IJETST- Vol.||02||Issue||09||Pages 3208-3216||September||ISSN 2348-9480 2015

Open access Journal International Journal of Emerging Trends in Science and Technology

DOI: http://dx.doi.org/10.18535/ijetst/v2i9.12

Rhizosphere Microbiome and Plant Nutrition

Authors
Badaru Suleiman[1], Buhari Lawan Muhammad[2], Bello Hassan Jakada[3], Dr. N. L. Vyas[4]
[1]Jodhpur National University, Faculty of Applied Sceinces,
Jhanwar Road Village Narnadi, Near Boranada, Jodhpur, (Raj) India
Email: *suleiman.badaru@yahoo.com*
[2]Jodhpur National University, Faculty of Applied Sceinces,
Jhanwar Road Village Narnadi, Near Boranada, Jodhpur, (Raj) India
Email: *buharilawan20@gmail.com*
[3]Jodhpur National University, Faculty of Applied Sceinces,
Jhanwar Road Village Narnadi, Near Boranada, Jodhpur, (Raj) India
Email: *bellojakada@gmail.com*
[4]Jodhpur National University, Faculty of Applied Sceinces,
Jhanwar Road Village Narnadi, Near Boranada, Jodhpur, (Raj) India
Email: *vyasnandlal@gmail.com*
Corresponding Author
Badaru Suleiman
Jodhpur National University, Faculty of Applied Sceinces,
Jhanwar Road Village Narnadi, Near Boranada, Jodhpur, (Raj) India
Email: *suleiman.badaru@yahoo.com*

Abstract

Rhizosphere microorganisms can affect agricultural productivity by assisting and controlling nutrient availability/acquisition for instance results of experiments suggest that Arbuscular mycorhizae (AM) fungi absorb N, P, K, Ca, S, Cu, and Zn from the soil and translocate them to associated plants. However, the most prominent and consistent nutritional effect of AM fungi is in the improved uptake of immobile nutrients, particularly P, Cu, and Zn [2]. The fungi enhance immobile nutrient uptake by increasing the absorptive surfaces of the root. Rhizosphere bacteria participate in the geochemical cycling of nutrients and determine their availability for plants and soil microbial community. For instance, in the rhizosphere there are organisms able to fix N_2 *forming specialized structures (e.g., Rhizobium and related genera) or simply establishing associative relationships (e.g. Azospirillium, Acetobacter). On the other hand, bacterial ammonifiers and nitrifiers are responsible for the conversion of organic N compounds into inorganic forms (*NH_4^+ *and NO3-) which are available for plants. Rhizosphere bacteria can also enhance the solubility of insoluble minerals that control the availability of phosphorus (native or applied) using organic acids or producing phosphatases that act on organic phosphorus pools. The availability of sulfur, iron and manganese are also affected by redox reactions carried out by rhizosphere bacteria.*

Keywords: *Rhizosphere, Microbiome, Mycorhizae, Bacteria*

1. Introduction

Rhizosphere is the region that surrounds plant roots, where materials released from the roots, and the root metabolic activities, change the characteristic of the soil. Microbes take advantage of the nutrients that the plant provides and on their own part, assist the plant in making more essential nutrients available for plant use [4]. The microbes in the rhizosphere also contribute to soil fertility and are important in long term maintenance and improvement of the soil environment. The rhizosphere thus forms an important part of the first “world” with which the plant roots interact. It is possible to view it as a cloud of microbes, which literally surrounds the plant root and is vital for the plant survival and growth. The microbes in the rhizosphere grow using the available mineral deficient root materials such as carbon and energy source and then develop enzymes to degrade the nutrient rich (but carbon poor) resistant soil organic matter. In this process, the essential nutrients are changed from complex to simpler forms, which are used by the microbes. The microbes assimilate the nitrogen and other essential nutrients in the forms that the plant can use; the process of mineralization.

Although the presence of microbes in plants is initially related to the occurrence of diseases, it is now recognized that the vast majority of microbial organisms are not causal agents of damage in plants. Several functions have been attributed to microbial cells in close association with plants, for instance, their ability to provide nutrients, such as phosphorus solubilization and nitrogen fixation, their support of nutrient uptake from the soil, as described for the mycorrhiza; and their capacity to promote plant protection by hindering agents of plant stresses, such as infection by pathogens and pests[22].

1.1The Rhizosphere

The rhizosphere is the zone of soil surrounding a plant root where the biology and chemistry of the soil are influenced by the root. This zone is about 1 mm wide, but has no distinct edge. Rather, it is an area of intense biological and chemical activity influenced by compounds exuded by the root, and by microorganisms feeding on the compounds. As plant roots grow through soil they release water soluble compounds such as amino acids, sugars and organic acids that supply food for the microorganisms. The food supply means microbiological activity in the rhizosphere is much greater than in soil away from plant roots. In return, the microorganisms provide nutrients for the plants. All this activity makes the rhizosphere the most dynamic environment in the soil. Because roots are underground, rhizosphere activity has been largely overlooked, and it is only now that we are starting to unravel the complex interactions that occur. For this reason, the rhizosphere has been called the last frontier in agricultural science.

1.2 The Microbiome

The word ‘microbiome’ was first used by Joshua Lederberg as the “*ecological community of commensal microorganisms, symbionts or pathogens that literally occupy a space in our body*[20]. Hence, the human body is a great reservoir of microbes, recently broadly studied by the Human Microbiome project, which linked several features of the host to the presence of specific sets of microbial groups [32]. More recently, the use of this term has been broadly applied to different sets of microbes found in specific hosts or inhabiting a given environment. It is Proposed that the best definition of ‘microbiome’ would relate to the set of genes encountered in association with the host or a defined environment, thus diminishing the importance of the link between taxonomy and functionality of the microbial community members. These assumptions made feasible the application of the microbiome concept to plants, which carry out several essential functions in association with distinct microbial groups.

Mycorrhizae As A Member Of The Rhizosphere Microbiome

The term “mycorrhiza” was coined by A. B. Frank, a scientist in Germany, more than 100 years ago. It literally means fungus-root, and describes the mutualistic association existing between a group of soil fungi and higher plants. The association is based on the plant component providing carbohydrates and other essential organic compounds to the fungi. In return, the fungal component, which colonizes both the root and the adjacent soil, helps the plant take up nutrients by extending the reach of its root system. Although mycorrhizal associations were discovered over 100 years ago, their role in plant productivity did not receive the attention until the past 30 years. Today, hundreds of scientists all over the world are engaged in the study of mycorrhizal associations, and any discussion of plant productivity that does not include mycorrhizal associations can hardly be considered complete.

2.1 Types of mycorrhizae

Mycorrhizae are commonly diviede into endomycorrhizae, ectomycorrhizae and ectendomycorrhizae

Endomyorrhizae

In this type of mycorrhizae the hyphae of the fungus penetrate the cell wall and invaginate the membrane. Endomycorrrhizae is further divided into

1. Arbuscular mycorrhizae
2. Ericoid mycorrhizae
3. Arbutoid mycorrhizae
4. Monotropoid mycorrhizae and
5. Orchidaceous mycorrhizae

Arbuscular mycorrhizae (AM)

This is the commonest mycorrhizae. They are also called vesicular-arbuscular mycorrhizae (VAM). Vesicular-arbuscular mycorrhizal (VAM) fungi colonize plant roots and ramify into the surrounding bulk soil extending the root depletion zone around the root system. They transport water and mineral nutrients from the soil to the plant while the fungus is benefiting from the carbon compounds provided by the host plant. Therefore VA-fungi have a pervasive effect upon plant form andfunction[11]. Fungi are the members of glomeromycota. AM are found in 85% of plant families and occure in many plant species.

Ericoid mycorrhizae

These are the mycorrhizae of Erica, Calluna and Vaccinium plants. That is, plants that endure acidic soil or similar challenging environments. Fungi are members of the Ascomycota. The fungus digest polypeptides saprophytically and passes absorbed nitrogen to the plant host. In extremely harsh condition the mycorrhizae may provide the host with carbon sources by metabolizing polysaccharides and proteins for their carbon sources.

Arbutoid mycorrhizae

These are mycorrhizae found in plant genera Arctostaphylos and Arbutus of the order Ericales. The fungi are members of basidiomycetes. In arbutoid mycorrhizae part of the hyphae penetrate the root cells while some part found at the root surface.

Monotropoid mycorrhizae

This is the mycorrhizae of the family monotropaceae. Until recently monotropoid are previously classified as arbutoid. The major difference difference is that monotropoid hyphae do not show deep penetration as arbutoid. Example of plants are *Monotropa hypopitys* and *M. Uniflora.* The monotropaceae members are mostly achlorophylous as such they use their mycorrhizae to tap carbon supplies of nearby plants via their roots.

Orchidaceous mycorrhizae

This is the mycorrhizae of orchid plants. They are similar to ericoid mycorrhizae but their carbon nutrition is more dedicated to supporting the host plant as the young seedling is non-photosynthetic and depends on the fungus which utilize complex carbon sources making carbohydrate available to the plant. The fungus is of Basidiomycetes (Genus rhizoctonia).

Ectomycorrhizae

In ectomycorrhizal associations, the fungi invade the cortical region of the host root without penetrating cortical cells. The main diagnostic features of this type of mycorrhiza are the formation within the root of a hyphal network known as the Hartig net around cortical cells and a thick layer of hyphal mat on the root surface known as *sheath* or *mantle*, which covers feeder roots. Infection of host plants by ectomycorrhizal fungi often leads to changes in feeder roots that are visible to the naked eye. Feeder roots colonized by the fungi are thicker and more branched than uncolonized roots; ectomycorrhizal feeder roots also tend to be colored differently. This type of mycorrhizae occur in about 3% of seed plants.most common are forest and ornamental trees as well as some members of family Rosaceae and Leguminaceae. The fungus are members of Basidiomycetes.

Ectendomycorrhizae

These are found in coniferous and deciduous plants in nurseries and burned forest sites. They exhibit characteristics of ectomycorrhizae and endomycorrhizae. That is the fungus sheath covered the root surface but shows intracellular penetration of the fungal hyphae into the living cells of the host. The fungus hyphae are septate and produce chlamydospores bothe on root surface and within the tissues. These mycorrhizae is replaced by ectomycorrhizae as the seedling matures. Fungus are members of Ascomycetes.

2.2 Role of mycorrhizae in plant nutrition

AM fungi absorb N, P , K, Ca, S, Fe, Mn, Cu, and Zn from the soil and then translocate these nutrients to the plants with whose roots they are associated. Their most consistent and important nutritional effect is to improve uptake of immobile nutrients such as P, Cu, and Zn.AM fungi have their greatest effect when a host plant not associated with them is deficient in P. They are also very useful to plant species that inherently lack either morphological or physiological mechanisms for efficient P uptake. Consequently, enhancement of growth of plants associated with AMF is explained in most instances by improved P nutrition[25].

Another advantage to associated plants is improved maintenance of a balanced supply of nutrients. This occurs because plants grown in association with AMF can grow with only a fraction of the P required for growth by plants lacking a mycorrhizal association. Moreover, when P is applied at high concentrations, as is commonly done when growing plants in soil where AMF are absent, it can cause nutritional disorders because of its antagonistic interactions with other nutrients, or because it inhibits mycorrhizal formation[6].

Studies with the forage tree *Leucaena leucocephala*, which is highly dependent on mycorrhizal association, have shown that the AMF symbiosis can decrease the plant's external P requirement, reducing it to as much as 40 times less than the plant would require for good growth in the absence of AMF. The ability of AMF to reduce plants' external P requirement has an important environmental benefit. High levels of P in soils can result in pollution of bodies of water when eroded soil rich in P is deposited in them. P enrichment of water bodies causes eutrophicationdue to excessive development of algae, cyanobacteria, and aquatic plants, and this condition impairs the usefulness of these waters. When plants rely on AMF association rather than heavy P fertilization, risks to water quality are reduced. Arbuscular mycorrhizal fungi, therefore, are an important component of nutrient management programs that aim to reduce environmental pollution[3].

2.3 Mechanisms of enhanced P uptake

In soils not adequately supplied with P, plant demand for this nutrient exceeds the rate at which it diffuses into the root zone, resulting in zones of P depletion surrounding roots. It is believed that AMF help overcome this problem by extending their external hyphae from root surfaces to areas of soil beyond the P depletion zone, thereby exploring a greater volume of the soil than is accessible to the unaided root [15]. The external hyphae of some AMF may spread 10–12 cm from the root surface. Assuming a radial distribution of hyphae around roots, it has been estimated that the volume of soil explored by the mycorrhizal root exceeds that explored by the unaided root by as much as 100 times [9].

AM fungal hyphae are 2.5–5 times smaller in diameter than plant roots and therefore have a greater surface area per unit volume. This surface area makes the fungi much more efficient than roots in the uptake of P. Moreover, the smaller diameter of AMF hyphae allows them to explore micropores in the soil that are not accessible to roots. And, studies carried out in solution culture have shown that AMF hyphae have a higher affinity for P than do roots [30].

AM fungi may have biochemical and physiological capabilities for increasing the supply of available P or other immobile nutrients. These mechanisms may involve acidification of the rhizosphere, increases in root phosphatase activity, and excretion of chelating agents.

2.4 Roles not directly related to nutrition

A growing body of research suggests that AMF could contribute to plant health and productivity independently of their role in enhancing nutrient uptake. For example, the fungi have been found to be involved in the suppression of plant diseases, including nematode infection.AMF stimulate hormone production in plants, aid in improving soil structure, enhance leaf chlorophyll levels, and improve plant tolerance to water stress, salinity, soil acidity, and heavy metal toxicity [10].Some of these functions may be the indirect effects of improved P nutrition.

3. Bacteria As Member Of The Rhizosphere Microbiome

A variety of symbiotic (Rhizobiumsp.) and non-symbiotic bacteria (Azotobacter, Azospirillum, Bacillus, and Klebsiellasp., etc.) are now being used worldwide with the aim of enhancing plant productivity[7]. Free-living soil bacteria beneficial to plant growth are usually referred to as plant growth promoting rhizobacteria (PGPR), capable of promoting plant growth by colonizing the plant root [16]. PGPR are also termed as plant health promoting rhizobacteria (PHPR) or nodule promoting rhizobacteria (NPR) and are associated with the rhizosphere.

According to their relationship with the plants,PGPR can be divided into two groups: symbiotic bacteria and free-living rhizobacteria [1]. PGPR can also be divided into two groups according to their residing sites: iPGPR (i.e., symbiotic bacteria), which live inside the plant cells, produce nodules, and are localized inside thespecialized structures; and ePGPR (i.e., free-living rhizo- bacteria), which live outside the plant cells and do not produce nodules, but still promote plant growth [8]. The best-known iPGPR areRhizobia, which produce nodules in leguminous plants. A variety of bacteria have been used as soil inoculants intended to improve thesupply of nutrients to crop plants. Species of Rhizobium (Rhizobium, Mesorhizobium, Bradyrhizobium, Azorhi- zobium, Allorhizobiumand Sinorhizobium) have beensuccessfully used worldwide to permit an effective establishment of the nitrogen-fixing symbiosis with leguminous crop plants [27]. On the other hand, non-symbiotic nitrogen-fixing bacteria such asAzotobacter, Azospirillum, Bacillus, and Klebsiellasp. are also used to inoculate a large area of arable land in the world with the aim of enhancing plant productivity [20]. In addition, phosphate-solubilizing bacteria such as species of Bacillusand Paenibacillus (formerly Bacillus) have been applied to soils to specifically enhance the phosphorus status of plants [23].PGPR have the potential to contribute in the development of sustainable agricultural systems. Generally, PGPR function in three different ways i.e. synthesizing particular compounds for the plants, facilitating the uptake of certain nutrients from the soil, and lessening or preventing the plants from diseases [18].

3.1 The Uptake of Various Nutrients By Rhizosphere Bacteria For The Plant Use

Nitrogen fixation

Nitrogen is one of the most limiting plant nutrients for plant growth [17]. Some rhizosphere bacteria have the ability to fix N_2 into organic forms that can then be used by plants. The rhizosphere conditions favor the N_2 fixation because it is carried out by heterotrophic bacteria that use organic compounds as source of electrons for the reduction of N_2. Prominent among these microorganisms are the N_2 fixers of the genera Rhizobium, Bradyrrhizobium, Mesorhizobium, Allorhizobium, Sinorhizobium, and Mesorhizobium that form symbiosis with legumes. In this case the concentration of O_2 is regulated by hemoglobin and the supply of carbonaceous compounds occurs in the interior of nodules avoiding competition of other microorganisms [26]. They are perhaps the most studied interaction between plant and bacteria.

Another N_2 fixer is *Azotobacter paspali*, which grows in the rhizosphere of tropical grasses, such as *Paspalum notatum* and Digitaria species, which exhibit certain degree of specificity [5]. Although fixation of 5- 25 kg N ha-1 year-1 are widely accepted, values as high as 90 kg N ha-1 year–1 have been reported. *Azotobacter diazotrophicus* is a N_2 fixer that can grow inside of the root tissue (endorhizosphere) of sugarcane, including vascular tissues. For its particular location, *A. diazotrophicus* has the advantage of a supply of carbon without microbial competition and apparently can tolerate high concentration of O_2 than other bacteria. Sugarcane can derive as much as 100- 150 kg N ha-1 from this association.

Manganese

The availability of manganese (Mn) in the rhizosphere is affected by two major factors: redox condition and pH [13]. In oxidized soils manganese is present in its oxidized form, Mn4+, in the lowsoluble mineral Pryolusite. Some rhizosphere bacteria (Bacillus, Pseudomonas, and Geobacter) can reduce oxidized Mn4+ to Mn2+, which is the chemical form that is metabolically useful for plants.Mn plays an important role in the resistance of plants to plant disease. Mn, as well as Cu, is required for the synthesis of lignin, which increase the resistance of the root tissues to the penetration of pathogens, consequently Mn-deficient plants are more susceptible to the attack of plant pathogens. *Gaeumannomyces graminis*, like many other soilborne pathogenic fungi, is a powerful oxidizer of Mn that impairs the lignification of root at infection sites [29]. Effective rhizosphere Mn-reducers (e.g., Pseudomonas sp.) could have beneficial effects not only on plant nutrition but also on biocontrol of pathogens [14]. In addition, roots and rhizosphere bacteria can produce chelating-agents (phenolic compounds, organic acids) that form soluble complex with Mn and other elements avoiding the reprecipitation of Mn [14].

In contrast, in flooded soils where the availability of Mn2+ can be high, the Mn-oxidization by rhizosphere bacteria would favor plant growth. Rice roots release O_2 in the rhizosphere avoiding Mn-toxic effects. On the other hand, Mn-oxidizing bacteria in the rhizosphere of plants grown in M-deficient soils can play an important role in plant disease control [10]. By reversing reaction, these bacteria reduce the availability of Mn^{2+} for fungal pathogens limiting its ability to attack roots.

Iron:The dynamics of iron in the rhizosphere is very similar to that of manganese [13]. Soil Fe is present in oxidized forms Fe^{3+} as a component of the structure of insoluble minerals Goethite (FeOOH) or hematite (Fe_2O_3). Rhizosphere bacteria (Bacillus, Pseudomonas, Geobacter, Alcaligenes, Clostridium, and Entero-bacter) can reduce Fe^{3+} to Fe^{2+}, the form required by plants. Electrons and protons are available in the rhizosphere and consequently iron is reduced, however it can be reprecipitated [24].

Under Fe-deficiency, rhizosphere bacteria, particularly fluorescent Pseudomonas, produce chelating agents (side-rophores) that form soluble complexes with Fe^{2+} and that are available for these bacteria [14]. Scher 1986, found in Fusarium-suppressive soils that Pseudomonas putida produced a siderophore that sequestered iron. The complex siderophore-Fe can only be used by P. putida but no by Fusarium, which requires iron to synthesize enzymes that degrade the plant cell walls. However, when Fe-EDTA (an iron fertilizer) was applied, the biocontrol was lost because Fusarium could use this fertilizer.

Solubilization of phosphates by rhizosphere bacteria

In recent years, great attention has been dedicated to study the role that soil microorganisms play in the dynamics of phosphate (P), particularly those able to solubilize insoluble P forms. These microorganisms are bacteria and fungi that inhabitant the rhizosphere. Most soil bacteria can solubilize insoluble phosphates, particularly active are those that belong to the genera Pseudomonas, Enterobacter and Bacillus[31]. The mechanisms involved in the microbial solubilization of P are the production of organic acids and the release of protons to the soil solution [21]. Inoculation with phosphate solubilizing rhizosphere bacteria (PSRB) and other soil microorganisms, such as arbuscular mycorrhizal fungi (AMF), might enhance even more the benefits of this P solubilization.

4. Conclusion

The diversity of microbes associated with the plant roots is enormous. This complex plant associated microbial community also referred to as the second genome of the plant is crucial for plant nutrition. For instanceMycorrhizal fungi occur in most of the soils and colonize roots of many plant species. Mycorrhiza are the structures resulting from the symbiosis between these fungi and plant roots, and are directly involved in plant mineral nutrition. The symbiotic root-fungal association increases the uptake of less mobile nutrients, essentially phosphorus (P) but also of micronutrients like zinc (Zn) and copper (Cu), the symbiosis has also been reported as influencing water uptake. AMF can also benefit plants by stimulating the production of growth regulating substances, increasing photosynthesis, improving osmotic adjustment under drought and salinity stresses and increasing resistance to pests and soil borne diseases. These benefits are mainly attributed to improved phosphorous nutrition. Most horticultural and crop plants establish the symbiosis with AMF. Although mycorrhizal associations were discovered over 100 years ago, their role in plant productivity did not receive the attention it should until the past 30 years. Today, hundreds of scientists all over the world are engaged in the study of mycorrhizal associations, and any discussion of plant productivity that does not include mycorrhizal associations can hardly be considered complete.

Rhizosphere bacteria also participate in the geochemical cycling of nutrients and determine their availability for plants and soil microbial community. For instance, in the rhizosphere there are organisms able to fix N_2 forming specialized structures (e.g., Rhizobium and related genera) or simply establishing associative relationships (e.g. Azospirillium, Acetobacter). On the other hand, bacterial ammonifiers and nitrifiers are responsible for the conversion of organic N compounds into inorganic forms (NH_4^+ and NO_3^-) which are available for plants. Rhizosphere bacteria can also enhance the solubility of insoluble minerals that control the availability of phosphorus (native or applied) using for that organic acids or producing phosphatases that act on organic phosphorus pools. The availability of sulfur, iron and manganese are also affected by redox reactions carried out by rhizosphere bacteria.

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Author Profile

Badaru Suleiman received his B.sc in Botany at Bayero University Kano, (BUK) Nigeria in 2012. He Worked at Kano State Ministry of Environment as an industrial training student in 2011 and currently studying M sc. Botany at Jodhpur National University, Rajasthan India

Buhari Lawan Muhammad received his Bsc, in Botany at Bayero University Kano (BUK). Nigeria, in 2010. In 2010 He worked at International Institute of Tropical Agriculture, as Industrial Training Student, Currently he is a Student of Msc Botany at Jodhpur National University (JNU), Jodhpur city (Rajasthan), India.

Bello Hassan Jakada received his B.sc in Botany at Bayero University Kano, (BUK) Nigeria in 2012. He Worked at Kano State Ministry of Environment as an industrial training student in 2011 and currently studying M sc. Botany at Jodhpur National University, Rajasthan India.