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FUNCTIONING OF MICROORGANISMS IN THE RHIZOSPHERE OF PLANTS

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ABSTRACT

The functioning of living organisms in nature is possible only due to active interaction with microbiota. It is typical for phytobionts, the microbial cenosis of which is even more diverse. Plants contribute to the spread of microorganisms in the rhizosphere by releasing root exudates. The chemical composition of these exudates varies in different plant species and depends on the significant number of factors that affect their growth and development. The components of the plant root exudates stimulate expansion in the rhizosphere of microorganisms, useful for the plant growth. This microbiota improves the mineral life of plants considerably, stimulating their growth with biologically active compounds, increasing the availability of a number of microelements for them, protecting the growth of plants from phytopathogens and phytophages. It provides significant stimulation for the growth and development of phytobionts. It has been shown that microbial groups in the rhizosphere can induce some changes in the composition of plant root exudates.

Keywords: microorganism, plants, root exudates, plant-microbial interaction

INTRODUCTION

The functioning of living systems in nature is possible only on condition of active interaction with microbiota. Microorganisms play an essential role in numerous interactions between plants and soil (**Lambers *et al.*, 2009; Ma et al., 2022**). This interaction is most typical in plant coenoses, which are characterized by a significant diversity of microbes in the soil and around the root system (**Lynch, 1990; Torsvik *et al.*, 1990**). One gram of soil contains more than a billion cells of microorganisms (**Myshustin, 1972**), which belong to about 4,000 types of microorganisms (**Tate, 1997; Roesch *et al.*, 2007**). Bacteria and fungi are the most dominant parts of the rhizosphere; however, in addition to them, there are archaea, oomycetes, nematodes, and protists, which are also crucial for the functioning of the microbiome (**Fitzpatrick *et al.*, 2020; Nayfach *et al.*, 2020**).
Two types of microbial coenoses are formed in soil conditions. One of them is created in soils distant from the root zone of plants due to the presence of organic remains of previously growing plants. This microbial coenosis is significantly different from the microbial community of the rhizosphere soil, which largely depends on the content of plant root exudates. This microbiota affects the growth and development of plants most noticeably (**Lynch, 1990; Mikkelsen *et al.*, 2015**). At the same time, an important role is also attributed to the microorganisms of rhizoplanes that control the penetration of other prokaryotes and micromycetes into plant roots (endorhiza) (**Zhang *et al.*, 2017**). Soil microorganisms are the main participants of the carbon cycle on earth. They account for more than half of the total soil organic carbon (**Liang *et al.*, 2019**).

Microorganisms of the plant rhizosphere

The rhizosphere is the zone of the root system in the soil where the functioning of soil microorganisms is determined by the influence of plant exudates. This zone extends up to several millimeters from the root surface and includes the soil attached to the root surface. It is essential for the interaction of plants with microbiota since the roots of plants release a significant amount of metabolites, affecting the functioning of various microorganisms considerably (**Lynch, 1990; Gray *et al.*, 2005; Canarini *et al.*, 2019; Seitz *et al.*, 2021**). Among this microbiota, gram-negative microorganisms of the genera *Pseudomonas*, *Agrobacterium*, *Klebsiella*, and others are most widely represented (**Katsy, 2003**).
The dynamic zone of contact between plant roots and the soil is known as the rhizobiome. Complex interactions between roots, bacteria, fungi, and other representatives of the microbiota take place in this zone (**Raaijmakers *et al.*, 2008**).
Plants are characterized by a significant diversity of microbes around their root system. Some microorganisms can be pathogenic for plants, while others are significant for their growth and development. To modulate their microbiome, plants use many defense reactions as structural modifications, among which exudation into the root zone of secondary metabolites plays an important role (**Pascale *et al.*, 2020**).
Modern ecological theories associate root exudates with benefits for plants due to their stimulating the functioning of beneficial microorganisms (e.g., symbionts), contributing to the obtainment of nutrients, and providing recognition between their own and neighboring roots (**Shirokych *et al.*, 2007; Mommer *et al.*, 2016**).
Microorganisms in the plant rhizosphere promote the growth, development, and productivity of plants. A certain part of the microbiota can fix atmospheric nitrogen, improving nitrogen nutrition of plants (**Jenkinson, 1973; Kurdish, 2001; Kurdish, 2019; Volkogon, 2006; Umarov *et al.*, 2007**).
An important role in the growth and development of plants is attributed to phosphate-mobilizing microorganisms of the root zone. A part of this microbiota can dissolve sparingly soluble phosphorus compounds, contributing to the nutrition of plants (**Myshustin, 1972; Bulavenko *et al.*, 2000; Wakelin *et al.*, 2004; Rudresh *et al.*, 2005; Mikkelsen *et al.*, 2015**).
The microbiota of the rhizosphere is able to suppress phytopathogens and phytophages (**Kurdish, 2010; Innerebner *et al.*, 2011; Roy *et al.*, 2012; Kurdish *et al.*, 2021**), and affect the flowering of plants and their productivity (**Kurdish, 2010; Kurdish, 2019; Chuyko *et al.*, 2010; Lu *et al.*, 2018**).

Composition of root exudates

Root exudates are represented by a wide range of chemical compounds, the composition of which depends on a significant number of factors (**Kravchenko *et al.*, 2004; Sasse *et al.*, 2018**). On the example of wheat seedlings, it was shown that the transition to phototrophic nutrition occurs only on the 10-12th day of plant growth (**Shirokych *et al.*, 2007**).
The profiles of root exudates can contain up to 60 chemical components, unique for each species and genotype of plants (**Berg *et al.*, 2009; Micallef *et al.*, 2009**). Plant root exudates affect the composition of the rhizosphere microbiome and its activity (**Achouak *et al.*, 2019**). Changing the composition of root exudates, plants can influence soil properties by changing their pH and dissolving various substrates, chelating toxic compounds, attracting beneficial microbiota, and suppressing pathogens (**Vives-Peris *et al.*, 2019**).
According to the data of some researchers, root exudates can make up from 5 to 21% of the carbon fixed photosynthetically by plants (**Nguyen, 2003**). At the same time, according to the results of other researchers (**Badri, *et al.*, 2009**), during vegetation, plants can release from 3 to 40% of the photosynthesis products in the form of exometabolites into the root zone, where these compounds cause a significant impact on the plant-microbial interaction (rhizosphere effect). It remains unclear why and how plants invest up to 40% of their photosynthetically fixed C in root exudates (**Badri, *et al.*, 2009**).

The abovementioned differences can be conditioned by the fact that the quantitative composition of plant exudates depends to some extent on the substrate for their cultivation, the stage of plant development, growth conditions, and the physical and chemical properties of the environment in which the root system develops. Root exometabolites show different physiological and biochemical properties and are represented by a spectrum of organic compounds from different classes. These are water-soluble substances that enter the soil from the roots, as well as high-molecular compounds (**Miller *et al.*, 2019**).

Carbohydrates, amino acids, organic acids, phytohormones, aldehydes, alcohols, and phenols are widely represented among the low-molecular compounds of plant root exudates. High-molecular compounds include polysaccharides (mucigel), which form thin layers on the surface of the roots; exfoliating root cap cells that partially remain in the root zone; dying epidermal cells; and volatile metabolites of germinating seeds and roots (**Sasse *et al.*, 2018; Berg *et al.*, 2009; Vives-Peris *et al.*, 2019; Bais *et al.*, 2006; Haichar *et al.*, 2014; Hawes *et al.*, 2016; Ahmed *et al.*, 2018; Maurer *et al.*, 2021**). The root exudates of leguminous plants also include flavonoids, which play an essential role in the interaction between roots and microbes, activating *Rhizobium meliloti* genes responsible for the process of nodule formation (**Peters *et al.*, 1986**). So, root exudate luteolin induces the expression of rhizobia nodulation gene reguired nodule development (**Spini *et al.*, 2015**).

The volatile fraction of plant exudates contains several various compounds: carbohydrates, alcohols, aldehydes, ketones, and organic acids. These volatile compounds can also inhibit or stimulate plant growth (**Grodzinsky, 1965; Zhang *et al.*, 2022**). It should be noted that rhizodeposits, such as mucus of the root cap and dying cells of the epidermis, are an important source of nutrition for rhizosphere microbes and affect the relationship between roots and microorganisms (**Hawes *et al.*, 2016; Ahmed *et al.*, 2018**).

The composition of root secretions of plants largely depends on the conditions of their cultivation. For example, when corn growth was limited by phosphorus, nitrogen, potassium, or iron, the content of carbohydrates, amino acids, and organic acids in root exudates differed significantly (**Miller *et al.*, 2019; Carvalhais *et al.*, 2013**). The content of green manure proteins in the exudates of these plants increased when zinc content was limited during wheat cultivation (**Rengel *et al.*, 2000**).

The content of organic acids and carbohydrates in root exudates differs significantly in the process of plant vegetation. Non-protein amino acids are a valuable reserve of organic nitrogen in various ecosystems. Studies show that they play an essential role as metabolites, allelopathic chemicals, in the metabolism of nutrients, in signal transmission, and in plant responses to stress (**Vranova *et al.*, 2010**). It was established that the content of threonine in the root exudates of green mustard was four times higher than that of Khibiny cabbage, and the content of tyrosine and phenylalanine was almost five times higher (**Bylyanovskaya, 1983**).

Interaction between microorganisms and root exudates

Some molecules extracted by roots can act as antimicrobial substances against one microorganism and as stimulants to establish positive interactions with other organisms. For example, canavanine, a non-protein analog of arginine extracted by many varieties of leguminous seeds, acts as an antimetabolite in many biological systems and stimulates the adhesion of rhizobia (**Cai *et al.*, 2009**).

It was determined that exometabolites of various plant species could both suppress and stimulate the rate of radial mycelium growth. It was demonstrated that the exometabolites of wheat, oats, and onion plants significantly affected the reproductive activity of the micromycetes *Bipolaris sorokiniana* and *Alternaria alternata*, which led to a decrease in the sporulation of these phytopathogens down to 2.5 times per 1 sq. cm. of the colony area (**Horgan *et al.*, 2021**).

It was established that corn exometabolites significantly increased the efficiency of phenol removal by *Pseudomonas fluorescens* bacteria. At the same time, there was also a decrease in the content of reactive oxygen species in the environment (**Jin *et al.*, 2019**).

The quantitative and qualitative changes in the composition of root exudates are caused by the activation of biological defense systems through elicitors simulating stress in plants. Biotic and abiotic elicitors stimulate protective mechanisms in plant cells and significantly increase the variety and number of exudates (**Cai *et al.*, 2011**).

The composition of plant root exudates is different for various species and genotypes and depends on the growth conditions of phytobionts. Root exometabolites and their transformation products are the main sources of nutrition for the rhizosphere microflora (**Ma *et al.*, 2022**).

The dynamics of organic substances exudation is species-specific. The main components of root exudates are organic acids and carbohydrates, which serve as substrates for the rhizosphere microflora. The ratio between the amount of these isolated substances in the fraction changes significantly during the growing season of plants (**Ma *et al.*, 2022**). The exudation of organic acids contributes to an increase in the denitrifying activity of rhizosphere bacteria, while this activity significantly decreases with an increase in the content of carbohydrates (**Maurer *et al.*, 2021**).

It was established that corn root exudates improved the formation of *Bacillus amyloliquefaciens* SQR9 biofilm on the surface of plant roots, which was possibly due to the stimulating effect of exudates on bacterial growth and extracellular matrix production (**Zhang *et al.*, 2015**).

Exometabolites exudation mechanisms

Modern ecological theories associate the release of root exudates with benefits for plants due to the stimulation of the spreading of the microorganisms that improve plant growth and development (for example, symbionts), contributing to the obtainment of nutrients and providing recognition between their own roots and those of neighboring plants (**Ortíz-Castro *et al.*, 2009**).

A significant part of root exudates can be passively released into the soil due to the creation of a concentration gradient between root cells and the soil solution (**Jones *et al.*, 2004: Jones *et al.*, 2009; Canarini *et al.*, 2019**). Most of these compounds are represented by primary metabolites: sugars, amino acids, and organic acids. It was shown that they come passively from the root at its meristem tip (**Canarini *et al.*, 2019; Sasse *et al.*, 2018; Jones *et al.*, 2004; Jones *et al.*, 2009; McCully *et al.*, 1985; Darwent *et al.*, 2003**).

The root tip is the first part of the plant to explore the new soil environment and plays a critical role in root response to environmental stimuli. Most of the root exudation is localized at the apex of the root (**Canarini *et al.*, 2019; Darwent *et al.*, 2003; Baluška *et al.*, 2004; Baluška *et al.*, 2013**). The root cap acts as the most important organ of plants, which determines the influence of several physical factors and inorganic compounds, critical for plants (**Baluška *et al.*, 2013**).

The molecules of exometabolites pass through plasma membranes only through specific transmembrane proteins that form small pores in the lipid bilayer, providing for polar or charged molecules to cross the membrane without interacting with hydrophobic fatty acid chains of membrane phospholipids. Some root exudates, such as biologically active secondary compounds, are released from the roots by energy-consuming primary or secondary active transporters (**Sasse *et al.*, 2018**).

The root tip perceives the changes in the concentration of released metabolites and converts them into signals to alter root growth. The cells of the root cap participate in the synthesis of polysaccharide mucus, which makes up to 12% of the total amount of rhizodeposits (**Nguyen, 2003**). These cells affect the formation of rhizosphere microflora, suppressing the spread of phytopathogens (**Gunawardena *et al.*, 2002**).

Plants can change the concentration of metabolites by controlling their uptake processes or by expressing and regulating efflux carriers. Due to the flow of root exudate, plants can locally increase the concentration of many common metabolites, which can serve as sensors and integrators of the nutritional status of plants and the availability of these substances in the environment. Plant-associated microorganisms are also powerful absorbers of plant carbon, thereby increasing metabolite concentration gradients and affecting root exudation (**Canarini *et al.*, 2019**). It was shown that the introduction of microorganisms into the solution used to grow plants significantly increased root exudation compared to the variant without the microorganisms (**Groleau-Renaud *et al.*, 2000; Phillips *et al.*, 2004**). It has been established that benzoxazinoids, which are secondary metabolites of root exudates of wheat and sorghum cereal crops, are able to influence the composition of fungal and bacterial communities in the root zones of plants and enhance the transmission of jasmonate signals (**Hu *et al.*, 2018**). Root exudates have a significant effect on the growth and activity of soil microorganisms. Modern research methods have yielded much experimental evidence of changes in the structure of microbial communities of the rhizosphere depending on the composition of exometabolites of plants (**Berg *et al.*, 2009**).

The composition of root exudates of different types of plants differs significantly and also alters considerably depending on the conditions of their growth and the period of vegetation. Thus, in tomato and wheat plants, the ratio of organic acids and sugars has the opposite character. Organic acids, which are part of root exudates, are more effectively utilized by rhizobacteria compared to sugars (**Kravchenko *et al.*, 2003**).

It is known that phosphorus deficiency in the soil causes significant changes in root architecture, increasing the number of root hairs and lateral roots (**Nadira *et al.*, 2016**). It has been established that the exudation of organic acids by the roots of rape helps increase the mobilization of phosphate from poorly soluble compounds and improve its availability for plants (**Hoffland *et al.*, 1992**).

Influence of microorganisms on plant root exudation

Soil microbiota plays a key role in the relationship between plants and the soil. It has been shown that different microbial groups are able to cause specific differences in the composition of root exudates of plants. Thus, the colonization of the rhizosphere by bacteria of the genus *Bacillus* influenced the composition of carbohydrates in the exudates of these plants (**Korenblum *et al.*, 2020**).

The composition of plant root exudates affects the synthesis of antifungal substances by PGPR strains significantly. While developing in the rhizosphere of plants, PGPR strains can produce substances of an antifungal nature and also prevent the emergence and development of a fungal infection by competing for food sources and ecological niches in the rhizosphere zone due to the high colonizing activity of bacteria (**Souza *et al.*, 2015**).

The maximum inhibition of phytopathogens was observed when growing bacteria in media with organic acids, which are much more efficiently utilized by rhizobacteria compared to carbohydrates. In the environments with carbohydrates, this activity was lower, and in some cases, it was completely absent. The removal of *Pseudomonas fluorescens* from the culture medium of oxalic, fumaric, or citric acids reduced the content of bacterial reactive oxygen species in it (**Korenblum *et al.*, 2020**).
The main source of L-tryptophan, necessary for the synthesis of auxins, in the rhizosphere of plants, is found in root exometabolites. Its content in root exudates is fractions of a percent. Despite this, soil microorganisms in close contact with plant root systems activate auxin synthesis in the presence of tryptophan significantly (**Kravchenko *et al.*, 2004**).
In recent years, considerable attention has been paid to the role of root exudates in regulating the activity of beneficial rhizobacteria and their ability to protect plants from phytopathogens (**Bakker *et al.*, 2018**). However, the question of whether the rhizospheric microbiome is able to modulate root exudation remains poorly investigated. It has been shown that different microbial communities can promote specific systemic changes in tomato root exudation (**Korenblum *et al.*, 2020**).
In the root exudates of barley, colonized by the phytopathogenic micromycete *Fusarium culmorum* and the antagonistic bacterium *Pseudomonas fluorescens*, the presence of seven aromatic carboxylic acids, known for their antimicrobial activity, was established. In response to the colonization of the root zone by *P. fluorescens* PGPR strains, a lower amount of antimicrobial components was determined in barley exudates compared to *F. culmorum* colonization. All aromatic carboxylic acids inhibited the growth of this micromycete, while only two of them favored the growth of *P. fluorescens*. This indicates the ability of plants, due to the synthesis of exometabolites, to create the conditions favorable for the functioning of useful microbiota and unfavorable for the growth of phytopathogenic micromycetes in the rhizosphere (**Shaposhnikov *et al.*, 2020**).
It was shown that the content of aromatic acids (nicotinic, shikimic, salicylic, cinnamic, and indol-3-acetic) contributes to the reproduction of rhizosphere bacteria and their positive effect on plants (**Zhalnina *et al.*, 2018**). Competitive relationships between fungi and bacteria were established in model experiments. According to the authors, fungi and bacteria compete for nitrogen sources (**Shaposhnikov *et al.*, 2020**). At the same time, certain types of bacteria and micromycetes can increase the immunity of plants, activating their defenses against phytopathogens (**van Loon *et al.*, 1998**).
Microorganisms of the rhizosphere can improve plant growth conditions, reducing the impact of abiotic factors (for example, drought), and pathogens, and improving plant nutrition. This testifies to the positive influence of these microorganisms on the growth and development of plants (**Eichmann *et al.*, 2021**). Plant phytohormones, auxins, play a significant role in the regulation of these processes (**Baluška *et al.*, 2004**).
Microorganisms can affect the morphogenetic processes of plants due to the influence of homoserine lactone, which belongs to the class of bacterial quorum sensing signals from gram-negative bacteria. It was established that these metabolites could be recognized by plants and used to modulate defense systems and cell growth (**Ortíz-Castro *et al.*, 2009**).
Microorganisms of the root zone of plants can significantly influence the growth of phytobionts, in particular, by regulating the availability of iron ions necessary for biosynthetic processes. Iron ions are a vital trace element for plants and microorganisms, as they participate in the processes of photosynthesis, respiration, chlorophyll biosynthesis, etc. (**Kobayashi *et al.*, 2012**).
Despite the high content of iron compounds in the soil, this element is often a limiting factor for plant growth and development due to its low availability. It was shown that the inoculation of *Arabidopsis* plants with *Paenibacillus polymyxa* BFKC01 bacteria stimulated Fe absorption by plants. Under these conditions, the content of phenolic compounds increased in the root exudates of the inoculated plants, which contributed to the mobility of iron in alkaline conditions. It increased the photosynthetic activity of plants (**Zhou *et al.*, 2016**).
Microorganisms have active strategies to absorb Fe from the nutrients using chelating agents called siderophores. They are represented by molecules with a low mass (under 1,000 Da) and high specificity for chelation or binding of ferric iron with subsequent transfer and deposition of iron in the middle of bacterial cells (**Krewulak *et al.*, 2008**).
The release of siderophores by bacteria can stimulate plant growth, improving their nutritional conditions (direct effect) or suppressing the spread of phytopathogens due to sequestration (reduction in availability) of iron ions from the environment (**Dimkpa *et al.*, 2009**). Siderophores synthesized by nitrogen-fixing bacteria *Azotobacter vinelandii* significantly increase the availability of molybdenum and vanadium, necessary for the functioning of nitrogenase, an enzyme that fixes atmospheric nitrogen (**Bellenger *et al.*, 2008**).
Taking into account the significant influence of microorganisms on the growth and development of plants, as early as in 1896, it was proposed to use preparations of nitrogen-fixing bacteria in crop production (**Nobble, 1896**). In recent decades, microbial preparations have been widely used in agriculture to correct the microflora of the rhizosphere, improve the nutrition of plants with mineral elements, protect them from phytopathogens and phytophages, and the influence of other negative factors (**Kloepper *et al.*, 1989; Kurdish, 2019; Volkogon, 2006; Iutynska, 2006**).

CONCLUSION

An important role in the growth and development of plants is attributed to their interaction with the microbiota of the root zone. Plant root exudates, the share of which can be up to 40% of the total content of photosynthesis products, largely determine the formation of the rhizospheric microbiome. Root exudates include carbohydrates, organic acids, amino acids, phenolic acids, and other compounds. The review analyzes the release mechanisms of root exudates, their influence on the functioning of plant rhizosphere microorganisms. Due to the release of these compounds, the rhizosphere microbiome improves nitrogen and phosphorus nutrition of plants significantly, stimulates their growth with biologically active substances and phytohormones, protects plants from phytopathogens and phytophages, and increases the productivity of phytobionts. It is shown that some microbial groups of the rhizosphere can cause certain changes in the composition of plant root exudates. However, the mechanisms of root exudation regulation, the influence of rhizosphere microbiota and microorganisms, introduced into the agroecosystem, on this process require further research.

REFERENCES

Achouak, W., Abrouk, D., Guyonnet, J., Barakat, M., Ortet, P., Simon, L., Lerondelle, C., Heulin, T., & Haichar, F. el Z. (2019). Plant hosts control microbial denitrification activity. FEMS Microbiology Ecology, 95(3). https://doi.org/10.1093/femsec/fiz021
Ahmed, M. A., Passioura, J., & Carminati, A. (2018). Hydraulic processes in roots and the rhizosphere pertinent to increasing yield of water-limited grain crops: a critical review. Journal of Experimental Botany, 69(13), 3255–3265. https://doi.org/10.1093/jxb/ery183
Badri, D. V., & Vivanco, J. M. (2009). Regulation and function of root exudates. Plant, Cell & Environment, 32(6), 666–681. https://doi.org/10.1111/j.1365-3040.2009.01926.x
Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology, 57(1), 233–266. https://doi.org/10.1146/annurev.arplant.57.032905.105159
Bakker, P. A. H. M., Pieterse, C. M. J., de Jonge, R., & Berendsen, R. L. (2018). The Soil-Borne Legacy. Cell, 172(6), 1178–1180. https://doi.org/10.1016/j.cell.2018.02.024
Baluška, F., & Mancuso, S. (2013). Root Apex Transition Zone As Oscillatory Zone. Frontiers in Plant Science, 4. https://doi.org/10.3389/fpls.2013.00354
Baluška, F., Mancuso, S., Volkmann, D., & Barlow, PW. (2004). Root apices as plant command centres: The unique 'brain-like' status of the root apex transition zone. Biologia (Bratislava), 59 Supplement 13, 7-19.
Bellenger, J. P., Wichard, T., Kustka, A. B., & Kraepiel, A. M. L. (2008). Uptake of molybdenum and vanadium by a nitrogen-fixing soil bacterium using siderophores. Nature Geoscience, 1(4), 243–246. https://doi.org/10.1038/ngeo161
Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiology Ecology, 68(1), 1–13. https://doi.org/10.1111/j.1574-6941.2009.00654.x
Bulavenko, L.V., Bega, Z.T., & Kurdish, I.K. (2000). Mobilization of phosphorus by some microorganisms from sparingly soluble inorganophosphates. Bull. agricultural microbiology, 6, 55-56.
Bylyanovskaya, T.M. (1983). The quality composition of the roots of selected vegetable crops. On Sat. The role of plant and microbial toxins in allelopathy. Kyiv. Scientific opinion, 99-101.
Cai, T., Cai, W., Zhang, J., Zheng, H., Tsou, A. M., Xiao, L., Zhong, Z., & Zhu, J. (2009). Host legume-exuded antimetabolites optimize the symbiotic rhizosphere. Molecular Microbiology, 73(3), 507–517. https://doi.org/10.1111/j.1365-2958.2009.06790.x
Cai, Z., Kastell, A., Knorr, D., & Smetanska, I. (2011). Exudation: an expanding technique for continuous production and release of secondary metabolites from plant cell suspension and hairy root cultures. Plant Cell Reports, 31(3), 461–477. https://doi.org/10.1007/s00299-011-1165-0
Canarini, A., Kaiser, C., Merchant, A., Richter, A., & Wanek, W. (2019). Root Exudation of Primary Metabolites: Mechanisms and Their Roles in Plant Responses to Environmental Stimuli. Frontiers in Plant Science, 10. https://doi.org/10.3389/fpls.2019.00157
Carvalhais, L. C., Dennis, P. G., Fan, B., Fedoseyenko, D., Kierul, K., Becker, A., von Wiren, N., & Borriss, R. (2013). Linking Plant Nutritional Status to Plant-Microbe Interactions. PLoS ONE, 8(7), e68555. https://doi.org/10.1371/journal.pone.0068555
Chuyko, N.V., Bega, Z.T., Bulavenko, L.V., & Kurdish, I.K. (2010). Influence of bacterial preparation of complex action on decorative plants growth. Microbiology Biotechnology, 2(10), 43–50. https://doi.org/10.18524/2307-4663.2010.2(10).98795
Darwent, M. J., Paterson, E., McDonald, A. J. S., & Tomos, A. D. (2003). Biosensor reporting of root exudation from Hordeum vulgare in relation to shoot nitrate concentration. Journal of Experimental Botany, 54(381), 325–334. https://doi.org/10.1093/jxb/erg017

Dimkpa, C. O., Merten, D., Svatoš, A., Büchel, G., & Kothe, E. (2009). Siderophores mediate reduced and increased uptake of cadmium byStreptomyces tendaeF4 and sunflower (Helianthus annuus), respectively. Journal of Applied Microbiology, 107(5), 1687–1696. https://doi.org/10.1111/j.1365-2672.2009.04355.x
Eichmann, R., Richards, L., & Schäfer, P. (2021). Hormones as go-betweens in plant microbiome assembly. The Plant Journal, 105(2), 518–541. Portico. https://doi.org/10.1111/tpj.15135
Fitzpatrick, C. R., Salas-González, I., Conway, J. M., Finkel, O. M., Gilbert, S., Russ, D., Teixeira, P. J. P. L., & Dangl, J. L. (2020). The Plant Microbiome: From Ecology to Reductionism and Beyond. Annual Review of Microbiology, 74(1), 81–100. https://doi.org/10.1146/annurev-micro-022620-014327
Gray, E. J., & Smith, D. L. (2005). Intracellular and extracellular PGPR: commonalities and distinctions in the plant–bacterium signaling processes. Soil Biology and Biochemistry, 37(3), 395–412. https://doi.org/10.1016/j.soilbio.2004.08.030
Grodzinsky, A.M. (1965). Allelopathy in the life of plants and their communities. Kyiv. Scientific opinion, 168.
Groleau-Renaud, V., Plantureux, S., Tubeileh, A., & Guckert, A. (2000). Influence of microflora and composition of root bathing solution on root exudation of maize plants. Journal of Plant Nutrition, 23(9), 1283–1301. https://doi.org/10.1080/01904160009382100
Gunawardena, U., & Hawes, M. C. (2002). Tissue Specific Localization of Root Infection by Fungal Pathogens: Role of Root Border Cells. Molecular Plant-Microbe Interactions®, 15(11), 1128–1136. https://doi.org/10.1094/mpmi.2002.15.11.1128
Haichar, F. el Z., Santaella, C., Heulin, T., & Achouak, W. (2014). Root exudates mediated interactions belowground. Soil Biology and Biochemistry, 77, 69–80. https://doi.org/10.1016/j.soilbio.2014.06.017
Hawes, M., Allen, C., Turgeon, B. G., Curlango-Rivera, G., Minh Tran, T., Huskey, D. A., & Xiong, Z. (2016). Root Border Cells and Their Role in Plant Defense. Annual Review of Phytopathology, 54(1), 143–161. https://doi.org/10.1146/annurev-phyto-080615-100140
Hoffland, E. (1992). Quantitative evaluation of the role of organic acid exudation in the mobilization of rock phosphate by rape. Plant and Soil, 140(2), 279–289. https://doi.org/10.1007/bf00010605
Horgan, T.M., Beznosenko, I.V., Bilenka, O.M., & Blaginina, A.A. (2021). Influence of exometabolites of different varieties of cultural plants on the growth and development of pathogenic micromycetes Bipolaris sorokiniana and Alternaria alternata. Agriciltural Microbiology, 33, 96–105. https://doi.org/10.35868/1997-3004.33.96-105
Hu, L., Robert, C. A. M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., van der Heijden, M. G. A., Schlaeppi, K., & Erb, M. (2018). Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nature Communications, 9(1). https://doi.org/10.1038/s41467-018-05122-7
Innerebner, G., Knief, C., & Vorholt, J. A. (2011). Protection of Arabidopsis thaliana against Leaf-Pathogenic Pseudomonas syringae by Sphingomonas Strains in a Controlled Model System. Applied and Environmental Microbiology, 77(10), 3202–3210. https://doi.org/10.1128/aem.00133-11
Iutynska, G. O. (2006). Soil microbiology. Kyiv: Aristei, 284.
Jenkinson, D.C. (1973). Organic matter and nitrogen in soil of the Rothemsted classical exseriments. J. Sci. Food and Agr., 24, 1149-1150.
Jin, J., Wang, M., Lu, W., Zhang, L., Jiang, Q., Jin, Y., Lu, K., Sun, S., Cao, Q., Wang, Y., & Xiao, M. (2019). Effect of plants and their root exudate on bacterial activities during rhizobacterium–plant remediation of phenol from water. Environment International, 127, 114–124. https://doi.org/10.1016/j.envint.2019.03.015
Jones, D. L., Hodge, A., & Kuzyakov, Y. (2004). Plant and mycorrhizal regulation of rhizodeposition. New Phytologist, 163(3), 459–480. Portico. https://doi.org/10.1111/j.1469-8137.2004.01130.x
Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). Carbon flow in the rhizosphere: carbon trading at the soil–root interface. Plant and Soil, 321(1–2), 5–33. https://doi.org/10.1007/s11104-009-9925-0
Katsy, E.I. (2003). Molecular genetic processes influencing the associative interaction of soil bacteria with plants. Saratov: Publishing House of Saratov University, 127.
Kloepper, J. W., Lifshitz, R., & Zablotowicz, R. M. (1989). Free-living bacterial inocula for enhancing crop productivity. Trends in Biotechnology, 7(2), 39–44. https://doi.org/10.1016/0167-7799(89)90057-7
Kobayashi, T., & Nishizawa, N. K. (2012). Iron Uptake, Translocation, and Regulation in Higher Plants. Annual Review of Plant Biology, 63(1), 131–152. https://doi.org/10.1146/annurev-arplant-042811-105522
Korenblum, E., Dong, Y., Szymanski, J., Panda, S., Jozwiak, A., Massalha, H., Meir, S., Rogachev, I., & Aharoni, A. (2020). Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. Proceedings of the National Academy of Sciences, 117(7), 3874–3883. https://doi.org/10.1073/pnas.1912130117
Kravchenko, L.V., Azarova, T.S., Leonova-Erko & E.I. (2003). Root secretions of tomatoes and their influence on the growth and antifungal activity of Pseudomonas strains. Microbiol., 72(1), 48-53. https://doi.org/10.1023/A:1022269821379
Kravchenko, L.V., Azarova, T.S., Makarova, N.M. & Tikhonovich I. A. (2004). The Effect of Tryptophan Present in Plant Root Exudates on the Phytostimulating Activity of Rhizobacteria. Microbiology, 73, 156–158. https://doi.org/10.1023/B:MICI.0000023982.76684.9d
Krewulak, K. D., & Vogel, H. J. (2008). Structural biology of bacterial iron uptake. Biochimica et Biophysica Acta (BBA) - Biomembranes, 1778(9), 1781–1804. https://doi.org/10.1016/j.bbamem.2007.07.026
Kurdish I.K. (2010). Introduction of microorganisms into agroecosystems. Kyiv. Scientific opinion, 253.
Kurdish, I. K. (2019). Interaction of Microorganisms with Nanomaterials as a Basis for Creation of High-Efficiency Biotechnological Preparations. Nanotechnology in the Life Sciences, 259–287. https://doi.org/10.1007/978-3-030-17061-5_11
Kurdish, I. K., Roy, A. A., & Skorochod, I. A. (2021). Efficiency of the Complex Bacterial Preparation Azogran Application in Protecting Potatoes from the Colorado Potato Beetle Depending on the Stage of Its Development. Mikrobiolohichnyi Zhurnal, 83(1), 3–11. https://doi.org/10.15407/microbiolj83.01.003
Kurdish, I.K. (2001). Granular microbial preparations for crop production: science and practice. Kiev KVIC, 141.
Lambers, H., Mougel, C., Jaillard, B., & Hinsinger, P. (2009). Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant and Soil, 321(1–2), 83–115. https://doi.org/10.1007/s11104-009-0042-x
Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. Global Change Biology, 25(11), 3578–3590. Portico. https://doi.org/10.1111/gcb.14781
Lu, T., Ke, M., Lavoie, M., Jin, Y., Fan, X., Zhang, Z., Fu, Z., Sun, L., Gillings, M., Peñuelas, J., Qian, H., & Zhu, Y.-G. (2018). Rhizosphere microorganisms can influence the timing of plant flowering. Microbiome, 6(1). https://doi.org/10.1186/s40168-018-0615-0
Lynch, J.M. (1990). The rhizosphere. Wiley-Interscience, 458.
Ma, W., Tang, S., Dengzeng, Z., Zhang, D., Zhang, T., & Ma, X. (2022). Root exudates contribute to belowground ecosystem hotspots: A review. Frontiers in Microbiology, 13. https://doi.org/10.3389/fmicb.2022.937940
Maurer, D., Malique, F., Alfarraj, S., Albasher, G., Horn, M. A., Butterbach-Bahl, K., Dannenmann, M., & Rennenberg, H. (2021). Interactive regulation of root exudation and rhizosphere denitrification by plant metabolite content and soil properties. Plant and Soil, 467(1–2), 107–127. https://doi.org/10.1007/s11104-021-05069-7
McCully, M. E., & Canny, M. J. (1985). Localisation of translocated 14C in roots and root exudates of field-grown maize. Physiologia Plantarum, 65(4), 380–392. https://doi.org/10.1111/j.1399-3054.1985.tb08661.x
Micallef, S. A., Channer, S., Shiaris, M. P., & Colón-Carmona, A. (2009). Plant age and genotype impact the progression of bacterial community succession in the Arabidopsis rhizosphere. Plant Signaling & Behavior, 4(8), 777–780. https://doi.org/10.4161/psb.4.8.9229
Mikkelsen, M., & Coyne M.S. (2015). Soil microorganisms contribute to plant nutrition and root health. Better Crops, 99, 18-20.
Miller, S. B., Heuberger, A. L., Broeckling, C. D., & Jahn, C. E. (2019). Non-Targeted Metabolomics Reveals Sorghum Rhizosphere-Associated Exudates are Influenced by the Belowground Interaction of Substrate and Sorghum Genotype. International Journal of Molecular Sciences, 20(2), 431. https://doi.org/10.3390/ijms20020431
Mommer, L., Kirkegaard, J., & van Ruijven, J. (2016). Root–Root Interactions: Towards A Rhizosphere Framework. Trends in Plant Science, 21(3), 209–217. https://doi.org/10.1016/j.tplants.2016.01.009
Myshustin, E.N. (1972). Microorganisms and agricultural productivity. M.: Nauka, 342.
Nadira, U. A., Ahmed, I. M., Wu, F., & Zhang, G. (2016). The regulation of root growth in response to phosphorus deficiency mediated by phytohormones in a Tibetan wild barley accession. Acta Physiologiae Plantarum, 38(4). https://doi.org/10.1007/s11738-016-2124-8
Nayfach, S., Roux, S., Seshadri, R., Udwary, D., Varghese, N., Schulz, F., Wu, D., Paez-Espino, D., Chen, I.-M., Huntemann, M., Palaniappan, K., Ladau, J., Mukherjee, S., Reddy, T. B. K., Nielsen, T., Kirton, E., Faria, J. P., Edirisinghe, J. N., … Henry, C. S. (2020). A genomic catalog of Earth's microbiomes. Nature Biotechnology, 39(4), 499–509. https://doi.org/10.1038/s41587-020-0718-6
Nguyen, C. (2003). Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie, 23, 375-396. https://doi.org/10.1051/agro:2003011
Nobble, F., & Hiltner, L. (1896). Inoculation of the cultivating leguminous plants. U.S. Patent 570 813.
Ortíz-Castro, R., Contreras-Cornejo, H. A., Macías-Rodríguez, L., & López-Bucio, J. (2009). The role of microbial signals in plant growth and development. Plant Signaling & Behavior, 4(8), 701–712. https://doi.org/10.4161/psb.4.8.9047
Pascale, A., Proietti, S., Pantelides, I. S., & Stringlis, I. A. (2020). Modulation of the Root Microbiome by Plant Molecules: The Basis for Targeted Disease

Suppression and Plant Growth Promotion. Frontiers in Plant Science, 10. https://doi.org/10.3389/fpls.2019.01741
Peters, N. K., Frost, J. W., & Long, S. R. (1986). A Plant Flavone, Luteolin, Induces Expression of Rhizobium meliloti Nodulation Genes. Science, 233(4767), 977–980. https://doi.org/10.1126/science.3738520
Phillips, D. A., Fox, T. C., King, M. D., Bhuvaneswari, T. V., & Teuber, L. R. (2004). Microbial Products Trigger Amino Acid Exudation from Plant Roots. Plant Physiology, 136(1), 2887–2894. https://doi.org/10.1104/pp.104.044222
Raaijmakers, J. M., Paulitz, T. C., Steinberg, C., Alabouvette, C., & Moënne-Loccoz, Y. (2008). The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant and Soil, 321(1–2), 341–361. https://doi.org/10.1007/s11104-008-9568-6
Rengel, Z., & Römheld, V. (2000). Root exudation and Fe uptake and transport in wheat genotypes differing in tolerance to Zn deficiency. Plant and Soil 222, 25–34. https://doi.org/10.1023/A:1004799027861
Roesch, L. F. W., Fulthorpe, R. R., Riva, A., Casella, G., Hadwin, A. K. M., Kent, A. D., Daroub, S. H., Camargo, F. A. O., Farmerie, W. G., & Triplett, E. W. (2007). Pyrosequencing enumerates and contrasts soil microbial diversity. The ISME Journal, 1(4), 283–290. https://doi.org/10.1038/ismej.2007.53
Roy, A.A., Pasychnyk, L.A., Tserkovniak, L.S., Khodos, S.F., & Kurdish I.K. (2012). The effect of bacteria of the genus Bacillus on the causative agents of bacterial cancer of tomatoes. Mikrobiolohichnyi Zhurnal, 74(5), 74-80.
Rudresh, D. L., Shivaprakash, M. K., & Prasad, R. D. (2005). Tricalcium phosphate solubilizing abilities of Trichoderma spp. in relation to P uptake and growth and yield parameters of chickpea (Cicer arietinum L.). Canadian Journal of Microbiology, 51(3), 217–222. https://doi.org/10.1139/w04-127
Sasse, J., Martinoia, E., & Northen, T. (2018). Feed Your Friends: Do Plant Exudates Shape the Root Microbiome? Trends in Plant Science, 23(1), 25–41. https://doi.org/10.1016/j.tplants.2017.09.003
Seitz, V. A., McGivern, B. B., Borton, M. A., Chaparro, J. M., Daly, R. A., Sheflin, A. M., Kresovich, S., Shields, L., Schipanski, M. E., Wrighton, K. C., & Prenni, J. E. (2021). Variation in root exudate composition influences soil microbiome membership and function. https://doi.org/10.1101/2021.11.04.467385
Shaposhnikov, A. I., Shakhnazarova, V. Yu., Vishnevskaya, N. A., Borodina, E. V., & Strunnikova, O. K. (2020). Aromatic Carboxylic Acids in Barley-Root Exudates and Their Influence on the Growth of Fusarium culmorum and Pseudomonas fluorescens. Applied Biochemistry and Microbiology, 56(3), 344–351. https://doi.org/10.1134/s0003683820030138
Shirokych, A.A., Merzaeva, Sh.V., & Shirokych, I.G. (2007). Methodical approaches to the study of microorganisms in the root zone of plants. Agricultural biology, 1, 43-54.
Souza, R. de, Ambrosini, A., & Passaglia, L. M. P. (2015). Plant growth-promoting bacteria as inoculants in agricultural soils. Genetics and Molecular Biology, 38(4), 401–419. https://doi.org/10.1590/s1415-475738420150053
Spini, G., Decorosi, F., Cerboneschi, M., Tegli, S., Mengoni, A., Viti, C., & Giovannetti, L. (2015). Effect of the plant flavonoid luteolin on Ensifer meliloti 3001 phenotypic responses. Plant and Soil, 399(1–2), 159–178. https://doi.org/10.1007/s11104-015-2659-2
Tate, R. L. (1997). Soil microbial diversity research: whither to now? Soil Science, 162(9), 605–606. https://doi.org/10.1097/00010694-199709000-00001
Torsvik, V., Goksøyr, J., & Daae, F. L. (1990). High diversity in DNA of soil bacteria. Applied and Environmental Microbiology, 56(3), 782–787. https://doi.org/10.1128/aem.56.3.782-787.1990
Umarov, M.M., Kurakov, A.V., & Stepanov, A.L. (2007). Microbiological transformation of nitrogen in soil. M.: GEOS, 137.
van Loon, L. C., Bakker, P. A. H. M., & Pieterse, C. M. J. (1998). Systemic resistance induced by rhizosphere bacteria. Annual Review of Phytopathology, 36(1), 453–483. https://doi.org/10.1146/annurev.phyto.36.1.453
Vives-Peris, V., de Ollas, C., Gómez-Cadenas, A., & Pérez-Clemente, R. M. (2019). Root exudates: from plant to rhizosphere and beyond. Plant Cell Reports, 39(1), 3–17. https://doi.org/10.1007/s00299-019-02447-5
Volkogon, V.V. (2006). Microbial preparations in agriculture: theory and practice. K. Agrarian science, 312.
Vranova, V., Rejsek, K., Skene, K. R., & Formanek, P. (2010). Non-protein amino acids: plant, soil and ecosystem interactions. Plant and Soil, 342(1–2), 31–48. https://doi.org/10.1007/s11104-010-0673-y
Wakelin, S. A., Warren, R. A., Harvey, P. R., & Ryder, M. H. (2004). Phosphate solubilization by Penicillium spp. closely associated with wheat roots. Biology and Fertility of Soils, 40(1), 36–43. https://doi.org/10.1007/s00374-004-0750-6
Zhalnina, K., Louie, K. B., Hao, Z., Mansoori, N., da Rocha, U. N., Shi, S., Cho, H., Karaoz, U., Loqué, D., Bowen, B. P., Firestone, M. K., Northen, T. R., & Brodie, E. L. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nature Microbiology, 3(4), 470–480. https://doi.org/10.1038/s41564-018-0129-3
Zhang, N., Yang, D., Wang, D., Miao, Y., Shao, J., Zhou, X., Xu, Z., Li, Q., Feng, H., Li, S., Shen, Q., & Zhang, R. (2015). Whole transcriptomic analysis of the plant-beneficial rhizobacterium Bacillus amyloliquefaciens SQR9 during enhanced biofilm formation regulated by maize root exudates. BMC Genomics, 16(1). https://doi.org/10.1186/s12864-015-1825-5
Zhang, X., Yan, J., Khashi u Rahman, M., & Wu, F. (2022). The impact of root exudates, volatile organic compounds, and common mycorrhizal networks on root system architecture in root-root interactions. Journal of Plant Interactions, 17(1), 685–694. https://doi.org/10.1080/17429145.2022.2086307
Zhang, Y., Xu, J., Riera, N., Jin, T., Li, J., & Wang, N. (2017). Huanglongbing impairs the rhizosphere-to-rhizoplane enrichment process of the citrus root-associated microbiome. Microbiome, 5(1). https://doi.org/10.1186/s40168-017-0304-4
Zhou, C., Guo, J., Zhu, L., Xiao, X., Xie, Y., Zhu, J., Ma, Z., & Wang, J. (2016). Paenibacillus polymyxa BFKC01 enhances plant iron absorption via improved root systems and activated iron acquisition mechanisms. Plant Physiology and Biochemistry, 105, 162–173. https://doi.org/10.1016/j.plaphy.2016.04.025