

How Rhizosphere Affects Microbes' Population and Availability of nutrients in the soil to Plants; A Review

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Abstract- The rhizosphere is the area of soil surrounding plant roots that is influenced by the plant's activities and the microorganisms living in close association with the roots. It is a dynamic zone where biological, physical, and chemical interactions occur between plants, soil, and microorganisms. The rhizosphere, which is located 2 mm from the root surface, is an important part of the plant environment. It controls the chemistry of plant nutrients and impacts plant development. In order to raise agriculture production worldwide and keep up with the expanding global demand for food, the nutrient requirements in agriculture have been rising and are anticipated to do so further. Most of the time, farmers apply fertilizers without understanding the function of the rhizosphere in a specific nutrient's chemistry or how accessible it is to plants. It can occasionally make a nutrient unavailable to a plant exhibiting deficient signs, lowering production. Plants can release lipids, vitamins, amino acids, and carbohydrates through their roots to promote the activity of microorganisms in the soil. Bacteria in the rhizosphere participate in the geochemical cycling of nutrients, particularly nitrogen, phosphorus, and micronutrients, including iron, manganese, zinc, and copper. Plants and microbial populations in the soil decide whether they are available. It raises the availability of nutrients to plants, generates growth hormones, and functions as a bioagent to manage diseases, increasing crop output. By modifying the rhizosphere environment through agronomic or/and breeding procedures, it is possible to increase the effectiveness of nutrient uptake.

Keywords; Rhizosphere, microorganism, plant nutrients, root exudates, nutrients availability

I. INTRODUCTION

The rhizosphere is a unique and dynamic soil volume in time and space, continuously shaped by the interaction between plants, soil, and microorganisms. In this peculiar soil volume, fluxes and gradients along the root (longitudinal) and away from the root (radial), together with physical, chemical, and biochemical interactions, trigger rhizosphere processes influencing, for instance, the biogeochemical cycles of nutrients, their solubility, soil transport and ultimately plant uptake and nutrient allocation. These processes are often the bottleneck of nutrient mobilization, impacting crop yield and quality of yields. Understanding these processes is thus critical and fundamental to adequately feeding the organisms living on them. The management of rhizosphere processes has recently been considered one of this decade's most important scientific frontiers (Mcneer, 2013).

Plant developmental processes are controlled by internal signals that depend on the adequate supply of mineral nutrients from the soil to root and root to shoot. Consequently, the availability of

plant nutrients may be a significant barrier to plant development in many different locales worldwide, particularly in the tropics, where nutrient-deficient soils reduce agricultural yield. Plants absorb most mineral nutrients through the rhizosphere, where microbes and root exudates interact. The complex mixture of organic acid anions, Phyto-siderophores, sugars, vitamins, amino acids, purines, nucleosides, inorganic ions (such as HCO_3^- , OH^- , and H^+), gaseous molecules (such as CO_2 and H_2), enzymes, and root border cells that makeup plant root exudate has a significant direct or indirect impact on the acquisition of the mineral nutrients needed for plant growth (Dakora and Phillips, 2002). Rhizosphere was described for the first time by Lorenz Hiltner in (1904). It varies with the plant species and the soil, generally considered at a 2 mm distance from the root surface, known as a rhizoplane. Researchers have shown that the influence can be up to 10 mm (Hartmann et al. 2008; Niu et al. 2013).

Root exudates represent one of the main driving forces of rhizosphere processes (and the so-called rhizosphere effect on plants). Their quality-quantitative composition depends on many factors, for instance, plant species, plant age, and environmental conditions (e.g., type of substrate, soil chemical characteristics, temperature, carbon dioxide (CO_2) concentration, and light conditions) (Mimmo et al. 2011). Besides being involved in the modulation of nutrients, root exudates are also involved in other fundamental functions, such as the protection of roots against toxic agents (metals like zinc (Zn), cadmium (Cd), aluminum (Al) (Jones, 1998) and pathogens and the attraction and pulsion of microorganisms (Bais et al. 2004). Nutrient availability differs between rhizosphere and bulk soil due to the interactions between soil, plants, and microorganisms (Jones et al. 2004). Therefore, standard chemical soil analysis of bulk soil samples does not exhaustively represent what occurs at the soil-root interface and only provides a rough approximation of the thioplast's available fraction of nutrients. Furthermore, this fraction depends on the soil's chemical-physical properties, the plant genotypes and species cultivated, and the agronomic practices adopted. Thus, root activity and the consequent rhizosphere processes cannot be excluded when setting up fertilization strategies to optimize, for instance, the exploitation of the nutrients' endogenous fraction of soil and the fertilizer use efficiency.

In particular, this review focuses on the rhizosphere effect on microbial population and diversity, the role of root exudates in mobilizing nutrients, microbe-plant interactions, focusing on healthy microbial communities and their association with plants, rhizosphere effect on plant nutrient availability and rhizosphere processes triggered when nutrients reach toxic concentrations focusing on copper (Cu) toxicity. These aspects are also discussed, considering the contribution of the metabolic changes triggered by nutrient shortage to the root exudation phenomenon.

II. Rhizosphere Effect on Microbial Population and Diversity

The micro-organism diversity is higher near the rhizoplane. It decreases with increased distance from the rhythm plane (Chowdhury et al. 2009; Paul and Clark, 1994) (Table 1). The interaction between plant nutrients in soil and plant exudates modifies the microclimate of the rhizosphere (Shukla et al. 2013). The soil volume is affected by the root exudates. Microorganisms exert influence on plants. The root-secreted organic compound enhances the microorganism population in the rhizosphere zone due to the increased availability of carbon (C) for food and energy (Aira et al. 2010). The plant secretes 10–30 % of photosynthates through the root system into the rhizosphere soil (Bowen and Rovira, 1999). The microorganism population is more in rhizosphere soil than the bulk soil. It determines the influence of the rhizosphere and the availability of nutrients. The rhizosphere effect on soil microbial population can be measured by comparing the population density [colonies forming units (CFU)] between the rhizosphere soil (R) and the bulk soil (S), for which the ‘‘R/ S ratio’’ (Table 2) is employed (Atlas and Bartha, 1997). The rhizosphere effect is higher for bacteria, fungi, actinomycetes, and protozoa. By contrast, algae exhibit more population in bulk soil than in rhizosphere soil. The type of associated plant can also affect the R/S ratio, which is directly related to the amount and type of root exudates (Rout and Katznelson, 1961). The activity of plant roots’ activity impacts the physicochemical conditions and the biological activity in the surrounding rhizosphere compartment and vice versa. These processes are determined by nutrient availability, cycling of nutrients, and solubility of toxic elements for plants and microorganisms, thereby creating a unique micro-ecosystem of rhizosphere which can exhibit completely different properties as compared with the bulk soil, not directly influenced by the activity of the roots (Neumann et al. 2009). The type and composition of root exudates, i.e., sugars, oligosaccharides, vitamins, nucleotides, flavones, auxins, and stimulators, mainly decide the diversity of microorganisms proliferating in the root zone (Dotaniya et al. 2013; Ueno et al. 2007). The decomposition of organic matter serves as an energy source for the growth of microorganisms and supplies C for their cell synthesis (Rillig et al. 2007). Under aerobic conditions, microbes assimilate 20–40 % of the substrate C, and the residual amount is released as CO₂ to the atmosphere (Zak et al. 2000; Rajendiran et al. 2012). The Rhizosphere effect is mainly governed by plant carbonic organic compounds released from plants and siderophores produced by microorganisms. The root surface area determines the extension of the rhizosphere effect. Mycorrhizosphere is more affected by nutrient chemistry in the soil as compared to those bacteria in the rhizosphere. Microorganism population varies in the rhizosphere and bulk soil and contributes significantly to determining the rhizosphere effect on nutrient availability and plant uptake (Vega, 2007; Gray and Williams, 1971). The plant species belonging to Gramineae, Solanaceae, and Leguminosae families had a higher rhizospheric effect on soil-available phosphorus (P) and biological properties than those belonging to Cruciferae and Compositae (Safari and Rashidi, 2012). Phyto-siderophores are organic substances [such as nicotinamide, mugineic acids (MAs) and avenic acid, etc.] produced by plants (Mori and Nishizawa, 1987) under iron (Fe)- deficient conditions, which can form

organic complexes or chelates with Fe³⁺, and increase the movement of iron in the soil (Ueno et al. 2007). Non-proteinous, low molecular weight acids are released by the graminaceous species under the iron and Zn deficiency stress (Wallace, 1991). The type of siderophore affects the plant nutrient uptake from the rhizosphere. *Rhizopus arrhizus* has a slightly higher affinity towards Fe compared to Phyto-siderophores. Rhizoferrin is a good Fe source for barley, probably because of the iron exchange (Fe) from rhizoferrin to the Phyto-siderophore (Yehuda et al. 1996). Anthropogenic activities have caused the concentration of atmospheric CO₂ to increase from 280 ppm at the beginning of the industrial revolution to over 370 ppm at present (Rouhier et al. 1994). Current estimates suggest that the atmospheric CO₂ concentration range will lie between 450 and 600 ppm by 2050 (Kattenberg et al. 1995). Microorganisms in soil regulate the dynamics of organic matter decomposition and plant nutrient availability and play a key role in the responses of ecosystems to global climate changes (Sadowsky and Schortemeyer, 1997). Elevated CO₂ affects soil microorganisms indirectly through increased root growth and rhizodeposition rates because the CO₂ concentration in soil is much greater than the atmospheric CO₂ (van Veen et al. 1991).

Table 1 Diversity in bacterial population with increasing distance from root surface (Paul and Clark, 1994)

Distance (mm)	CFU 10 ⁹ cm ⁻³ soil	Morphological types
0–1	120	11
1–5	96	12
5–10	41	5
10–15	34	2
15–20	13	2

Table 2 Number of bacteria (CFU×10⁶ g⁻¹ soil or root dry mass) in the rhizoplane and rhizosphere of different plants, and the bulk soil (S) and their R/S ratio

Plant species	Rhizoplane	Rhizosphere	Bulk soil	R/S ratio
Red clover (<i>Trifolium pratense</i>)	3844	3255	134	24
Oats (<i>Avena sativa</i>)	3588	1090	184	06
Flax (<i>Linum usitatissimum</i>)	2450	1015	184	05
Wheat (<i>Triticum aestivum</i>)	4119	710	120	06
Maize (<i>Zea mays</i>)	4500	614	184	03
Barley (<i>Hordeum vulgare</i>)	3216	505	140	03

(Rouat and Katznelson, 1961).

The impact of elevated CO₂ in soil ecosystems focuses primarily on plants and various microbial processes. The processes considered include changes in the microbial biomass of C and N, soil enzyme activity, microbial community composition, organic matter decomposition, and functional groups of bacteria mediating trace gas emission in terrestrial and wetland ecosystems (Paterson et al. 1997). At present, elevated concentrations of atmospheric gases like CH₄, N₂O, etc., also

play a significant role in global climate phenomena (Kundu et al. 2013). It affects root secretion from plant and rhizospheric microbial populations (Mandal et al. 2013). Studies revealed that the increased temperature accelerates the rate of microbial decomposition, thereby increasing CO₂ emitted by soil respiration and producing positive feedback to global warming (Allison et al. 2010). Response of biological systems with reference to temperature is expressed as a Q₁₀ function (Prosser, 1991).

$$Q_{10} = K_2/K_1^{10} (T_2 - T_1)$$

Q₁₀ is the relative change in decomposition rate with a 10 °C rise. k₂, k₁ are the rate constants for a process of interest at two observed temperatures, T₂ and T₁ are temperature increases in soil respiration exponentially. The concentration of heavy metal in the rhizosphere, change in the microbial population and root exudates from plants, and reduced plant nutrient uptake and crop growth (Leita et al. 1995 and Algaidi, 2010).

III. Role of root exudates in mobilizing nutrients

Plants can adapt to soil conditions characterized by low nutrient availability triggering the release of a myriad of low molecular weight (e.g., organic acids, amino acids, phenolics, Phyto siderophores, flavonoids, etc.) and high molecular weight (e.g., carbohydrates, enzymes) organic compounds (Dakora and Phillips, 2002). By influencing the soil-root interface's chemical, physical, and biological characteristics, they favor the mobilization of nutrients from sparingly available sources via acidification, reduction/ complexation, and/or ligand exchange reactions (Terzano et al. 2015a). In this respect, the white lupin plant species example is very interesting. These plants are very efficient in phosphorous(P)-mobilization thanks to both morphological and physiological modifications: on one side, they develop bottlebrush-like roots - the so-called cluster roots - increasing the soil volume being explored by the roots, and on the other side, these plant species concentrate the release of organic compounds (organic acids, flavonoids, and protons) from specific root segments of the clusters (Tomasi et al. 2009a). Furthermore, white lupin seems to even counteract the microbial degradation of organic acids around their cluster roots by releasing specific flavonoids (Cesco et al. 2010, 2012; Tomasi et al. 2008). Organic acids have a short half-life (Mimmo et al. 2014) since they are an easily accessible carbon source for microorganisms (Colombo et al. 2014). Yet, flavonoids are compounds that also have complexing and/or reducing properties and might, therefore, also impact the cycling of many mineral nutrients (Tomasi et al. 2008; Terzano et al. 2015b). Notwithstanding the mechanisms and the regulation of the root exudation process that has been largely investigated in model plants (Tomasi et al. 2009a; Wang et al. 2007; Weisskopf et al. 2006), the information regarding fruit crops is still limited. A recent study pointed out that iron (Fe) and P-deficient strawberries release citric acid and acidify their rhizosphere in response to nutrient shortages (Valentinuzzi et al. 2015a). The same authors identified five strawberry genes clustering in the multidrug and toxic compound extrusion (MATE) subfamily involved in citric acid transport and nine putative plasma membrane (PM) H⁺-ATPases. Among them, at least two members of the MATE transporter family and one of the PM H⁺ ATPases family were involved in responding to both P and Fe starvation in strawberry plants. Nutrient availability and, thus,

the nutritional status of the plant's impact, the yield, and the quality of fruit crops. The main nutrients being investigated are, however, only nitrogen (N) (Castellanos-Morales et al. 2010; Nestby et al. 2005), P and Fe (Valentinuzzi et al. 2015b); furthermore, most studies are limited to apple, pear, and peach (IvarezFernández et al. 2011), and there are only some reports on strawberry quality (Pestana et al. 2008; Valentinuzzi et al. 2015b). It has been demonstrated that the limited availability of Fe and P could positively affect both the nutritional and health parameters of strawberry fruits (Valentinuzzi et al. 2015b). While a decreased Fe content of strawberry fruits might not be a valuable option for the human diet (anemia), P-starved fruits have shown to be desirable both from a productive (increased fruit firmness and extended shelf life) and human health (more equilibrate vitamin D and Ca metabolism preserving the bone health) point of view (Valentinuzzi et al. 2015b). In addition, these fruits are also characterized by a high content of health-beneficial compounds (e.g., vitamin C and phenolic compounds) (Scalzo et al. 2005), which possess antioxidant (Diamanti et al. 2014), anticancer (Stoner and wang, 2013) and anti-inflammatory (Joseph et al. 2014) properties. A recent study pointed out that Fe and P-deficient strawberry fruits accumulate catechins, benzoic acids, anthocyanins, and flavonols (Valentinuzzi et al. 2015b), molecules well known for their health-beneficial properties. As mentioned earlier, root exudates are involved in nutrient mobilization processes. Yet, the mobilization efficiency depends on the type of root exudate and the soil characteristics for instance; citric acid has shown to be more efficient than oxalic and malic acid in mobilizing micronutrients such as Fe, manganese (Mn) and copper (Cu) from acid soil. On the contrary, in alkaline soil, the mobilizing efficiency changes depending on the nutrient considered: citric acids showed the highest mobilizing efficiency for Fe and Mn. In contrast, oxalic acid performed better for Cu (Terzano et al. 2015b). These different mobilization efficiencies are related to the different mineral weathering processes occurring in the rhizosphere. In fact, mineral alterations can occur within a few days (Hinsinger and Jaillard, 1993), particularly at the expense of amorphous soil fractions (Gattullo et al. 2016). Furthermore, root exudation, a process involving a complex cocktail of different compounds' classes, synergic, antagonistic, and additive effects might be expected (Oburger et al. 2009; Terzano et al. 2015a). A synergistic effect has been, for instance, observed between organic acids and flavonoids. When citric acid was combined with either rutin or quercetin, the mobilizing efficiency of Mn was almost two-fold greater compared to the single exudate (Terzano et al. 2015b). The authors have demonstrated that combining the two compound classes might induce a reductive-complexing process rather than a simple complexing-dissolution process. It is well known that the release of root exudates is far from uniform along plant roots (Marschner, 2011). For this reason, it is predictable that heterogeneous exudation can easily cause, together with other rhizosphere processes (e.g., pH modifications, water uptake, plant nutrient uptake, etc.), radial and longitudinal gradients of nutrients along the roots. For instance, depending on their mobility, nutrients might accumulate or deplete within the rhizosphere (Hinsinger et al. 2009). Radial gradients might vary, extending from less than one

mm for nutrients with low solubility (like phosphate) to several mm for very mobile nutrients like nitrate (Hinsinger et al. 2009). Furthermore, such gradients vary temporally and spatially due to the dynamic interplay between plant roots, soil, and microorganisms. Indeed, in many plant species, root exudation follows a diurnal rhythm, implying a diurnal pattern of nutrient gradients. Fe-deficient graminaceous plants give one well-described example: barley plants, very efficient Fe-mobilizing plants, since these plant species concentrate their release of phytosiderophores (PSs – not proteinogenic amino acids) between 2-4 h after the onset of light (Marschner et al. 1986). Also, white lupin plants are characterized by spatial and temporal exudation patterns. The release of citric acid is mainly concentrated around mature cluster roots (Massonneau et al. 2001) with an exudation burst five h after light onset (Tomasi et al. 2009a).

IV. Plant-microorganisms-soil interactions driving nutrient availability

Soil microorganisms are crucial actors in either enhancing or restricting rhizosphere processes. In fact, they play an important role in the organic matter turnover (mineralization) in soil, affecting, in turn, nutrient availability. Both structure and concentration of soil microbiome differ between the bulk soil and the rhizosphere since they feed on root debris and exudates, representing a very labile carbon source. It is interesting to note that plants of different crop species are characterized by distinct Fe acquisition strategies (dicots: Fe III-reduction-based mechanism named Strategy I; monocots: PSs-based Fe chelation mechanism named Strategy II – Marschner, (2012) when exposed to a nutritional disorder can use a qualitatively different root exudation to pursue the same objectives (in the case described by Pii et al. (2016) to affect the rhizosphere microbial community in order to cope with the low nutrient availability). Yet, microorganisms also release organic compounds, which can influence nutrient availability thanks to their complexing, solubilizing, reducing, and/or oxidizing properties (Colombo et al. 2014). Rhizobacteria, which positively affect plant health and growth (by increasing the plant nutrient uptake), is commonly known as plant-growth-promoting rhizobacteria (PGPR). Pii et al. (2015a) provide a detailed overview of the effects of PGPRs on the nutrient acquisition processes. The organic compounds released in the rhizosphere by plants and microorganisms can also be envisaged as an intricate exchange of molecular signals that establishes interaction between the two actors. Such molecular crosstalk is also believed to influence both interacting partners' molecular and biochemical responses (Venturi and Keel, 2016). A recent study showed that Fe-deficient cucumber plants grown on either a PGPR-inoculated soil or a non-inoculated one had different root exudation profiles, which eventually led the former to a quicker and more efficient recovery from the nutritional disorder (Pii et al. 2015b). Indeed, the altered exudation profile, at both qualitative and quantitative levels, could also be ascribable to bacterial metabolism (i.e., use of organic substrate as carbon (C) source, excretion of metabolites). Interestingly, this analysis confirmed the involvement of organic acids in the mobilization processes of mineral elements from soil particles. Nonetheless, it was also highlighted that amino acids could have a role in the rhizosphere

processes, particularly by functioning as both chemo-attractants for bacteria, as in the case of glutamate (Carvalho et al. 2011), and mobilizing agents, as for glycine (Pii et al. 2015b). Fe deficient monocots release glycine, and it was argued that complex Fe with efficiency similar to that of citrate is known to play an important role in Fe mobilization, uptake and translocation within plants (Mimmo et al. 2014; Fan et al. 2001; Tomasi et al. 2009b; Tomasi et al. 2014). These pieces of evidence suggest that besides playing a determinant role in the biogeochemical cycles of elements, microbes might also promote the absorption of nutrients by affecting plants' molecular pathways (Pii et al. 2015a). In this regard, the filamentous fungus *Trichoderma asperellum* was shown to enhance plant growth and Fe nutrition in both cucumber and white lupin by stimulating the activity of root Fe-chelate reductase (de Santiago et al. 2013; Zhao et al. 2014). Further evidence obtained in the model plant *Arabidopsis thaliana* demonstrated that the inoculation with the rhizobacteria *Bacillus subtilis* GB03 could induce Fe-sufficient plant to transiently activate the typical mechanisms widely described for dicots, as, for instance, the induction of Fe-chelate reductase activity, proton extrusion and genes expression, to cope with Fe shortage (Zhang et al. 2009). A deeper investigation of the mechanisms triggered by PGPR in cucumber plants demonstrated that microorganisms could affect both the growth and the architecture of the root system and the ability of plants to absorb Fe (Pii et al. 2016). The root morphology assessment demonstrated that PGPR enhanced root growth, allowing plants to explore a larger soil volume for nutrient interception. Interestingly, this effect was different depending on the Fe nutritional status of the plants: in Fe deficient plants, PGPR promoted the lengthening (elongation) of pre-existing lateral roots, whilst, in case of Fe sufficient plants, PGPR triggered the initiation of new lateral roots. Besides enhancing the root surface available for nutrient absorption, PGPR stimulated molecular and biochemical mechanisms underpinning the acquisition of the microelement. Inoculated Fe deficient plants expressed the genes encoding for the PM H⁺-ATPase and the ferric chelate reductase (FRO) at higher levels than control plants, determining stronger rhizosphere acidification and Fe reduction capacity (Pii et al. 2016).

V. Rhizosphere Effect on Plant Nutrient Availability

The rhizosphere is a densely populated area in which the roots must compete with the invading root system of neighboring plant species for space, water, mineral nutrients, and soil-borne microorganisms, including bacteria, fungi, and insects feeding on an abundant source of organic material (Ryan et al. 2001). Thus, root-root, root-microbe, and root-insect communications will likely occur continuously in this biologically active soil zone. However, due to the underground nature of roots, these intriguing interactions have largely been overlooked (Pradhan et al. 2013). Root-root and root-microbe communication can either be positive (symbiotic) to the plant, such as the association of epiphytes, mycorrhizal fungi, and nitrogen-fixing bacteria with roots, or negative to the plant, including interactions with parasitic plants, pathogenic bacteria, fungi, and insects (Walker et al. 2003). Some of the nutrient availability modified due to rhizosphere influence in the soil is described in the present paper. It determined the nutrient conversion of non-labile pools to

available form, which is helpful to enhance biochemical activities and nutrient uptake in plants.

A. Nitrogen

It is one of the important plant nutrients which limits crop growth and quality. The nitrogen uptake efficiency is 50% despite good management practices (Gillian et al. 1985). Oertli and Lunt (1962) showed that in sandy soils receiving 100–120 cm annual rainfall, the efficiency of N uptake might not exceed 20–30%. Additional application of nitrogenous fertilizers increases the cost of cultivation. The rhizospheric bacteria fix atmospheric N₂ in the soil in organic form, and plants easily use it (Cheng and Walker, 1998; Beauchamp et al. 2006). The rhizosphere conditions favor the N₂ fixation mainly by the *nifH* gene control process in soil because it is carried out by heterotrophic bacteria that use organic compounds as a source of electrons to reduce nitrogen (Kizilova et al. 2012; Vitousek et al. 2013). The protease, urease, and dehydrogenase activities in rhizosphere soil increase with wheat growth, maximize at jointing and heading stages, respectively, and decrease thereafter. Catalase activity increases with wheat growth and shows a peak at maturing stage (Gahoonia et al. 1992). In another experiment, the protease, catalase, and dehydrogenase activities in the rhizosphere soil of the two cultivars show an increase with increasing nitrogen application rate (Tai et al. 2013). Urease activity also increases with increasing nitrogen application rate. Its maximum activity is 360 kg N ha⁻¹ (Guo et al. 2008). Application of (NH₄)₂SO₄ reduces the rhizosphere pH by 0.22–0.29 unit and urea by 0.08–0.18 unit. The treatment with KNO₃ increased rhizosphere pH in bean plants (Thomson et al. 1993). Nitrogen fertilizers leave a residual effect on soil which modifies the rhizosphere pH through chemical reactions (Gundersen et al. 2006). The redox potentials (Eh) remain lower in the rhizosphere than in bulk soil, showing no direct relationships between Eh and nitrogen forms (Ring et al. 2013). Nitrogen fertilizers enhance the N concentration in soil solution but remain lower in the rhizosphere. Phosphorus always shows depletion in the rhizosphere, and the depletion zone remains larger in (NH₄)₂SO₄ than in the KNO₃ plot. The responses of potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), zinc (Zn), manganese (Mn), and Fe concentrations in the rhizosphere to nitrogen fertilizers vary with species of apple seedlings and treatments (Dong and Shu, 2001). Populations of anaerobic nitrogen-fixing bacteria and *Azospirillum sp.* and *Azotobacter sp.* were stimulated in such a combination. It is also suggested that rhizosphere pH gets altered using N-source fertilizers. Soil N availability and its uptake by plant tissues decline under elevated CO₂ in grasslands (Hu et al. 2001). It is linked to microbial N immobilization, which changes the soil's quality and quantity of exudates (Dijkstra et al. 2010). Some grazing-tolerant grass species have been shown to immediately increase C inputs to the soil. This stimulates microbial activity within the plant's rhizosphere and affects plant nutrient availability (Henry et al. 2008). In pulse crop microbial activity and plant, biomass can potentially increase soil N mineralization in the rhizosphere, thereby enhancing N uptake by the plant (Hamilton and Frank, 2001). However, the magnitude and direction of herbivore effects on the rhizosphere process can vary with plant species identity and defoliation intensity (Guitian et al. 2000).

B. Phosphorus

Its deficiency is one of the major limiting nutritional problems for plants, particularly in acidic and calcareous soils where P retention and precipitation are high ((Marschner, 1997). In recent years great attention has been dedicated to enhancing phosphorus use efficiency (PUE), which is nearly 15-20%. Phosphorus absorption by plants depends on its concentration gradient and diffusivity in the soil near the roots (Barber, 1995 and Narolia et al. 2013). Under such conditions, root-soil interactions in the rhizosphere noticeably affect the availability of P to plants (Marschner, 1997). In this relation, soil microorganisms play a vital role in the dynamics of P, particularly those which can solubilize insoluble P forms. The mycorrhizosphere favor nutrient uptake, particularly P, Cu and Zn (Lucas et al. 2011). The mycorrhizal association is a natural strategy in which fungal hyphae are extensions of the root system that increase soil volume, release organic acids, and mobilize insoluble P into plant-available P (Jiang et al. 2012). Root exudates composed of low molecular weight organic substances (LMWOS) represent a significant source of easily degradable organic C (Dotaniya et al. 2013). Small additions of LMWOS, such as amino acids or monosaccharides, to the soil, have been shown to strongly increase available phosphorus in soil (Blagodatskaya et al. 2009 and Dorodnikov et al. 2009). Especially glucose, an energy source for microorganisms, strongly affects microbial activity and phosphorus mineralization in the rhizosphere region (Pirainen et al. 2007). In contrast, amino acids mainly used as N and, less importantly, as C sources by microorganisms have a smaller effect on P mineralization from organic sources (Hamer and Marschner, 2005).

Studies revealed that plant species significantly decrease all the inorganic P (Pi) fractions in the rhizosphere soil compared to the bulk soil (Safari and Rashidi, 2011). Soil bacteria; that belong to the genera *Pseudomonas*, *Enterobacter*, *Bacillus Penicillium*, *Aspergillus*, and soil fungi solubilize insoluble phosphate (Whitelaw, 1999). The mechanism involved in the microbial solubilization of P is the production of organic acids and the release of protons to the soil solution. The alkaline phosphatase activity increases from 102 to 325% and acid phosphatase activity from 205 to 455% in the soil adhering to the root mat compared to the non-rhizosphere soil (Silber et al. 2004).

C. Iron

Its availability remains low in most aerobic soil. Microorganisms and plants release low molecular weight compounds (chelators), increasing Fe availability (Marschner et al. 2010). In plants, there are two different strategies in response to Fe deficiency. The strategy I plant (dicots and non-graminaceous monocots) releases organic acid anions which chelate Fe. Iron solubility is also increased by decreasing the rhizosphere pH, and Fe uptake is enhanced by reducing the roots' capacity (Fe³⁺Fe²⁺). Strategy II plants (Poaceae) release phytosiderophores that chelate Fe³⁺. It is taken up in the chelated form of Fe Phyto-siderophore (Von et al. 1993). Phyto-siderophores are released only a few hours daily at the root tip (Roemheld, 1991). Iron in young rice plants may be transported in phloem sap as deoxy-MA Fe in phloem sap has almost an equi-molar amount of Fe to deoxy-MA. Phloem sap of rice has a high pH (about 8) and under such conditions, Fe will preferentially bind with MAs rather than with other organic acids such as citrate or malate (Takagi et al. 1981). Some rhizosphere bacteria, particularly *Pseudomonas*, produce chelating agents

(siderophores) that form soluble complexes with Fe^{2+} and are available in iron-deficient soils (Dinlaker et al. 1989). The Fe and Zn contents of both shoot and root remain inversely proportional to rhizosphere pH. The Mn contents also increase with increasing pH, but a sharp decrease was apparent below pH 5.5. In the shoot of French bean (*Phaseolus vulgaris* L.) Fe, Zn and Mn contents remain significantly correlated with the extractable levels determined in the rhizosphere and non-rhizosphere soil (Sarkar and Wynjones, 1982).

D. Manganese

It plays an important role in plant growth and reduces the occurrence of plant diseases (Welch, 1995). The dynamics of Mn in the rhizosphere are very similar to that of Fe (Mackay and Barber, 1985). Its availability in soil solution increases with increasing acidic conditions. The rhizosphere effect is beneficial in alkaline soils where Mn is usually insoluble. However, its excessive reduction in acidic soil with abundant Mn can induce Mn toxicity in sensitive plants (Millaleo et al. 2010). The availability of Mn in the rhizosphere is affected by important factors like redox condition and pH, moisture, temperature, other nutrients, and heavy metal concentrations in soil solution. In oxidized soil, Mn is present in its oxidized form, Mn^{4+} in the low-soluble mineral pyrolusite. Some rhizosphere bacteria like *Bacillus*, *Pseudomonas*, and *Geobacter* reduce oxidized Mn^{4+} to Mn^{2+} , which is the chemical form metabolically useful for plants. The reaction is as follows:



This reaction is mediated in the rhizosphere, where the reduction of Mn requires electrons and protons, which are supplied through the decomposition of carbonaceous compounds and organic secretion from roots [60]. Several Mn reducing bacteria (*Pseudomonas sp.*) and fungi (*Gaeumannomyces graminis*) play a crucial role in enhancing its availability and crop uptake from the soil solution (Clair and Lynch, 2010).

E. Zinc

It attracts much interest in diverse disciplines of the scientific community. It has an integral role in various plant metabolic activities, including membrane integrity gene expression, carbohydrate, photosynthetic metabolism, detoxification of reactive O_2 species, phytohormone activity, and proper functioning of several enzymes and reduces the P toxicity (Prasad, 2006). Its deficiency causes crop yield reduction (Silber et al. 2012). In general, sandy loam and organic soils are more likely to be Zn deficient than silty or clayey soil. However, it can be enhanced by modifying the rhizosphere soil by the change in physiochemical parameters (White et al. 1997). Zinc is commonly provided to plants through fertilization with chelating agents (mainly EDTA or DTPA) (Cakmak, 2008). Zinc adsorption is affected by various factors such as soil mineralogical and chemical composition, organic matter content, and pH (Graham et al. 2001). Zinc availability in rice flowers is strongly associated with the pH in the root environment and ions present in soil solution (Silber et al. 2004). Zinc deficiency is common in neutral and calcareous soil, intensively cropped soil, paddy soil and poorly drained soil, sodic and saline soil, peat soil, soil with high available phosphorus and silicon, sandy soil and highly weathered acid and coarse-textured soil (Singh et al. 2005).

In deficiency conditions, Zn efficiency has been related to the various mechanisms operative in the rhizosphere and the plant system. Long and fine plant roots with architecture favoring exploitation of Zn from larger soil volume, higher synthesis, and release of Zn-mobilizing Phyto-siderophore by the roots in rhizosphere region promotes Zn uptake as Zn- Phyto-siderophore complex (Cakmak et al. 1996). Due to higher rhizosphere pH, the application of $\text{Ca}(\text{NO}_3)_2$ enhances the Zn concentration in *Thlaspi caerulescens*. The Zn concentration in the shoot increases as the rhizosphere pH increases. The $\text{Ca}(\text{NO}_3)_2$ is more effective treatment than urea or EDDS for enhancing Zn phytoextraction in mildly acidic soil (Monsanto, 2008). The plant uptake of Zn and Mn is a complex reaction both are positive cations, and competition for the uptake from soil solution depends on the concentration of the ions. The reason for the dissimilarity between Zn and Mn acquisitions by rice flower plants is not clear because it is to be expected that rhizosphere pH should control the availability of both micronutrients (Lindsay, 1979). The stability constants of Zn with EDTA or citrate and malate show important root excreted ligands higher than Mn (II) (Jones, 1998; Bar-Yosef, 1996). Thus, at equal solution concentration and based on thermodynamic consideration, it is expected that the Zn solubility in the root environment should be at least equal to that of Mn and Fe. The uptake of these metals by the plant depends mainly on the activity of the metal ion in the solution (Welch, 1995). Utilizing the chelated metals involves two steps: the liberation of the metal from the complex and reduction (Neumann et al. 2000). Hence, the rice flower plants' enhanced uptake of Fe and Mn may result from reduced extracellular reductase and the roots' release of phenolics and organic acids (Marschner, 1988). The NH_4OAc extraction procedure was satisfactory for predicting Cd and Zn bioavailability in rhizosphere soil (Liu et al. 2011). Low concentrations of Zn (below $10 \mu\text{mol l}^{-1}$) benefit plants, animals and humans, but the high concentration contaminates many environmental systems (Shivay et al. 2007).

F. Copper

Its dynamics are similar to that of zinc. It is also a micronutrient cation. The root exudation in the rhizosphere increases its availability and plant uptake (Jones, 1998). The root exudation of dicotyledons enhances the mobilization and uptake of Cu in nutrient solutions and calcareous soil as Cu-organic ligands (Degryse et al. 2008). Some of the Cu bacteria are found in a high concentration of Cu, soil which reduces the Cu concentration in soil. The Cu concentration decreases up to 36 % in the presence of bacterial strain MS12 and *Ampicillin* together compared with bacterial inoculation alone (Chen et al. 2005). When Ampicillin and the bacterial strains were added to the nutrient solution, the Cu concentration in the root and shoot of Ampicillin-treated plants was lower than those in inoculated plants. When Ampicillin was added to the nutrient solution, Cu accumulation was inhibited by about 24–44 % in shoots and 20–44 % in roots (Tarnawski et al. 2006). In the wheat root zone, Cu fractions are more affected by root activities as it modifies the concentration compared to bulk soil. In the rhizosphere of amended soil, the average of residual Cu, associated with iron–Mn oxides, organic matter, carbonates, and exchangeable Cu were 18.8, 2.1, 1, 0.37, and 0.24 mg kg^{-1} as compared to that of

the bulk soil as 18.1, 2.43, 0.8, 0.42 and 0.3 mg kg⁻¹ respectively (Motaghian and Hosseinpur, 2013).

VI. When nutrients reach toxic concentrations: in the case of copper

Both macro- (Mg, Ca, N, S, P, K) and micronutrients (Fe, Mn, Zn, Cu, Mo, B) contribute to an equilibrate plant growth and development as well as to several other important physiological and metabolic plant activities (Marschner, 2012). Yet, considering the micronutrients, even though essential to plants, they might become toxic at increasing concentrations. Copper, for instance, is an essential micronutrient involved in many metabolic processes, such as photosynthesis, respiration, carbohydrate metabolism, and reproduction (Kabata-Pendias, 2000). However, when soils with high levels of available Cu-fraction are considered, plants might accumulate the metal with biochemical and physiological impacts (Tiecher et al. 2016). Besides inhibiting plant growth by interfering in processes like membrane permeability, protein synthesis and the activity of enzymes involved in photosynthesis and respiration (Yruela, 2005). The excess of Cu causes oxidative stress ascribable to an imbalance between the antioxidant responses and the increased production of reactive oxygen species (Girrotto et al. 2013). Many agricultural soils worldwide – especially vineyard soils – face problems related to Cu toxicity due to the intense and long-lasting use of Cu-containing fungicides. While Cu concentrations range between 5 and 30 mg kg⁻¹ in most not contaminated agricultural soils, vineyard soils often reach Cu concentrations exceeding 200 mg kg⁻¹, far beyond the trace amount required for optimal plant growth (Brunetto et al. 2016). Hyperaccumulators, for instance, adopt an internal detoxification strategy since they can take up and translocate high Cu amounts (with concentrations up to a few percent of the shoot biomass) to the shoots without exhibiting any toxicity symptoms. Moreover, these plant species might even enhance the mobility and replenishment of Cu in their rhizosphere by releasing organic chelating compounds, further increasing the acquisition and hyperaccumulation (Wenzel et al. 2003). Excluder plants, on the contrary, adopting the so-called external tolerance mechanism, immobilize and decrease the bioavailability of Cu in the rhizosphere by chelating the metal with organic compounds. An interesting case is represented by some coniferous trees that release oxalic acid (Heim et al. 2001) when subjected to toxic Cu concentrations. Differently, some metallophytes exuded both citric and oxalic acid and phenolic compounds like cinnamic acid, coumaric acids and catechin in response to Cu (Meier et al. 2012). Also, amino acids have been detected in the root exudates of some Cu tolerant plant species (Huang et al. 2016). Despite the evidence of the huge importance of low-molecular-weight compounds in modulating Cu availability in the rhizosphere, most of the results are based on hydroponic experiments. Soil-based experiments are crucial to confirm their role in alleviating Cu toxicity at the field scale.

Conclusion

The increasing world population and increasing food demand will be a great challenge for agricultural soils. In the last decades, significant agricultural production was achieved only by applying high fertilizers and agrochemicals. Yet, from an economic and environmental point of view, there is an urgent

need to move towards more sustainable agricultural systems that also consider the exploitation of endogenous sources of nutrients in soils. In this respect, considering that the availability of nutrients is a consequence of chemical, physical and biological interactions occurring in the rhizosphere, the knowledge of these phenomena is crucial to predict the nutrient cycling in the agroecosystems and to set up agronomic practices and actions, including breeding programs for crops, to ensure yields qualitatively adequate to the needs. The rhizosphere effect on nutrient mobility and plant nutrient uptake is a key activity in crop production. The manipulation of root activities and its exudation from the plant root by biotechnological tools or evolved nutrient-efficient varieties in nutrient-deficient conditions enhance nutrient use efficiency through improved plant root architecture in terms of thinner and longer roots having a larger surface area of nutrient absorption or utilization. Screening high organic compound-producing bacteria and their utilization is beneficial in seed treatment. More precise research should be done on challenges of plant sciences in rhizosphere areas like in situ detection and quantification of root distribution; monitoring of root activity, reflected by root-induced physicochemical changes in the rhizosphere, characterization of the underlying regulatory mechanisms at the physiological and molecular level and knowledge transformation into modeling approaches and strategies of rhizosphere management.

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