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Rhizosphere microbial communities: A review

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ABSTRACT

Rhizosphere is the region of soil immediately surrounding plant roots. There are more microorganisms in the rhizhosphere than in the rhizosphere free soil. Some microorganisms found in the rhizosphere are, bacteria (e.g. species of *Azotobacter, Rhizobium, Pseudomonas, Bacillus*), actinomycetes (e.g. species of *Actinomyces*, *Nocardia* and *Streptomyces*), fungi (e.g. species of *Aspergillus, Penicillium, Fusarium, Cladosporium*), protozoan (e.g. species of *Entamoeba, Euglena*) and viruses (e.g. bacteriophage, species of *Myxovirus*). However, bacteria are the predominant microorganisms. Plants secrete many compounds into the rhizosphere which serve as food for the microorganisms, e.g. amino acids, organic acids, carbohydrates/sugars, nucleic acid derivatives, growth factors, vitamins and mucilage. Microorganisms in return fix nutrients to the plants. There are several ecological relationships between plant roots and microorganisms in the rhizosphere e.g. mycorrhizae (fungi and plant root). Several relationships exist between microflora of the rhizosphere, this may be beneficial (e.g. cometabolism and mutualism) or detrimental (e.g. predation, amensalism and competition). The factors that affect the microbial floral of the rhizosphere are soil type, moisture, soil amendments/fertilizers, rhizosphere pH, proximity of root with soil, plant species, age of plant and root exudates.

KEYWORDS

Rhizosphere;
Exudates;
Microorganisms;
Plant roots;
Ecological relationships.

INTRODUCTION

Rhizosphere can be defined as the region of soil surrounding plant roots[3,24], it is the zone of soil surrounding a plant where the biology and chemistry of the soil are influenced by the roots[9,24,29]. This definition encompasses not only the roots and region of nutrient uptake by the roots, but extends into soils by action of root products and the trophic interactions that are affected by these products or by roots[28]. This zone is about 1mm away from the root and about 5mm wide, but has no distinct edge. Rather, it is an area of intense biological chemical activity influenced by compounds exuded by the root and by microorganisms feeding on the compound (www.agric.nsw.au/reader/soil-biology).

The rhizoplane is the root epidermis and outer cortex where soil particles, bacteria and fungal hyphae adhere[43,39]. The rhizosphere can be divided into endorhizosphere, i.e. the root itself with associated microorganisms, the rhizoplane, i.e. the root surface and the ectorhizosphere, i.e. the soil in close vicinity to roots. The abundance of microorganisms in the rhizosphere depends on the amount and composition of rhizodeposits with generally higher numbers of microbes near the root tip, branching points and root base[38].

MICROBIAL COMMUNITIES IN THE RHIZOSPHERE

The rhizosphere is a centre of intense biological activity due to the food supply provided by the root exudates. Bacteria, actinomycetes, fungi, protozoa, slime moulds, algae, nematodes, enchytraeid worms, earthworms, millipedes, centipedes, insects, mites, snails, small animals and soil viruses can be found in the rhizosphere, they compete constantly for water, food and space[24] and carry out fundamental processes that contribute to nutrient cycling, plant growth, and root health[27].

Bacteria

Bacteria are the most numerous organisms in the soil[3] averaging between 1 x 10^6 and 1x10^9 organisms per gram of rhizosphere soil. Due to their small mass, they only account for a small amount of the biomass of soil. Many studies indeed suggest that the *Proteobacteria* and the *Actinobacteria* form the most common of the dominant populations (>1%, usually much more) found in the rhizosphere of many different plant species[40].

Diverse plant growth promoting *rhizobacteria* PGPR strains have been used successfully for crop inoculations[3]. These comprise members of the bacterial genera *Azospirillum*, *Bacillus*[3,13], *Pseudomonas*[3,17,23], *Rhizobium*[3,23], *Serratia* and *Stenotrophomonas*[36].

Actinomycetes

Actinomycetes population has been identified as one of the major groups of the soil population[44]. This replenishes the supply of nutrients in the soil and is an important part of humus formation. Actinomycetes are numerous and widely distributed in soil and are next to bacteria in abundance. *Streptomyces* have been used successfully as a strain for crop inoculations as PGPR[37] and are responsible for earthy / musty odor / smell of freshly ploughed soils (www.agriInfo.in). Several species of actinomycetes such as *Streptomyces*, *Acitinomadura*, *Microbispora*[17,18] *Micromonospora*, *Nocardia*, *Nonomurea* and *Arthrobacter cupressi* have been isolated from various rhizosphere[18,31,50].

Fungi

Both pathogenic and symbiotic fungi associate with the rhizosphere[41]. They average between 10^5 and 10^6 organisms per gram of rhizosphere soil. Zygomycetes and hyphomycetes establish the most readily in the rhizosphere because they metabolize simple sugars[43]. The fungal populations in the rhizosphere and rhizoplane ranged from 5.0 x 10^2 to 4.5 x 10^4 cfu/g and 2.0 x 10^2 to 2.0 x 10^4 cfu/g respectively[41].

Many plant pathogens are fungi, but only a few fungi are pathogens. A special group of fungi particularly beneficial in agriculture are those that form a mycorrhizal symbiosis with plant roots[3]. Some important fungi in rhizosphere are species of *Aspergillus*[26], *Rhizopus*[41], *Geotrichum*, *Mucor*, *Penicillium*, *Acremonium*[41], *Curvularia*[26], *Trichoderma*[26], *Saccharomyces*[26], *Rhodotorula*[3,41].

Protozoa

Protozoa typically range in size from 25mm to 200mm and are grouped as naked amoebae, testate amoebae, ciliates, and flagellates based on mode of locomotion. In general, protozoa are classified as small unicellular eukaryotes with a maximum size of 50μm. Forest soil samples typically harbour between 1.0 x 10^4-1.0 x 10^7 cfu/g[1]. The importance of protozoa in terrestrial ecosystems results mainly from their feeding activities. The direct effect relates to the enhancement of nutrient availability to plants by reducing the amount of nutrients bound in bacterial tissue whereas indirect effects relate to grazing-mediated shifts in the composition and activity of microbial communities[8].

Recent findings by[15], demonstrated an up regulation of secondary metabolites of *Pseudomonas fluorescens* in the presence of predators. *Amoebae* colonize with the help of their pseudopodia the water film surrounding soil particles, dying roots, organic material and reach high densities in the rhizosphere of plants[14]. At low soil moisture or low food availability they form resistant cysts awaiting more favourable conditions[14].

Viruses

Viruses can also be found in the rhizosphere of roots. Viruses are of great importance as they may influence the ecology of soil biological communities through both an ability to transfer genes from host to host and as a potential cause of microbial mortality. Consequently, viruses are major players in global geochemical cycles, influencing the turnover and concentration of nutrients and gases. Despite this importance the area of soil virology is understudied. The most abundant viruses in the rhizosphere are the bacteriophages. This is due to the fact that bacteria constitutes the largest population in the rhizosphere[24].

THE ROLE OF ROOT EXUDATES IN RHIZOSPHERE INTERACTIONS

The exudates have several functions.

Parasitic plant-host interactions

Root exudates are essential in the development of associations between parasitic plants and their plant hosts, an association that is negative for the host and positive for the parasite[4]. Root cells are under continual attack from microorganisms and survive by secreting defence proteins and other antimicrobial chemicals[24].

Attract and repel particular microorganisms

High levels of moisture and nutrients in the rhizosphere attract much greater numbers of microorganisms than elsewhere in the soil. The composition and pattern of root exudates affect microbial activity and population numbers which, in turn, affect other soil organisms that share this environment[24].

Keep the soil around the roots moist

Exudates released from roots at night allow expansion of roots into the soil. When transpiration resumes with daylight, the exudates begin to dry out and adhere to the soil particles in the rhizosphere. As the soil dries and its hydraulic potential decreases, exudates lose water to soil[24].

Obtain nutrients

The exudates help roots adsorb and store ions for plant use. For instance, flavonoids in legume roots activate *Rhizobium meliloti* genes responsible for root nodulation that enable the plant roots to obtain nitrogen from the air. Exudates enable the transfer of up to 20% of all photosynthetically fixed carbon to the rhizosphere. Exudates may also be responsible for encouraging vesicular arbuscular mycorrhizae that colonise roots and send out miles of thread-like hyphae into the soil, increasing the surface area and distance covered by the roots and taking up nutrients for the plant[24]. Besides, root exudates makes organic acids, phosphorus, phytosiderophores and micronutrient available for the rhizosphere[4]. Organic acids can act as metal chelators in the rhizosphere, but are thought to have more important effects on phosphorus availability than on micronutrient availability. Phosphorus, like iron, is often relatively abundant in soils, but in unavailable forms. In particular, phosphorus is often bound in insoluble ferric, aluminum, and calcium phosphates, especially in soils with high pH. Organic acids such as citric, malic, and oxalic acid can form complexes with the iron or aluminum in ferric and aluminum phosphates, thus releasing plant-available phosphates into the soil. Organic acids may also increase phosphorus availability by blocking phosphorus absorption sites on soil particles or by forming complexes with cations on soil mineral surfaces. Several plants increase organic acid rhizosecretion substantially in response to phosphorus deficiencies, including *Lupinus alba* (white lupine), *Brassica napus*, and *Medicago sativa*[4].

Change the chemical properties of the soil around the roots

The rhizosphere environment generally has a lower pH, lower oxygen and higher carbon dioxide concentrations. However, exudates can make the soil in the rhizosphere more acid or alkaline, depending on nutrients roots are taking from the soil. For example, when a plant takes up nitrogen as ammonium it releases hydrogen ions which will make the rhizosphere more acid.

When a plant takes up nitrogen as nitrate, it releases hydroxyl ions which make the rhizosphere more alkaline. This action doesn't usually affect the bulk pH of the soil but is important for the small organisms that live in the rhizosphere because many soil organisms do not move far in the soil[26].

Stabilize soil aggregates around the roots

Sticky mucilage secreted from continuously growing root cap cells is believed to alter surrounding soil[24].

Inhibit the growth of competing plant species

Plant roots are in continual communication with surrounding root systems and quickly recognise and prevent the presence of invading roots through chemical messengers. This process is known as allelopathy. In agriculture it can be beneficial when crop plants prevent weeds from growing nearby; or detrimental when the weed plants prevent crops growing[24].

RHIZOSPHERE ECOLOGICAL RELATIONSHIP

Between plant root and microorganisms

Microorganisms present in the rhizosphere play important roles in ecological fitness of their plant host. Important microbial processes that are expected to occur in the rhizosphere include pathogenesis and its counterpart, plant protection/growth promotion, as well as the production of antibiotics, geochemical cycling of minerals and plant colonization. Some microbes directly interact with plants in a mutually beneficial manner whereas others colonize the plant only for their own benefit. In addition, microbes can indirectly affect plants by drastically altering their environments. Understanding the complex nature of plant–microbe interactions can potentially offer new strategies to enhance plant productivity in an environmentally friendly manner[32]. Many pathogenic organisms, bacteria as well as fungi, have coevolved with plants and show a high degree of host specificity[34].

Plants secrete metabolites to defend themselves against soil-borne pathogens, which can adversely affect plant growth and fitness, but also to establish mutualistic associations with beneficial soil microorganisms[16]. Plant-microbe interactions may thus be considered beneficial, neutral, or harmful to the plant, depending on the specific microorganisms and plants involved and on the prevailing environmental conditions[4]. Some of these relationships are discussed below;

Mycorrhizae

Mycorrhizae are mutualistic symbioses between fungi and plant roots. About 90% of all plant species harbour this type of symbiont, which are in general considered as beneficial. However, the mutualistic character of the symbiosis may depend on the conditions, so that the benefit can be unilateral in some cases. There are several types of mycorrhizae, the most important for crop plants being the arbuscular mycorrhizae, where the fungal partner is a zygomycete, member of the order Glomales. These fungi are not cultivable in the absence of plant roots. In most cases, the symbiosis is mutualistic, the plant bringing organic compounds as carbon and an energy source to the fungus, whereas the latter, through its mycelium extending in the surrounding soil, takes up water and minerals and transfers them to the root. They are particularly important in orthophosphate-deficient soils. However, fungal partners can also bestow other advantages to their host, like protection against root parasites. They also allow nutrient transfers between different plants harbouring common mycorrhizae, e.g. in prairie ecosystems. In this manner, mycorrhizal plants may out compete non-mycorrhizal plants by forming successful guilds sharing the same mycorrhizal partners. Recently, it was shown that bacterial populations can be associated with mycorrhization, and help establishment and functioning of the symbiosis. Mycorrhizal root exudates and the cell membrane is the main physiological control of heavy metals into the plant root cell unit[3,26].

The mutualistic symbionts of nitrogen fixing bacteria

Symbiotic nitrogen fixation is a well-known process exclusively driven by bacteria, the only organisms possessing the key enzyme nitrogenase, which specifically reduces atmospheric nitrogen to ammonia in the symbiotic root nodules[22]. The bacteria responsible belong to the genera *Rhizobium*, *Sinorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Azorhizobium*, collectively termed *rhizobia*. The signaling processes evolutionary history[8,35] and, particularly, the molecular aspects determining host specificity in the rhizobial–legume symbiosis have been reviewed recently. Other bacteria (actinomycetes) of the genus Frankia form nodules on the root of 'actinorrhizal' plant species, which are of great ecological importance. The genetics and genomics of their root symbiosis is a matter of current attention[35].

Plant growth promoting *Rhizobacteria* (PGPR) interaction with plants

Plant growth-promoting rhizobacteria are thus free-living, soil-borne bacteria which when applied to seeds/

soils or crops, enhance the growth of the plant directly by providing nutrients to plants or indirectly by reducing the damage from soil-borne plant pathogens[2,10,25]. Mechanisms of biological control by which rhizobacteria can promote plant growth indirectly, i.e., by reducing the level of disease, include antibiosis, induction of systemic resistance, and competition for nutrients and niches[25]. Beneficial, root colonizing, rhizosphere bacteria, the PGPR (plant growth promoting rhizobacteria), are defined by three intrinsic characteristics: (i) they must be able to colonize the root (ii) they must survive and multiply in microhabitats associated with the root surface, in competition with other microbiota, at least for the time needed to express their plant growth promotion/protection activities and (iii) they must promote plant growth[2,3,37]. Examples of direct plant growth promotion include (a) biofertilization, (b) stimulation of root growth, (c) rhizoremediation, and (d) plant stress control[25].

Among microorganisms in the rhizosphere

Direct interactions occurring between members of different microbial types often result in the promotion of key processes benefiting plant growth and health. It is obvious that all interactions taking place in the rhizosphere are, at least indirectly, plant-mediated. However, this section will deal with direct microbe–microbe interactions themselves, with the plant as a 'supporting actor' in the rhizosphere. There are different ways of microbial and microbial interactions in the rhizosphere, some of these interaction may be beneficial or detrimental.

Beneficial interaction

Mutualism

An example is the interaction between PGPR and *Rhizobia*. Symbiotic nitrogen fixation in legumes is accomplished by *Rhizobia* inside root nodules. This process is dependent on the efficiency of the *Rhizobium* strain involved and on its competitiveness for nodulation against indigenous soil *Rhizobia*, and is influenced by environmental factors. Increasing symbiotic nitrogen fixation is rational since legume crops are an important source of protein and are environmentally safe, avoiding the use of nitrogen fertilizers. Rhizobial strain selection and legume breeding are conventional approaches to improve this process and, more recently; molecular approaches have demonstrated their potential. The exploitation of PGPR in combination with *Rhizobium* also constitutes an interesting alternative to improve nitrogen fixation. The mechanisms involved in the beneficial interaction *Azospirillum-Rhizobium* with clovers have received considerable world-wide attention. However, negative effects of *Azospirillum* on nodulation of clover have also been reported[3,20].

Cometabolism

Cometabolism is defined as the simultaneous degradation of two compounds, in which the degradation of the second compound (the secondary substrate) depends on the presence of the first compound (the primary substrate). For example, in the process of metabolizing methane, propane or simple sugars, some bacteria, such as *Pseudomonas stutzeri* OX1, can degrade hazardous chlorinated solvents, such as tetrachloroethylene and trichloroethylene, that they would otherwise be unable to attack. They do this by producing the methane monooxygenase, enzyme which is known to degrade some pollutants, such as chlorinated solvents, via cometabolism. Cometabolism is thus used as an approach to biological degradation of hazardous solvents.

Another example is *Mycobacterium vaccae*, which uses an enzyme to oxidize propane. Accidentally, this enzyme also oxidizes, at no additional cost for *M. vaccae*, cyclohexane into cyclohexanol. Thus, cyclohexane is co-metabolized in the presence of propane. This allows for the commensal growth of *Pseudomonas* on cyclohexane. The latter can metabolize cyclohexanol, but not cyclohexane[5].

Detrimental interactions

Predation

Predation describes a biological interaction where a predator (an organism that is hunting) feeds on its prey (the organism that is attacked). Predators may or may not kill their prey prior to feeding on them, but the act of predation often results in the death of its prey and the eventual absorption of the prey's tissue through consumption. Other categories of consumption are herbivory (eating parts of plants) and detritivory, the consumption of dead organic material (detritus). All these consumption categories fall under the rubric of consumer-resource systems[11]. It can often be difficult to separate various types of feeding behaviors. For example, some parasitic species prey on a host organism and then lay their eggs on it for their offspring to feed on it while it continues to live or on its decaying corpse after it has died. The key characteristic of predation however is the predator's direct impact on the prey population. On the other hand, detritivores simply eat dead organic material arising from the decay of dead individuals and have no direct impact on the "donor" organism(s). A typical example of predation is protozoa feeding on bacteria and small fungi[14].

Amensalism

Amensalism is a relationship in which a product of one organism has a negative effect on another organism[48]. It is specifically a population interaction in which one organism is harmed, while the other is neither affected nor benefited. Usually this occurs when one organism exudes a chemical compound as part of its normal metabolism that is detrimental to another organism. *Penicillium* is a common example; *Penicillium* secretes penicillin, a chemical that kills bacteria[48].

Competition

Competition can be defined as an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Limited supply of at least one resource (such as food, water, and territory) used by both usually facilitates this type of interaction, although the competition may also exist over other 'amenities', such as females for reproduction (in case of male organisms of the same species)[6]. Competition is one of many interacting biotic and abiotic factors that affect community structure. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. The magnitude of competition therefore depends on many factors in the rhizosphere. According to the competitive exclusion principle, species less suited to compete for resources should either adapt or die out[6].

APPLICATIONS OF THE RHIZOSPHERE

Phytoremediation (plant-assisted bioremediation) refers to the use of plants to stabilise/immobilise contaminants in soils or sediments, to remove organic pollutants via microbial degradation in the plant rhizosphere or by metabolising them after uptake in plant organs, to volatilise some metals and metalloids by the formation of volatile compounds by the action of rhizosphere microorganisms or after uptake in plant organs, or to extract metals/metalloids via uptake in harvestable plant parts, i.e. typically shoots[33,47].

Phytoremediation is generally considered as an environmentally friendly, gentle management option for polluted soil as it uses solar-driven biological processes to treat the pollutant. Phytoremediation appears attractive because in contrast to most other remediation technologies, it is not invasive and, in principle, delivers intact, biologically active soil. The process involved in phytoremediation is described below:

Phytostabilisation (and immobilisation) is a containment process using plants-often in combination with soil additives to assist plant installation-to mechanically stabilising the site and reducing pollutant transfer to other ecosystem compartments and the food chain;

Phytoextraction is a removal process taking advantage of the unusual ability of some plants to (hyper-) accumulate metals/metalloids in their shoots;

Phytovolatilisation/rhizovolatilisation is a removal process which involves employing metabolic capabilities of plants and associated rhizosphere microorganisms to transform pollutants into volatile compounds that are released to the atmosphere;

Phytodegradation/rhizodegradation refers to the use of metabolic capabilities of plants and rhizosphere microorganisms to degrade organic pollutants[25,46,47].

FACTORS AFFECTING MICROBIAL FLORA OF THE RHIZOSPHERE

Rhizosphere microbial communities can be regarded as a subset of the soil microbial community, therefore they too are influenced by soil chemical and physical properties[27,29] and consequently, changes microbial community structures in rhizosphere can affect the plant[49].

Soil type and its moisture

In general, microbial activity and population is high in the rhizosphere region of the plants grown in sandy soils and least in the high humus soils, and rhizosphere organisms are more when the soil moisture is low. Thus, the rhizosphere effect is more in the sandy soils with low moisture content[7,28,19].

Soil amendments and fertilizers

Crop residues, animal manure and chemical fertilizers applied to the soil cause no appreciable effect on the quantitative or qualitative differences in the microflora of rhizosphere. In general, the character of vegetation is more important than the fertility level of the soil[30].

Rhizosphere pH

Respiration by the rhizosphere microflora may lead to the change in soil rhizosphere pH. If the activity and population of the rhizosphere microflora is more, then the pH of rhizosphere region is lower than that of surrounding soil or non-rhizosphere soil. Rhizosphere effect for bacteria and protozoa is more in slightly alkaline soil and for that of fungi is more in acidic soils[30].

Proximity of root with soil

Soil samples taken progressively closer to the root system have increasingly greater population of bacteria, and actinomycetes and decreases with the distance and depth from the root system. Rhizosphere effect decline sharply with increasing distance between plant root and soil[30].

Plant species

Different plant species inhabit often somewhat variable microflora in the rhizosphere region. The qualitative and quantitative differences are attributed to variations in the rooting habits, tissue composition and excretion products[27,30].

Age of plant

The age of plant also alter the rhizosphere microflora and the stage of plant maturity controls the magnitude of rhizosphere effect and degree of response to specific microorganisms. The rhizosphere microflora increases in number with the age of the plant and reaching at peak during flowering which is the most active period of plant growth and metabolism. Hence, the rhizosphere effect was found to be more at the time of flowering than in the seedling or full maturity stage of the plants[27,30]

Root exudates

One of the most important factors responsible for rhizosphere effect is the availability of a great variety of organic substances at the root region by way of root exudates/excretions[16,24,27,30].

CONCLUSION

The rhizospheric community is complex and is made up of a myriad of organisms and plants secretions. The activities of microorganisms in the rhizosphere is like a two edged sword playing several ecological roles which could be detrimental and also beneficial.

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