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Role of microorganisms in communication between soil and plants

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Keywords

Plants interaction; Rhizosphere microorganisms; Exudates; Radical colonisation

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REVIEW ARTICLE

Role of Microorganisms in Communication Between Soil and Plants

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Abstract

Microbial population in the rhizosphere establishes a number of important interactions with plants, whose study is crucial in perspective of sustainable agricultural production. Studies on various plant crops have revealed that, despite the complex microbial biodiversity of the soil, the bacterial microbiome is characterised by multiple functionalities. A better understanding of the molecular mechanisms, underlying the interactions between plants and the microbiome, could enable better development of plants, related to the beneficial action of microorganisms. Therefore, this review aims to describe the characteristics of the rhizosphere microbiome with the interactions that occur between soil and roots, as well as the signals that influence bacterial activities, and the importance of molecular techniques for analysing microbial activities.

Keywords: Plants interaction, Rhizosphere microorganisms, Exudates, Radical colonisation

1. Introduction

The rhizosphere is the part of the soil surrounding the root and is influenced by the root itself. The plant releases carbon-based exudates that influence the surrounding microbial community [1]. These can be found on the surface of the roots or growing in the surrounding areas. Novel analysis methodologies enable the study of various microbial communities independent of their cultivation. This greatly extends the possibility of studying the interactions in the rhizosphere between plants and microorganisms [2,3]. As soon as seeds germinate and rootlets begin to grow, the release of organic material influences the activity of microbial populations around the root, generating the so-called rhizospheric effect [4]. This can depend both on the development and extension of the roots and the type of soil, which can interfere with the speed and diffusion of the substances in the exudates. There are billions of bacteria belonging to thousands of different species in the soil [5]. This biodiversity is often related to the plant species to which the root belongs and differs substantially from that of the surrounding soil not affected by the presence of the root. There are functional associations with certain bacterial groups that have been investigated the most and described in this review [6,7]. Among the various examples, the plant growth-promoting rhizobacteria are certainly of great interest, particularly the genus *Burkholderia*, which is capable of stimulating plant growth, acting with biocontrol activities on plant pathogens, and contributing to the decontamination of soil pollutants [8]. The activity of *Burkholderia* from the studies carried out seems to be influenced by soil type, plant species and plant development stage, aspects also found in other bacteria and fungi colonising the rhizosphere [9]. In this review, we describe the possible interactions that take place between plants and soil microorganisms, emphasising their benefits in plant cultivation and defence, and improvements in fertility. Interactions between microorganisms and root systems is relevant in order to make the most of the application of microbial strains in agriculture.

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2. Root activity and the effect of exudates on microbial activity

The ability of roots to influence the characteristics of the surrounding soil is extremely variable, partly due to differences in morphology, physiology and longevity [10,11]. The characteristics of the rhizospheric soil are modified by the release of exudates, which may consist of cells, mucilage or components of various kinds. Nutritional and other environmental factors such as temperature, light, water resources and the presence of toxic contaminants can be relevant on the quantity and quality of rhizodepositions [12]. Root exudates include mucilage composed mainly of polysaccharides, generally permeated by microorganisms or organic and inorganic soil particles [13]. The main component of root exudates is sugars, organic acids, amino acids and rhizodeposits may vary depending on the plant species, plant age, nutritional status and environmental conditions. Part of the released compounds can be reabsorbed by the roots (Table 1). The rhizodepositions represent an important source of energy for the microorganisms in the rhizosphere, which can vary depending on the presence of the different exudates [14]. Microbial species may differ depending on the root tract and influence plant activity by favouring water and nutrient supply processes, increasing resistance to stress situations and acting as mediators in exchanges with microorganisms [15]. Usually, the presence of mucilage improves the structure of the rhizospheric soil, leading to situations that favour root growth, particularly by reducing the friction between the root apex and soil particles. In practice, an environment is created between soil and root where the uptake of nutrients, even difficult ones such as phosphorus and iron, is easier. Roots are not the only source of enzymes in the rhizospheric environment; they can also originate from microorganisms colonising areas around the root [16,17]. Exudates can play specific roles in the acquisition of nutrients and, in particular, in the communication between root cells and microorganisms in the rhizosphere. Roots can modify the conditions of the rhizosphere, influencing the availability of certain nutrients, and can also release metal-binding compounds, leading to increased availability [18]. Much research shows how the action of a substance released by roots is influenced by a number of situations, including microbial activity, the site of release and chemical alterations. Therefore, studies concerning the relationships between plants and microorganisms must consider all these aspects and study the mechanisms that mediate the passage from the root cells to the external medium [19]. Different classes of compounds that are released from roots can cross membranes in different ways; they are influenced by external and internal factors and the chemical characteristics of the compound [20–22]. While substances, such as amino acids and organic acids, are released from the roots by passive processes, the release of high molecular weight compounds such as polysaccharides, mucilages and proteins is influenced by exocytosis mechanisms, with the formation of membrane vesicles that allow the release of the contents into the soil [23].

Table 1. Rhizodepositions released by roots in the soil [24].

Rhizodeposition	Exudate type	Exudate description
Organic root exudates	Enzymes	Amylase, invertase, peroxidase
	Fatty acids	Linoleic, oleic, stearic
	Sterols	Campesterol, cholesterol
	Phenolic compounds	Flavonols, flavones
	Sugars	Glucose, fructose
	Amino acids	all essential amino acids
Inorganic root exudates		H^+, K^+, NO_3^-, OH^-
Mucilages		
Dead cells		

3. Influence of nutrient availability on the release of root exudates

In the soil, plants must resist hostile factors of various biological, chemical and mechanical natures that can affect their life and growth [25]. The plants, particularly the roots, develop forms of adaptation that are also reflected in changes in the conditions of the rhizosphere, which in this way create favourable environments for plant growth. Of particular importance are, above all, nutritional and environmental factors and the presence of toxic contaminants in the soil [26]. Mineral elements that can influence plant growth include iron and phosphorous. Plants respond differently to the limited availability of iron. Root responses are often localised in the sub-apical zones and associated with morphological changes [27]. An acidic soil contributes to increased iron solubility and, at the same time, contributes to the release of exudates by the roots that can complex it. These are strategies of certain plants, such as dicotyledons and non-gramineous monocotyledons, that are able to can increase the availability of iron in the soil through these mechanisms. Other modes of iron uptake are related to the release into the rhizosphere of considerable quantities of amino acids (phytosiderophores), characterised by their ability to complex trivalent iron [28]. This release varies from species to species, and studies show that differences in the phytosiderophores released and in the manner and amount of exudation exist. There is a close relationship between the number of phytosiderophores released and the ability to tolerate nutritional stress [29,30]. It has also been noted that nutritional stresses related to other elements such as copper can increase the release of phytosiderophores. Another element that can severely limit plant growth is the availability of phosphorous. It has also been observed that its deficiency can significantly alter the quantity and composition of root exudates so that the uptake of difficult-to-soluble forms of phosphorous increases [31]. There are differences in phosphorous deficiency between plants, involving modes, production and release of carboxylic acids and extent of acidification of the rhizosphere [32]. In *Aloe*, for example, these modes occur simultaneously, while in some vegetables, only acidity increases, and in cereals neither is observed. In several plant species, phosphorus deficiency also leads to the release of phenolic compounds from the roots, which play a role as signal molecules in the germination of and the growth of mycorrhiza hyphae [33]. During phosphorous deficiency, the rhizospheric soil can become enriched in enzymatic activities, which can contribute to increased uptake of this mineral element by the roots (Fig. 1).

The presence of toxic metals in the soil leads to increased production of exudates by the roots over a period ranging from a few minutes to a few hours [34]. The release may vary depending on the type or portion of the root; in some species, the release occurs in the immediate vicinity of the root portion, maintaining a high capacity to detoxify the areas most sensitive to toxic metals [35].

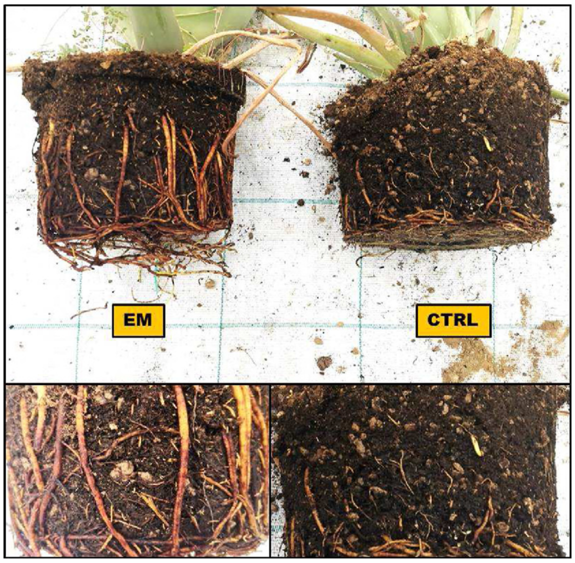

Fig. 1. Stimulating effects of rhizosphere bacteria (EM), Bacillus spp. and Pseudomonas spp., on Aloe arborescens roots under phosphorus deficient conditions. Increase in root volume and root hairs following microbial treatment (EM), compared to untreated control (CTRL).

4. Signs in the soil influencing root growth

Activities in the rhizosphere with regard to the concentration of nutrients and humic molecules can alter the development of the root system. Indeed, it is well known that root systems are highly plastic structures capable of responding to signals from the surrounding environment [36]. Nutrients of different types act as signals that can be perceived by the roots and induce molecular mechanisms that influence cell division and differentiation processes, thus having a considerable impact on the structure of the root system (Fig. 2). In particular, changes in nutrient concentrations can modulate processes such as root hair formation, main root growth and lateral root formation. Root responses can be mediated by the intervention of phytoregulators [37]. Recent research reveals the existence of individual nutrient-dependent signals whose function is to interpret changes in nutrient concentrations to modify root development. Other environmental signals can induce changes in root morphology, in particular, humic substances can play a key role [38]. Indeed, it has been shown that humic substances influence plant metabolism through a series of physiological processes, which can increase the number of nutrients absorbed by plants [39]. Small humic particles have been shown to increase lateral root proliferation, with a significant increase in root hair density. This ensures greater soil exploration and increased nutrient uptake. The characterisation of root exudates and the ability of roots to change soil structure are the basis of current research [40]. All of these studies can certainly lead to the

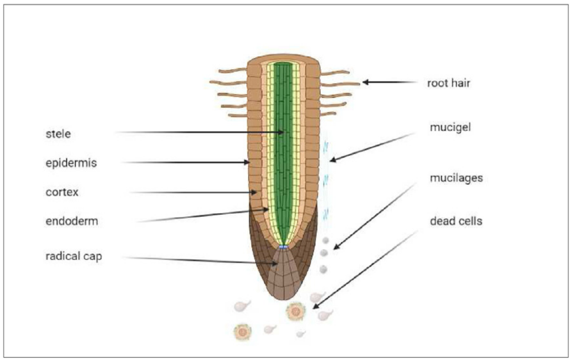

Fig. 2. Diagram of the various structures that make up the root and root hairs.

improvement of crops and the development of agronomic techniques that enable greater protection of the environment as well as of the available resources [41].

5. Beneficial influences of microorganisms in the soil

Various processes take place in the rhizosphere, related to the interactions that exist between plants and microorganisms. Among the most important situations, symbioses for nutrient uptake, stimulation in phytohormone production and biocontrol activity are of particular interest [42]. Root colonisation is the phenomenon whereby the root surface is colonised by microorganisms in the soil. Therefore, a good root growth-promoting microorganism, is first and foremost a good root coloniser. The mechanisms that enable efficient root colonisation bring together all those microorganisms that establish a close relationship with the roots, both beneficial and pathogenic [43]. Molecular biology studies have identified genes that are correlated to the function of moving and degrading soil matter. In particular, studies have shown that the presence of flagella, pili and fimbriae and chemotaxis are decisive for colonisation [44]. For example, bacteria of the genus Pseudomonas can pick up signals related to the presence of root exudates and transduce it within the cell, in order to create a certain metabolic pathway. Site-specific recombinases can also play an important role in radical colonisation, associated with DNA rear-rangements, which bring about morphological changes on the cell surface and appear to be useful in responding to environmental changes by favouring adaptation to new ecological niches. However, the colonisation process is very complex and requires the activity of a large number of genes linked to different metabolic and physiological functions, especially related to surface interactions and motility [45]. In recent years, increasing interest has been focused on the possible biological control of plant diseases. Biocontrol studies have led to more in-depth investigations both of the organism to be controlled and the network of interactions within the microflora on the plant surface, particularly on the root surface [46]. The best-known strains used in biocontrol normally belong to the genera *Pseudomonas*, *Bacillus* and *Streptomyces*, which have demonstrated disease control on various horticultural and ornamental plants, either through the production of antibiotics or through competition for space and resources in the rhizosphere. In addition to antibiotic production, it must be remembered that key elements for the success of a biocontrol strategy are also the survival and the ability to compete for resources in the rhizospheric environment. Interesting studies on *Agrobacterium* have also shown how non-pathogenic strains control the virulence of pathogenic strains without killing them, thus not triggering resistance mechanisms [47]. Microorganisms in the rhizosphere also play a key role in a number of biogeochemical cycles, in particular by enabling the solubilisation of both phosphate and insoluble organic compounds such as lignin and cellulose. Microorganisms that solubilise phosphate are abundant and ubiquitous in soils. They can be found especially in the rhizospheric zone where they provide phosphate that can be assimilated by the plant [48]. Phosphate-solubilising bacteria carry out this activity by acidifying the surrounding pH through the secretion of organic acids. Plants benefit from association with phosphate-solubilising microorganisms, as these provide access to phosphorous sources otherwise not available to them [49]. Studies of bulbous vegetable species inoculated with *Bacillus* strains solubilise phosphate significantly more than non-inoculated ones (Fig. 3). Research involving rhizospheric microorganisms has also revealed their importance in the degradation of insoluble compounds derived from plant tissue, such as lignin and cellulose [50]. The activity of cellulosol organisms then influences the activity of other microorganisms that utilise the by-products of degradation as a source of energy and carbon, increasing soil fertility and stimulating microbial activity [51].

6. Methods for analysing soil microbial variability

The study of microbial variability in the rhizosphere can provide a better understanding of the interactions between microorganisms and roots. In fact, in the rhizosphere, because of root exudates, there is an abundance of metabolic processes that regulate soil fertility [52]. The identification of microorganisms obtained by traditional cultivation methods can only give a partial description of rhizospheric microbial diversity. In fact, in the soil and rhizosphere, only a small proportion of the microorganisms can be cultivated in the laboratory, while the majority are viable but cannot be cultivated. It has been hypothesised that cellular communication mechanisms, mediated by small molecules, may be responsible for the unculturability of some microorganisms [53]. In particular, the mechanism of quoring sensins seems to be activated only at a certain population density; conversely, it also appears that when microbial populations reach a

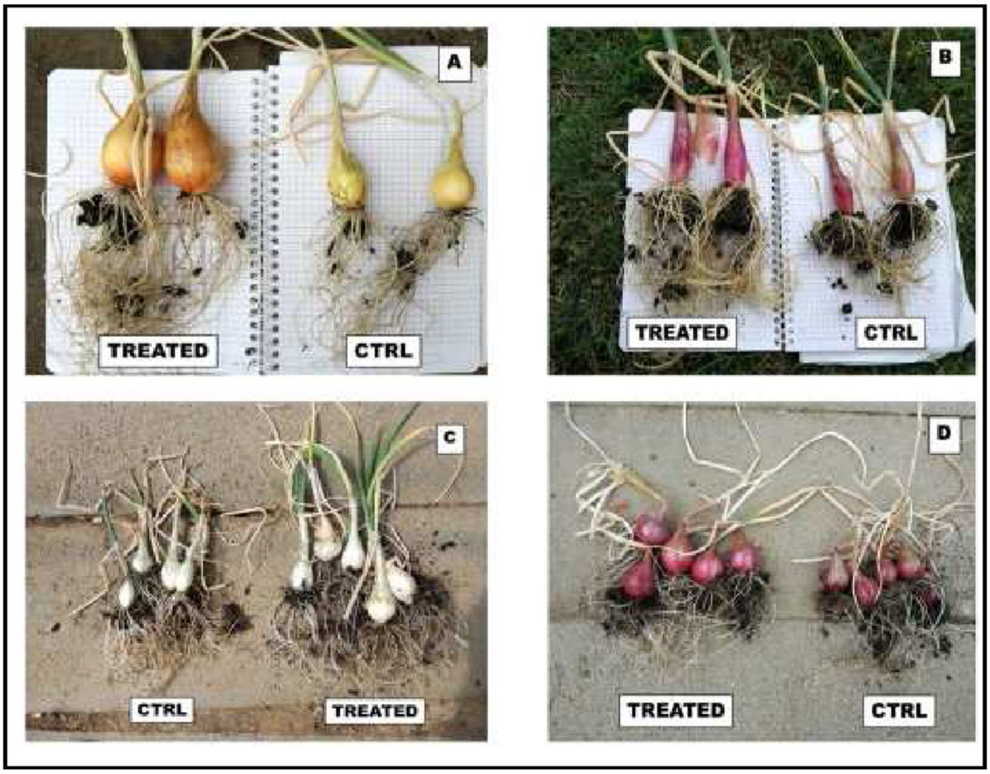

Fig. 3. Increase in root volume, root hairs and bulb size following microbial treatment with Bacillus strains (TREATED), compared to untreated control (CTRL), in various types of white, red and yellow onions.

certain size, this chemical signal is switched off, ceasing growth. A modern approach to the functional characterisation of complex microbial communities is the characterisation of their catabolic profile [54]. Typically, this type of characterisation is carried out by determining the substrate utilisation capacity of the microbial community. It can also be carried out by analysing lipid chemotaxonomic markers such as phospholipids or methyl esters of total fatty acids. These methods can reveal relevant properties of microbial communities, such as the quantity and quality of the biomass. They also make it possible to assess the viability of the biomass, as this correlates with the state of degradation of fatty acids, as well as the structure of the microbial community and its nutritional status [55]. It is possible to assess the complexity of the bacterial community by establishing the number of equivalents in the metagenome, through kinetic measures of reassociation of the total DNA extracted from the soil. In order to describe in detail the microbial diversity in the soil by including non-culturable populations in the analysis, the most comprehensive approach is to sequence the 16S rRNA gene of the microorganisms inhabiting the system and compare the sequences obtained with those deposited in databases [56]. Modern genomic sequencing techniques have enabled the introduction of new approaches for characterising complex communities. Metagenome sequencing, for example, allows the identification of entire genomes present in a community, generating a wealth of information that can be used to understand the functioning of the entire system. Recent approaches also allow the diversity of the microbial community to be correlated with certain functions. The construction of chromosome libraries has enabled the identification of different metabolic functions associated with previously unknown genes. One very interesting strategy is based on marking the nucleic acids of microorganisms that correspond to a specific growth substrate, for example, an environmental stimulus, a specific exudate, or physical factors such as water, heat and salt stresses [57].

7. Microbial populations and environment

Molecular methodologies enable the analysis of microbiology associated with plant roots, highlighting the sensitivity to different environmental factors and the differences in the rhizospheric microbial community compared to that of root-free soil. The microbial populations exhibit a different level of complexity depending on the age of the plant [58]. Around young *Aloe* roots, which can be associated with intense exudation and, thus, a relative abundance of nutrients, the microbial population has a relatively low degree of complexity with few genotypes. In contrast, a high diversity is observed in adult *Aloe* plants for which exudation is reduced. This is, probably, due to the more variable nutrient availability. In roots close to senescence, the detachment of localised cells in the soil and the presence of nutrient heterogeneity allow for a greater number of microbial types to thrive [59]. Under these conditions, the microbial community becomes more complex and more similar to that detectable in root-free soil. Another factor influencing the structure and diversity of root microorganisms is the soil type, whose chemical and structural characteristics are crucial in determining the selection of the microbial community [60]. At the rhizospheric level, the effect produced by the soil type on the microbial community is influenced by exudates, which determine greater selection than the soil type. The molecular approach was so sensitive that it was possible to distinguish between populations associated with different cultivars of the same species, an effect probably influenced by the different exudates produced by the different plants [61].

8. Conclusions

The interaction between plant roots and soil microbial activity influences their metabolism, resistance to biotic and abiotic stresses and agricultural production. Numerous studies have shown how the soil microbiota represent the main source of inoculum for plant-associated bacterial communities and, at the same time, how the physico-chemical characteristics of the soil affects the physiological responses of plants, microorganisms and their interactions. These considerations are described in studies that exhibit how the microbiome of plants, in different soils, differs in both quality and quantity. Soil tillage techniques, as well as the addition of organic and mineral fertilisers, can influence the interactions between plants and microorganisms. Plants of the same *Opuntia* variety grown conventionally have a different microbiome to plants grown in environments subject to more conservative cultivation techniques. Further studies have shown how plants of different species or genotypes of the same plant species recruit distinct microbial communities. Therefore, scientific studies are aimed at finding quick and inexpensive tools to help researchers monitor soil microorganisms. Indeed, the effects of microorganisms on plants are generally influenced by many factors such as temperature, soil type, the presence of indigenous microorganisms and the agricultural practices used. A better understanding of exchanges in the rhizosphere and microbial activities can certainly support those who wish to apply these cultivation techniques in a sustainable farming approach. The application of microorganisms in agriculture today plays a key role in both improving crop quality and reducing the use of synthetic fertilisers and plant protection products. A better understanding of how the interactions between roots and micro-organisms take place is relevant, especially in order to be able to make better use of them in cultivation. This review has highlighted the exchanges between plants and roots in the soil and their benefits, taking into account the difficulties that are present in the study of the ever rapidly changing underground world.

Conflict of interest

The author declares no conflict of interest.

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