulfate, including *Thiobacillus*, *Thiothrix*, *Chlorobiaceae*, *Beggiatoa*, *Chromatiaceae*, *Ectothiorhodospiraceae* has the enzyme Sox, while its SoxB component is activated by the *SoxB* enzyme (Meyer et al. 2007).

The pH at which the uptake of most macro and micronutrients by plant is optimal is the neutral. Accordingly, one of the suitable methods to increase the availability of soil nutrients to plant is the adjustment of soil pH by adding S or lime to the soil (Beller et al. 2006; Miransari and

Smith 2007; Salimpour et al. 2010). In addition, the biochemical processing in the rhizosphere of plants such as the production of enzymes such as arylsulfatases, which are partly produced by plant roots and mostly produced by soil microbes, can significantly influence the biogeochemical cycling of nutrients such as sulfur in the soil (Hinsinger et al. 2005). Arylsulfatases are able to turn the organic S to inorganic S (SO_4^{2-}) for the use of plant. Knauff et al. (2003) investigated the activity of the enzyme in the rhizosphere of different plant species with the highest related to *Brassica napus* and *Triticum aestivum*. Organic matter (compost) significantly increased the enzyme activity while soil sterilization significantly decreased the enzyme activity. The production of the enzyme is induced under S deficiency.

The genome sequence of the obligatory chemolithoautotrophic, *Thiobacillus dentirificans*, as a β-preteobacteria, is among the first sequences, which has been recently recognized for sulfur oxidizing bacteria. Such a discovery can help recognize the molecular pathways by which the bacteria can reduce sulfur compounds under aerobic and anaerobic conditions. Accordingly, it becomes likely to recognize bacterial importance for biogeochemical cycles, related to sulfur, carbon and nitrogen affecting the quality of ground water as well (Beller et al. 2006). The analysis of 2,909,809 pair genome of the bacteria can indicate the unusual properties of the bacteria including their ability to perform denitrification with sulfur oxidation. Some of the genes are able to activate *c*-type cytochromes, genes activating dehydrogenases, 50 genes oxidizing sulfur such as *sox* and *dsr*, genes responsible for the organic transport of ions and resistance to heavy metals, and genes related to the organic compounds and the obligate chemolithoautotrophy nature of bacteria (Beller et al. 2006).

Salimpour et al. (2010) found that treating canola (*Brassica napus* L.) with elemental sulfur inoculated with *Thiobacillus* spp. significantly affected the growth and production of canola (*Brassica napus* L.). Treatment including rock phosphate + elemental sulfur + *Thiobacillus* sp. + organic matter (tea waste) resulted in the highest amount of oil (39 % higher than control). They accordingly indicated that the combined use of biological fertilization with chemical fertilization is a favorite way of increasing crop and oil production with economical and environmental significance (Miransari 2011c).

Soil microbes and plant micronutrient uptake

Iron

Iron is an important micronutrient, which is especially deficient to plant under dry and calcareous conditions. It is because under such conditions the presence of carbonate and bicarbonate anions in the soil can result in the precipitation of iron and hence significantly decrease its availability to plant. Under iron deficient conditions, the signs of chlorosis appear on plant leaf. The highest iron solubility is related to humid conditions where the high uptake of iron by plant may result in some unfavorable effects on plant growth and hence yield production (Marschner 1995).

There is also some kind of interactions between phosphorus and iron and other micronutrients. Although the chemical properties of phosphorous is a determining factor in the uptake of micronutrients by plant, its effects on the root growth is also important affecting the uptake of different nutrients. The presence of P in the soil may decrease the availability of different micronutrients to the plant by increasing pH and production of compounds with little solubility. In addition, under phosphorous deficient conditions, the cluster growth of roots can also decrease the uptake of different nutrients including micronutrients (Marschner 1995; Shane and Lambers 2005; Miransari et al. 2009a, b).

Under Fe-deficient conditions, plants perform two types of strategies including strategy I and II. Strategy I plants acidify the rhizosphere and produce organic products such as phenolic compounds resulting in the activation of ferric chelate reductase and Fe(II) transporter in plant roots. However, strategy II plants handle the stress by producing siderophores and activating the Fe^{3+} siderophore transporter in the plasmalemma of root cells (Romheld and Marschner 1986).

The produced siderophores by plant roots can significantly increase Fe availability due to its high affinity to chelate Fe^{3+} and hence its efficient absorption by plant roots (Chen et al. 1998). Interestingly, plant may not sufficiently handle Fe stress using such strategies. For example, it has been indicated that under sterilized conditions, plants are not able to alleviate Fe stress indicating the role of soil microbes under such conditions (Jin et al. 2010). Fe concentration in plant may also affect Fe uptake by affecting the quality and quantity of root exudates and hence microbial activities in the rhizosphere (Yang and Crowley 2000). Similar to plants, PGPR are also able to produce siderophores, which increase the solubility and hence the availability of Fe for the use of plant (Abbas-Zadeh et al. 2010; Jalili et al. 2009; Zabihi et al. 2011).

The production of root exudates, including organic and amino acids and the secondary metabolites, can affect the combination of soil microbes in the rhizosphere of different plant species. Such products can also affect the solubility and availability of different nutrients in the plant rhizosphere. In addition, plant morphological and physiological properties may also be altered under nutrient deficiency

including iron. For example, under iron deficient conditions plant may produce more root hairs and products such as carboxylates and phenolic compounds as well as water (Lamont 2003; Badri and Vivanco 2009).

Interestingly, it must be mentioned that root properties are affected by microbial presence in the rhizosphere. For example, mycorrhizal fungi can alter root morphology by affecting the uptake of P by the host plant and the production of different products influencing the uptake of different nutrients including iron by plant (Miransari 2011b). Plant Fe status can determine soil microbial combination producing siderophores. Jin et al. (2010) found that in the rhizosphere of plants with iron deficiency the number of soil microbes, which produce siderophores, increases. This may be due to the fact that under such conditions phenolic compounds are produced by plant roots.

Zhang et al. (2009) indicated that the bacterium strain *Bacillus subtilis* GB03 is able to enhance Arabidopsis ability to assimilate nutrients such as iron more efficiency. Accordingly, the bacterium upregulates the transcription factor (FIT1), which is induced under Fe-deficient conditions and is required for the GB03 inducing of ferric reductase *FRO2* and the *IRT1* transporter of iron. GB03 is also able to increase iron mobility in the rhizosphere by acidifying, enhancing the proton production and direct acidification of bacteria. Hence, in plants treated with such bacteria the uptake of iron increases resulting in the higher rate of photosynthesis. It is hence resulted that the bacteria are able to control the uptake of Fe by plant and the rate of photosynthesis.

Zinc

Zinc is also among important micronutrients for plant growth and yield production and is also affected by soil microbial activities. Zn is necessary for plant growth for different functioning such as the activities of different enzymes. Such enzymes include the ones, which can alleviate the effects of different stresses on plant growth by controlling the production of products such as hydrogen peroxide. Some other examples are enzymes such as dehydrogenase, and RNA and DNA polymerase, which have also Zn in their structure (Marschner 1995).

Under stress, enzymes such as super oxide dismutase (SOD) are produced by plant to turn the products of stress into non-toxic ones. Hence, one of the most important effects of AM fungi on plant growth under stresses such as drought is through their alleviating effects on the oxidative stress (Sajedi et al. 2010). The adverse effects of oxidative stress on plant growth are by lipid peroxidation, protein denaturation and DNA mutation (Bowler et al. 1992). AM fungi such as *Glomus mosseae* have the CuZn-SOD enzyme, which can influence the host plant resistance to stresses such as drought (Sajedi et al. 2010). It has been indicated that mycorrhizal plants produce higher amounts of SOD enzyme in comparison with non-mycorrhizal ones. In addition, zinc presence in plants can also influence the activity of plant hormones such as auxin, affecting plant activities under stress (Sajedi et al. 2010).

AM fungi can enhance the uptake of different nutrients such as micronutrients including Zn by the host plant (Johnson 2010). Under nutrient deficiency, plants use different strategies to handle the stress (Table 2) (Marschner and Römheld 1994; Rengel 1999; Hartmann et al. 2009). He et al. (2010) indicated that the zinc-tolerant bacterial strains including *Bacillus cereus*, *B. subtilis*, *Flavobacterium* spp. and *Pseudomonas aeruginosa* can increase the availability of Zn in the soil and hence its uptake by plant, which is also of bioremediation significance.

At concentrations between 300 and 500 mg/kg, Zn is toxic to the plants (Pongrac et al. 2007; Miransari 2011d). The positive effect of mycorrhizal fungi on the alleviation of Zn pollution has been indicated in a polluted soil. It is important to select the right fungal species, which can survive under such a stress; they usually must be selected from a polluted soil. However, it must be mentioned that elevated levels of metal pollution may adversely affect the fungal performance (Chen et al. 2003). Under Zn stress, the related fungal genes are expressed and make the fungi survive the stress. Accordingly, the expression of the Zn transporter gene *GintZnT1* in *Glomus intraradices* indicated its role in the alleviation of stress. The related genes are able to result in the production of glutathione S-transferase, which is a Zn transporter (Gonzalez-Guerrero et al. 2005; Hildebrandt et al. 2006, 2007). Bi et al. (2003) indicated that mycorrhizal fungal absorption of Zn from soil solution affects Zn mobility by increasing pH and decreasing Zn uptake by plant.

Interestingly, there is some kind of controlling mechanisms between mycorrhizal fungi and the host plant under low and high levels of Zn. When there is low level of Zn in the soil, the fungi help the plant to absorb higher rates of Zn. However, with increasing the level of Zn in the soil (in a polluted soil), the fungi with the help of the plant roots make the plant to survive the stress by absorbing Zn, by increasing the plant growth and by controlling Zn uptake (Miransari 2011d).

Iqbal et al. (2010) compared different isolates of zinc phosphate solubilizing bacteria on the growth of *Vigna radiata* using their single or combined use with zinc phosphate. The inoculation of seedlings with isolate 102 (non-spore former) resulted in the highest plant growth. Isolate 111 (spore former) was the most efficient isolate to solubilize phosphate and isolate 36 (spore former) was the one with the greatest rate of Zn uptake.

Table 2 Mechanisms increasing the mobility of nutrients in the rhizosphere (Jones et al. 2004)

Nutrient	Metal complexation	Redox change	pH change	Biotic	Mycorrhiza	Root morphology
N				+++	+++	+++
P	++		+++ ↘	+++	+++	+++
K					++	
S				++		
Mg					++	
Ca					+	+++
Fe	+++	+++ ↘	++ ↘			+++
Mn	+++	+++ ↘	+++ ↘			+++
B						
Cl						
Zn	+++		+ ↘			+++
Cu	+++					
Mo			+ ↗			

+: low, ++: important, +++: very important, the arrows indicate the trend of solubility

Copper

Copper is also another necessary micronutrient for plant growth and yield production. However, compared with the other micronutrients it is necessary at less amounts by plant. It can regulate different plant activities including the activities of different enzymes as well as the process of symbiotic N fixation in legumes (Makoi and Ndakidemi 2007). The effects of soil microbes on copper availability in the soil are directly by the production of different compounds such as carboxylates and phenolic compounds or indirectly through affecting plant growth and hence the production of root exudates (Marschner 1995; Badri and Vivanco 2009).

Manganese

Similar to the other necessary micronutrients for plant growth, optimum amounts of manganese are also required for plant growth and yield production and at excess amounts it can adversely influence plant performance. Unlike the other soil micronutrients, manganese may not be deficient under dry climates and sometimes it can be found at high amounts. Soil biological activities can also affect Mn availability in the soil mostly by affecting plant growth and hence plant root exudates (Dutta and Podile 2010; Miransari 2011d).

While the process of manganese oxidation is biological, its reduction in the soil is both biological and chemical (Ghiorse 1988). Accordingly, it is likely to determine the availability of manganese in the soil using the ratio of soil oxidizing and reducing Mn bacteria (Rengel 1997). Interestingly, as the reduced form of manganese is available to plant, in the rhizosphere of manganese-efficient plants the number of manganese reducing microbes is higher than the oxidizing ones, which are higher in the rhizosphere of inefficient genotypes (Timonin 1946; Rengel et al. 1996).

As previously mentioned, the production of root and microbial exudates is an important parameter determining the availability of nutrients in the rhizosphere. Accordingly, it may be possible to enhance plant and microbial activity to increase nutrient availability in the rhizosphere and enhance their bioremediating ability; for example, by inserting the related genes. Divya and Kumar (2011) indicated that it is likely to increase the bioremediating ability of transgenic tobacco (for bisphenol and penta-chlorophenol) by inserting the laccase gene from *Coriolus versicolor*. The transgenic tobacco also indicated the expression of a manganese peroxidase gene from *Coriolus versicolor*. The production of such enzymes can be useful for the remediation of organic pollutants with small molecules (Iimura et al. 2002; Oller et al. 2005; Sonoki et al. 2005).

Conclusion

The effects of soil microbes on the properties of soil nutrients are presented in this review article. Soil microbes can significantly contribute to the availability of soil nutrients for plant use, which is of economical and environmental importance. Some of the most important details

and mechanisms, which may affect the availability of nutrients in the soil by microbial activities, have been presented. Different soil microbes can differently affect the properties of nutrients in the soil. This is particularly important for the production of biofertilizer as the most efficient strains must be selected for inoculum preparation (Miransari 2011c).

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