THE COMPLEXITY OF THE RHIZOSPHERE - THE "UNSEEN" PART OF THE SOIL – A SHORT REVIEW

MIHAI Luiza-Silvia, CIOBOIU Olivia

Abstract. Soil is where most of the biodiversity on Earth exists, and the rhizosphere is probably the most dynamic habitat and certainly the most important area in terms of defining the quality and quantity of terrestrial human food resources. Despite its central importance to all organisms, very little is known about the functioning of the rhizosphere. The processes taking place in the rhizosphere play a key role in the nutrient circuit in terrestrial ecosystems. There is a growing need to understand the processes in the rhizosphere area so that we can effectively manage ecosystems or harness their potential benefits, either to mitigate or stop the negative consequences of anthropogenic intervention.

Keywords: biodiversity, rhizosphere, rizodeposition, root exudates, soil.

Rezumat. Complexitatea rizosferei – partea „nevăzută" a solului – scurtă recenzie. Solul este locul unde există cea mai mare parte a biodiversității de pe Pământ, iar rizosfera reprezintă probabil cel mai dinamic habitat și cu siguranță este cea mai importantă zonă în ceea ce privește definirea calității și cantității resursei alimentare umane terestre. În ciuda importanței sale centrale pentru întreaga viață, se cunosc foarte puține despre funcționarea rizosferei. Procesele care se desfășoară în rizosferă joacă un rol cheie în circuitul nutrienților în ecosistemele terestre. Există o nevoie tot mai mare de a înțelege procesele din zona rizosferei, astfel încât să putem gestiona eficient ecosistemele fie pentru a le valorifica beneficiile potențiale, fie pentru a diminua sau stopa consecințele negative ale intervenției antropice.

Cuvinte cheie: biodiversitate, rizosferă, rizodepunere, exudatele rădăcinilor, sol.

INTRODUCTION

The term "rhizosphere" which comes from the Greek word "rhiza" means root and is defined as "the soil area in the vicinity of the roots strongly influenced by them". The rhizosphere is the volume of soil shaped by exudates resulting from plant root tissues and colonized by rhizobacteria (PRASHAR et al., 2014). This area is one of the most diverse habitats on the planet and is essential for ecosystem functioning (JONES & HINSINGER, 2008). A wide range of soil microorganisms and invertebrates coexist in the rhizosphere and exhibit a variety of interactions with each other as well as with plant species (SANTOYO et al., 2021), which is why it is considered the "hot spot" for microbial activity. It is the largest ecosystem on earth with a huge energy flux (PRASHAR et al., 2014; MUELLER et al., 2024). A rhizosphere is considered to be "born" when a root tip reaches a soil volume and "ended" when that root decays. Depending on the type of crop, the rhizosphere can persist for a long period of time (WATT et al., 2006).

The rhizosphere has been subdivided into the following three zones: endo-rhizosphere, rhizoplane and ecto-rhizosphere (PRASHAR et al., 2014; DENG et al., 2024) and hosts very complex relationships between plants and associated organisms (microorganisms, invertebrates) forming a network of complex interactions and exchanges of chemical substances (NICOARĂ et al., 2010).

Microorganisms in the rhizosphere zone can break down soil organic matter into plant-available nutrients promoting their development, and their activities can improve soil quality (HARTMANN et al., 2008; LIU et al., 2023). Plant roots and their surrounding rhizosphere are the main belowground components relevant to climate change adaptation and mitigation (GEORGE et al., 2024). YORK et al. (2016) distinguished between the abiotic rhizosphere, characterized by changes in soil structure, and the biotic rhizosphere, characterized by rhizodeposition and microbial communities.

METHODS

The literature review was conducted using Google Academic, Research Gate and Web of Science. In this study, there were no publication date restrictions applied to the scientific articles included in the bibliography. We reviewed both original articles and synthesis articles. To identify relevant publications in the field of interest, we used various combinations of keywords. Afterwards, the downloaded articles were stored in an Excel database and critically analysed.

RESULTS AND DISCUSSIONS

Timeline. Historically, the importance of belowground biotic interactions in plant growth and development has been overlooked due to the practical difficulties of below-ground investigations, especially in the context of the rhizosphere - a less "seen" part of the soil (the small size of invertebrates and microorganisms, the difficulty of studying this topic).

More recently, studies have bridged this knowledge gap, bringing greater attention to understanding this complex environment. It is vital for agriculture and other related sectors to understand the role this environment plays in plant physiology (CLARK & BENNETT, 2024). The interest in this soil area increased after 1990. Until then there was a very small number of works on roots or root systems (GREGORY, 2006).

A simple search for the word “rhizosphere” on Google Academic, by time intervals, for the period 1900-1950, yielded 339 results; in the period 1950-2000, 53,700 results appeared, and from 2000 to the present we identified 296,000 results, which confirms the researchers’ ever-increasing interest in this area of the soil (Fig. 1).

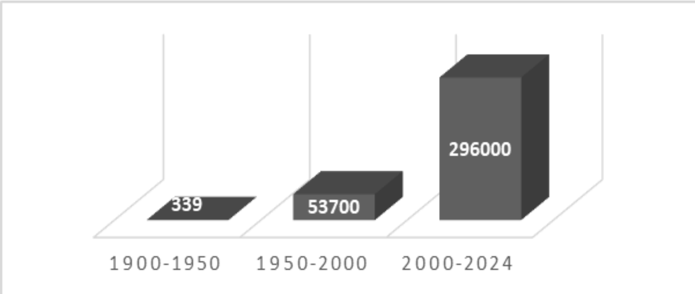

Figure 1. Search results for the word “rhizosphere” over time (original).

The role of microorganisms in the rhizosphere. Densities of soil microorganisms are much higher in the rhizosphere than in the rest of the soil (rootless soil) (JONES, 1998; TOAL et al., 2000). They also interact complexly and constantly with plants (KHAN et al., 2021). There are multiple mechanisms that microorganisms can use to provide benefits to plants: the production and modulation of phytohormones, the solubilization and increase of bioavailability of essential nutrients, the production of antibiotics, the synthesis of volatile compounds and secondary metabolites, and the improvement of soil properties (SANTOYO et al., 2021).

The role of invertebrates in the rhizosphere. Soil invertebrates are organisms that live permanently or temporarily in the soil or on its surface (LAVELLE et al., 2006, CORNU et al., 2020). They have a role in the regulation of ecosystem services (climate regulation by controlling the flow of greenhouse gases, carbon sequestration, flood control, etc.). They also contribute to cultural services, but to a lesser extent, due to society’s low interest in the sustainable use of this key resource (LAVELLE et al., 2006). Soil invertebrates can play two roles in the food web: shredding and moistening ingested plant debris, thus improving the substrate for bacterial activity (CULLINEY, 2013). They enhance microbial activity by accelerating decomposition and mediating soil transport processes (STORK & EGGLETON, 1992; STONE et al., 2020). They participate directly and indirectly in the decomposition process, soil genesis and soil characteristics (porosity, aeration, fertility, infiltration) and are involved in the nutrient cycle (MANU et al., 2019). Soil fauna increases nutrient release through litter fragmentation and improves soil structure (REICHLE, 1977; SETALA & HUHTA, 1991; BARDGETT & CHAN, 1999).

Soil microorganisms and invertebrates can interact with each other in several ways: negative interactions (competition or antagonism), positive interactions (symbiosis) and neutral interactions (commensalism) (HASSAN et al., 2019; CHEPSERGON & MOLELEKI, 2023). They also establish very close connections with vegetation.

The role of plants in the rhizosphere. Plants play a key role in soil mineral degradation and soil formation processes (pedogenesis) (HINSINGER et al., 2009). The rhizosphere influences biogeochemical cycling, plant growth and tolerance to biotic and abiotic stress (PHILIPPOT et al., 2013; ONETE et al., 2023).

Plant growth depends on light, moisture and nutrients available in inorganic form, released from organic matter through decomposition; therefore, they depend on the rate at which mineralization occurs in the soil (LAMBERS et al., 2008). Nutrient mineralization is the result of the activity of soil microflora. Nutrient absorption occurs in the rhizosphere, a region of intense interactions between roots and soil organisms (microorganisms, invertebrates) (BONKOWSKI, 2004).

Plants have a major influence on invertebrate groups. They release certain substances (*i.e.* amino acids and sugars) that serve as a source for microorganisms (NEHER & BARBERCHECK, 1998) and also select in this way certain groups of invertebrates to carry out their metabolic activity in their rhizosphere (HASSAN et al., 2019; SANTOYO et al., 2021). An example is the case of invasive species whose invasion can be faster and due to the fact that the invasive species can interrupt the interaction between the plant species and the native functional groups, thus cancelling biological control (DAWSON & SCHRAMA, 2016; ZHANG et al., 2019).

In the field, the rhizosphere of plants is much more complex than in the laboratory. Plants in the field have more roots, with a more complex architecture compared to those in the laboratory, a much wider range of exuded chemicals and a multitude of associated organisms (WATT et al., 2006). Although architectural phenotypes are promising targets for crop breeding, their effects on microbial associations are not well understood. Architecture determines the location of microbial associations in root systems, which determines the functions and metabolic capacity of microbial communities in the rhizosphere (GALINDO CASTAÑEDA et al., 2024).

The rhizospheres developed in the field show great differences in terms of environmental variables: temperature, diurnal and seasonal variations, the amount of water in the soil, especially in the surface areas that can go through very diverse periods from some very dry to some characterized by saturation in a very short period of time (hours to weeks) (WATT et al., 2006). The different types of roots, as well as the way they branch and their orientation, determine the degree of soil occupation, the rooting depth. Differences in soil structure, temperature, nutrients and water at different depths influence how soil organisms dynamically interact with roots (WATT et al., 2006).

During its growth and development, the plant goes through several stages (germination of seeds, growth of seedlings, etc.). During this process, a variety of organic compounds are released from the roots by exudation, secretion and deposition, making the rhizosphere rich in nutrients. This acts as a driving force for the formation of active microbial populations in the root zone, much larger compared to the soil without roots. This phenomenon of establishment of rich microflora in the rhizosphere under the influence of nutrients secreted by the root is called the rhizosphere effect or plant effect (PRASHAR et al., 2014).

The ecological role of the rhizosphere. The key biological functions of plant roots (absorption, respiration and exudation) can considerably modify the biogeochemical parameters of the soil in the vicinity of the roots: the concentration of nutrients, pollutants, pH and redox potential, gas partial pressures. Such parameters can also be directly influenced by the activity of soil invertebrates and microorganisms (HINSINGER et al., 2009). Although microorganisms are most numerous and ubiquitous in the subsurface, they are not uniformly distributed in all habitats. Most microbial populations are concentrated in nutrient-rich niches such as the rhizosphere, which has a constant supply of readily available nutrients (PRASHAR et al., 2014).

The rhizosphere influences the cycle of carbon, nitrogen and phosphorus, the rate of release of greenhouse gases and the decomposition of pollutants in the soil (TOAL et al., 2000; DE FARIA, 2021).

Roots change soil structure by increasing the connectivity between soil aggregates. They are a powerful management tool. Worldwide, alfalfa roots are used to create “biopores” in deeper soil layers that a subsequent crop can use. Root systems can also be used to improve soil structure at its surface (WATT et al., 2006).

Soil quality represents the ability to support agricultural crops and animal productivity, maintain and improve environmental sustainability, and improve human health worldwide (NICOARĂ et al., 2020; YANG et al., 2020). Agriculture is essential for food security. It has been predicted that, by 2050, the human population could reach 8 billion, which will pose a significant challenge to agricultural systems to produce enough food for this global population, especially given that there is a wide range of biotic and abiotic factors that have a significant negative impact on agricultural productivity. Currently, pest management is mainly carried out through the use of pesticides and agrochemicals, which do not completely solve the problems caused by various phytopathogens, as they can generate negative effects such as health problems, loss of ecological diversity and bioaccumulation of toxic substances (SANTOYO et al., 2021; PAUSCH et al., 2024).

Intensive agricultural practices that include prolonged use of inorganic fertilizers and chemical pesticides have resulted in huge agricultural and ecological damage. The excessive use of chemical fertilizers exerts harmful effects on soil microorganisms, altering soil fertility and polluting the environment. Sustainable food production has become the main need to improve food security globally, especially in developing countries (MANU et al., 2022; IGIEHON et al., 2024).

Farming systems offer the opportunity to significantly increase productivity in a sustainable way. Plants can alter their rhizosphere structure by shaping a beneficial microbial community to enhance resistance against soil pathogens. In this context, the selection and modification of the rhizosphere microbiome is an important strategy for improving crop health, since the rhizosphere and the root microbiome act as microbiological defences against pathogens (DE FARIA et al., 2021).

Root exudates. In nature, plants constantly release various compounds into the environment. This secretion process is known as exudation and can be carried out by different organs, including leaves, shoots or roots, which can secrete substances in solid, liquid or gaseous forms into the environment (VIVES-PERIS et al., 2020). Rhizo-deposits, root exudates and cells at the root margin are vital components of the rhizosphere that significantly affect the ability of microorganisms to colonize the root zone (HASSAN et al., 2019).

Root exudates include high molecular weight compounds such as proteins and polysaccharides and lower molecular weight compounds that are mainly composed of primary and secondary metabolites (amino acids, sugars, carboxylates, flavonoids, etc.). Root exudates can account for 20% to 40% of plant photosynthesis, depending on species and cultivars within species, and are highly controlled by environmental factors. Quantitative and qualitative changes in rhizodeposition in response to drought have been reported. Drought often leads to a decrease in absolute rhizodeposition due to decreased photosynthesis and carbon availability for exudation (AFFORTIT et al., 2024).

Plants have developed several mechanisms to secrete metabolites into the rhizosphere (passive and active transport). The secretion of root exudates has been considered a passive process, mediated by different pathways: transport through the root membrane by diffusion, ion channels and vesicle transport (GREGORY, 2006; VIVES-PERIS et al., 2020).

Metabolites secreted into the root rhizosphere are involved in several processes. By modulating the composition of root exudates, plants can modify soil properties to adapt and ensure their survival under adverse conditions. They use several strategies such as (1) changing soil pH to solubilize nutrients (2) chelating toxic compounds, (3) attracting beneficial microbiota or (4) releasing substances that are toxic to pathogens (VIVES-PERIS et al., 2020).

Rhizodeposition. The term rhizodeposition was first defined as “material lost from plant roots, including water-soluble exudates, secretions of insoluble materials, lysates, dead fine roots, and gases such as CO2 and ethylene”. More simply, it is defined as: “organic compounds released by the roots of living plants into the environment”. It is equivalent to nearly 15–60% of the total photosynthetic output of the plant and leads to the accumulation of substantial reserves of carbon and energy in the rhizosphere for the microflora (PRASHAR et al., 2014). Plant rhizo-deposits provide low molecular weight (LMW: organic acids, amino acids, sugars, phenolic acids, flavonoids, etc.) and high molecular weight

(HMW: carbohydrates, enzymes, etc.) carbon substrate. The composition of root exudates is highly variable depending on plant species and/or environmental conditions (e.g. substrate type, soil chemical characteristics, temperature, CO2 concentration, light conditions) (TOAL et al., 2000; PII, 2015).

CONCLUSIONS

Although the growth of plants by microorganisms has been studied in several articles, the roles played by them in the process of nutrient uptake by plants are not fully explored yet. There are still gaps in the knowledge of the mechanisms by which microorganisms in the rhizosphere zone increase the production and productivity of plants and their development under various environmental conditions. Also, answers are needed regarding the processes in the rhizosphere and the influence of the rhizo-deposits on the physiological state and diversity of the microorganisms in the rhizosphere. Also, there are many unknowns regarding the exudates of rhizosphere organisms, including: the distribution of exudates in the soil, the sites of synthesis and transport in and out of the root, the receptors within the plant, and the specificity of different compounds.

The rhizosphere is now seen as a key mechanism for solving critical issues faced by the planet, including the sustainability of agriculture and forests, improving water quality, mitigating climate change, conserving biodiversity and sustainable energy production. Due to their close proximity and/or continuous association with the plant, the various microorganisms found in the rhizosphere influence the host plant in a variety of ways. These can be broadly classified as beneficial effects leading to improved plant health and growth or harmful effects, i.e. pathogenic activities. Thus, it is very important to understand the composition, ecology, dynamics and activities of the rhizosphere microbial communities, before being able to exploit rhizosphere microflora as a tool for developing sustainable agricultural practices.

The rhizosphere microflora provides an important link between the plant and the soil, acting as an intermediary between the two. The rhizosphere is heavily loaded with nutrients obtained from plant roots through rhizo-position. Microorganisms are the most abundant rhizosphere-dwelling organisms that promote plant growth.

In the coming decades, food supply and agricultural productivity must meet the demands of human population growth. Plant growth and productivity depend on nutrient availability, and this is influenced by various factors, including the biological activities of both roots and rhizosphere microorganisms. To meet the challenge of the global food shortage crisis, chemical fertilizers have been widely applied to crops. However, excessive use of chemical fertilizers can lead to soil acidification and compaction, causing decreased microbial function and diversity and altering microbial assembly processes. These changes can negatively affect soil ecology and food safety. Organic fertilizers are mainly derived or composted from plant or animal materials, contain abundant nutrients and carry various beneficial microbes for plant growth. They are a promising alternative to chemical fertilizers; however, the effects of organic fertilizers from different biological sources on plants and their risks to soil ecology remain poorly understood.

Until now, crop nutrition has depended on the application of large amounts of fertilizers; however, to limit and/or prevent future environmental and economic problems, agricultural practices are moving towards more sustainable systems. In this context, the use of microorganisms as bioinoculants could represent a very promising approach, given that they are able to improve both plant development (increase in root and shoot biomass, more branched root system) and nutrient bioavailability.

Understanding how rhizodepositions, root exudates, and root margin cells interact in the rhizosphere in the presence of rhizobacterial populations is necessary to decipher their synergistic role in improving plant health. There is also a growing need to understand the rhizosphere, so that we can effectively manage ecosystems either to harness their potential benefits or to reverse the negative consequences of anthropogenic intervention.

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Mihai Luiza-Silvia
Bucharest Institute of Biology of the Romanian Academy, Splaiul Independenței 296, Bucharest, Romania.
E-mails: luiza.chiriac@ibiol.ro; luizaschiriac@gmail.com

Cioboiu Olivia
The Oltenia Museum, Craiova, Str. Popa Șapcă, No. 8, 200422, Craiova, Romania.
E-mails: oliviacioboiu@gmail.com; cioboiu.olivia@yahoo.com

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