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Agrobiology of Rhizosphere

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Modern trends in studying the rhizosphere agrobiology in accordance to the specificities and mechanisms of formation of natural functional and structural interspecies relations, the organizational components of soil formation system as well as plant-microbe interactions have been considered. It was demonstrated that the investigations at the interface of different fields of study (agriculture, soil science, microbiology, biogeochemistry, etc.) allow revealing the specificities of the formation of the structure of taxon-wise functional diversity of rhizobacterial groups as a constituent of the complicated system of rhizosphere organization and conducting effective integration and management of soil processes in agroecosystems.

Key words: rhizosphere, soil formation, plant-microbe systems, agroecosystems.

INTRODUCTION

Soil rhizosphere is the interface of the spheres of the plant root system and the microbial population in soil which is the center of the most intense biological, chemical and physical activity, life, interaction and metabolism. Complicated trophic chains, water potential and reduction-oxidation reactions distinguish this biological system from the ground biome in general. The rhizosphere is located in the framework of the root system; it is remarkable for the diversity of the activity and functionality of the biota. The populations of archaea, bacteria, fungus, protozoa, and animals live and function in the rhizosphere along with the plants; the activity of each species is relevant and, in its turn, has its impact on the formation of soil ecosystems in spatial and temporal scales and is related to a wide spectrum of taxons. The specificities of interaction and transformation of biogenic elements are implemented by means of such bioresources as organic carbon, mineral nutrients and water – using the rhizosphere biota they determine the pathways of energy flows and form the structure of cenosis, ecosystem, and its properties in general. The rhizosphere is the place for the information exchange between all the system participants via different mechanisms, including molecular, genetic mechanisms and the production of phytohormones. The impact of the life activity of rhizosphere biota is spread further beyond the boundaries of the very rhizosphere, the influence of which is reflected in space and time in the formation of the structure of biological community and the implementation of ecosystem processes as well as soil formation. The notion of biological, physical and chemical endo-soil processes in modern science is considerably behind the understanding of the processes above ground (i.e. understanding of the fact how functionally relevant it is for the management and removal of ecological problems in natural and agriculturally regulated ecosystems). At present the study of rhizosphere biology is multifaceted and related to different fields of science depending on geophysical specificities and properties of soil (both physical and chemical), biology of plants, functions and organization of the structure and texture in the soil profile of microbiota and fauna. Large-scale multifaceted and targeted investigations on rhizosphere [1–3] are also evidenced by the discovery of a complicated system of its organization; great interest has also been attracted to its applied relevance for the management of agrarian ecosystems. More current works are dedicated to the specialized branches of rhizosphere biology, which largely use reductive approaches in the study of specificities and mechanisms of the nature and functions of specific interspecies relations [4–6].

The studies on rhizosphere in the ecological aspect had their extensive and rapid development in the mid-80s of the previous century. They cover a wide range of biological and biochemical issues and changes, related to the production of bacterial enzymes (in the range from a microgram of soil to the landscape in the dynamics of soil genesis in the course of thousands of years).

The results of investigations on rhizosphere agrobiology, including relevant discoveries and interdisciplinary (poly-scale) research have been combined and focused for further application in the eco-taxonomy. The main kinds of rhizosphere study are related to very different spatial and temporal perspectives and on different levels of generalization they cover three fields of knowledge: 1) rhizosphere biogeochemistry of soil and physical structure; 2) taxonomic and functional diversity of rhizosphere biota; 3) integration and management of rhizosphere interactions.

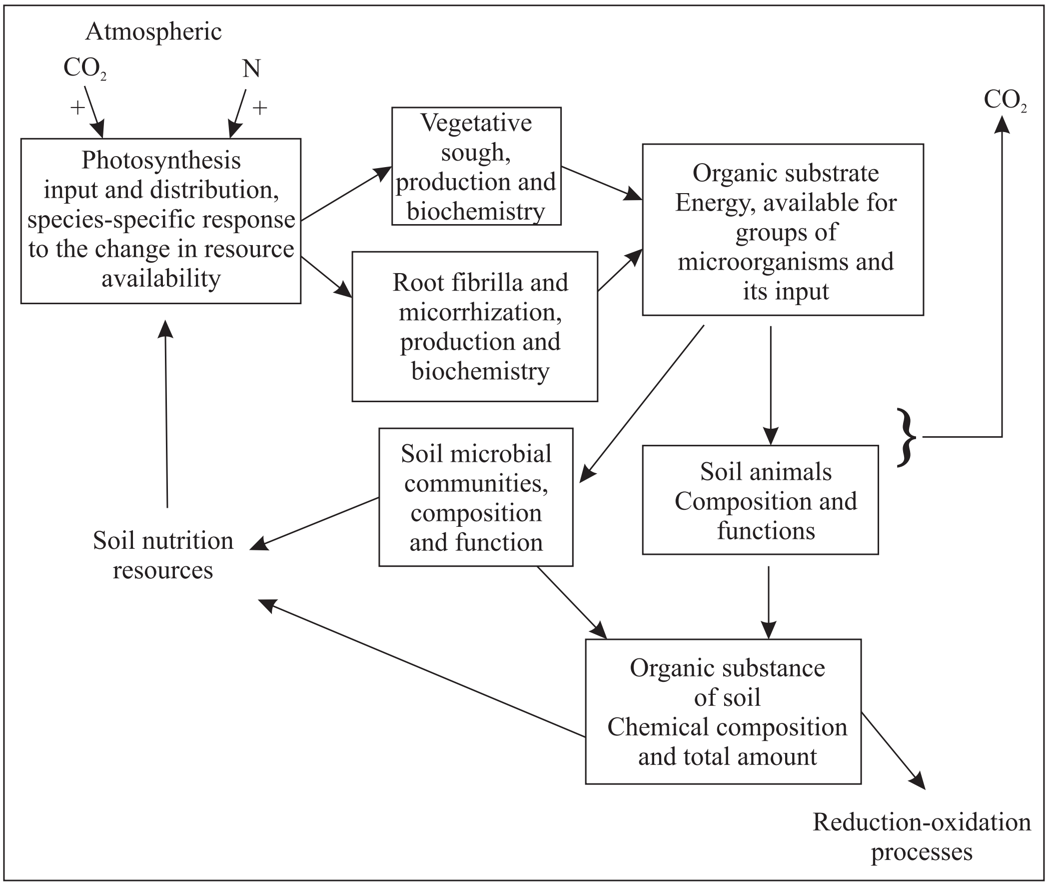
THE COMPOSITION OF MICROBIAL COMMUNITIES IN THE RHIZOSPHERE

In nature each plant species determines the formation of the structure of rhizosphere bacterial and (or) fungus groups (communities), having its positive or negative impact on them. The group composition of the rhizosphere microbiota is conditioned by the genotype of plants, the availability of nutrients, the presence of the pathogenic infectious agent and the mycorrhizal or nodulating symbiont. The groups of microorganisms occupy the plant root system [7, 8] in a differentiated way and have different texture (distribution) around the root. The highest amount of bacteria in rhizosphere is known to be located in the zone of root growth [9].

The study of organisms in rhizosphere and soil is the most complicated task. The colonization of the root system by the group of soil bacterial microflora may take the form of a biofilm or be partially present on the surface of the root, and the boundaries between the colonies are hard to distinguish. It is impossible to have physical differentiation of the impact of soil microorganisms on the rhizosphere of plants. Recent years have witnessed the development and popularity of the molecular research methods of estimating the biome and metagenome of soil organisms which allowed scientists “to break the existing boundaries” and to extend the spectrum of notions on the biodiversity of soil microflora, which is considerably richer than that for the groups of microorganisms, cultivated on elective culture media as well as starting the identification and study of populations and communities of microbes of the whole soil profile. The most common current method of genotyping allows characterizing complicated microbial groups of small and highly conservative 16S rRNA of ribosome subunits of DNA genes (rDNA 16S) which is important, taking into consideration the low level of the transfer of homologous genes and adequate reflection of the general phylogenic homology. The estimation of the 16S rRNA gene set by such methods as T-RFLP and DGGE or direct sequencing of the whole group or community from the library of clones may be used to characterize the community in general. Using these methods the researchers succeeded in coming closer to the understanding of the notion of population and ecology of microorganism groups [10], related to the rhizosphere microflora which is rather relevant for the formation of agroecosystems.

Most investigations of the microbial complex are focused on economically valuable organisms, which may be used in agriculture either for biological control or to enhance the growth of plants, including different species of symbiotic retainers of nitrogen [11], rhizobacteria, stimulating the growth and development of plants [12], organisms, controlling pathogenic rhizosphere bacteria [13], and bacteriophages [14]. The studies were also conducted on the level of populations, remarkable for rhizosphere bacteria that are useful for bioremediation of soil. For instance, Dalmastri *et al.* [15] demonstrated that high genotypic and phenotypic diversity of the population of *Burkholderia cepacia* in the agrocenosis system of corn rhizosphere testifies to the ecological significance of this group of prokaryotes for biocontrol and biological remediation.

The impact of microorganisms on rhizosphere is often synergetic; it occurs on the level of populations and has high ecological relevance. The groups of microorganisms in rhizosphere are maintained in a certain amount, comprising bacteria, stimulating the growth and development of plants, pseudomonades, nitrifying agents or mycorrhiza micromycete, which can be identified [16]. The microbiological characteristics of the microorganism groups are composed on the basis of their economic relevance pertaining to the crops of agricultural and industrial production (first of all, they include wheat, corn, alfalfa, barley, beets, rape, salad, peas, potatoes, rye, soybeans, tomatoes, etc.). The plants of natural habitat are paid less attention of the researchers [17, 18].



The model of interaction of ecosystems with the increase in CO_2 and nitrogen concentration in the atmosphere

The investigations on rhizosphere interactions, affecting the levels of ecosystems, are quite important, as they will allow revealing the corresponding mechanisms, controlling ecosystem functions, conditioned by the changes in the atmosphere of the Earth. The concentration of carbon dioxide in the atmosphere is rapidly increasing due to the active burning of fossilized fuel resources and changes in the soil management. In recent decades hundreds of experiments have proven that the concentration of CO_2 in the atmosphere will keep increasing with further unlimited use of natural resources [19–22]. The content of nitrogen in the atmosphere has also increased considerably in the ground ecosystems, which is greatly related to the human activity [23, 24]. The resources of the available nitrogen in soil affect the formation of the biomass of plants and play a key role in the regulation of the photosynthesis level [25], the growth rate for the biomass of plant tissue and respiration [26]. Nitrogen, available in soil, has also its impact on the distribution of carbon-containing substances and the level of interaction of the root system and microorganisms, the carbon emission into the atmosphere via the respiration of plants and microorganisms. Therefore, the increase in the concentration of CO_2 and nitrogen in the atmosphere may violate the biochemical cycles, directly changing the net primary productivity (NPP – the products of autotrophic organisms, mainly plants and chemosynthesizing bacteria). The plants in the ground ecosystems are generators, providing the energy for the microbial metabolism via the root exudation, accompanied by the metamorphoses in the root system. The increase in the concentration of atmospheric CO_2 and nitrogen will change NPP and carbon distribution in plants which, in its turn, will initiate a series of biochemical changes and metabolism disorder, food webs and the rate of passing the ecosystem cycles (Figure) in them. The conceptual model, presented in Figure, presupposes optimal physiological formation of the root system, biochemical reactions in the process of plant ontogenesis with the subsequent dying, which is of key functional relevance for the management of ecosystems and biogeochemical processes. In other words, the understanding of the ways for the root system and the dynamics of rhizosphere formation by the microorganism groups to respond to the increase in the concentration of atmospheric CO_2 and nitrogen is important for the notion on the biogeochemical interactions and the formation of relations between the cycles of these elements, which eventually define the evolution of ecosystems. The metamorphoses in the physiology and growth of the root system are defined by the conceptual mechanisms of microbial bioenergetics in rhizosphere, forming the corresponding systems and interactions. The analysis of relations and interactions of the root system of plants and microorganisms has been conducted on the level of ecosystems. The conclusion was made that the biochemical processes of the substance transformation in nature have direct effect on the functions, growth and development of the root system. The anthropogenic changes on the planet are considerably conditioned by the role of the factor of rhizosphere and microbial systems, established in the former, and the circulation and flows of carbon and nitrogen depend thereon.

The interaction of ecosystems is defined by the dominating plant species. Being the producers of secondary metabolites, the species of plants condition the amount and biochemical composition of the vegetative slough, which, in its turn, is the medium for the activity of soil microorganisms. The main role of soil microorganisms is to regulate the flows of nutrients and their immobilization. Therefore, it is supposed that the changes in the amount of the nitrogen, which is available in soil and is the main nutrition element on the background of the increase in CO_2 concentration in the atmosphere, correlate with the disorder in microbial bioenergetic flows in the processes of biosynthesis and destruction. The role of the effect of the ratio between the elevated atmospheric CO_2 and soil on the soil biological processes has not been adequately studied yet [28–30].

The conceptual model, based on the idea of changing the availability of the resources (increased concentration of CO_2 and nitrogen in the atmosphere), presupposes the change in the distribution of carbon in the plant and the initiation of the cycle of physiological and biochemical transformation in the vegetative biomass and the transformation of the vegetative slough. As shown in Figure, via biochemical modifications in soil the leaves, roots and the system of microorganisms of the rhizosphere play a key role in controlling the energy flows on the trophic level. The biochemical processes of synthesis and destruction condition the existence of reverse relations between the biochemical cycles of carbon and nitrogen, which eventually inhibit the response of ecosystems to the increase in the concentrations of CO_2 and nitrogen in the atmosphere. Deeper understanding of the physiological relations between the distribution of carbon in plants is primarily related to the study of the permanent biochemical and rhizosphere processes. A key moment in predicting the level of the soil processes at elevated CO_2 is the realization of the way, in which the level of availability of nitrogen-containing substances in soil will change. Although many researchers have made attempts to realize how the availability of soil nitrogen will change with the increase in the concentration of CO_2, the answer is yet to be found. At present there are neither theoretical nor conceptual notions, explaining the increase or decrease in the nitrogen availability in soil [27]. One might assume that the changes in the resource availability are related to the distribution of the photosynthesized substances, the accumulation of substances and defensive reactions of plants along with the microbial mechanisms of the formation of rhizosphere systems and the levels of their interaction on the background of bioenergetic flows. Once confirmed, it will allow formulating the conceptual fundamentals for possible interactions in the ecosystem and building long-term simulations of C and N cycles. At present the science is limited to the discussion of the role of the root system in rhizosphere and biogeochemical cycles and to the attempts of explaining how and why the increased concentrations of CO_2 and nitrogen in the atmosphere affect and change the physiological, biochemical processes as well as the production of root exudates. Along with a complicated cascade of mechanisms, launching the vegetative systems via the interaction with microbial soil communities, these changes define the trophic functional structure of the rhizosphere and the course of biogeochemical processes in ecosystems.

The elevated atmospheric CO_2 promotes enhanced formation and growth of roots with a small diameter (≤ 1 mm), which is remarkable for the whole series of plant species [28, 29]. It is directly related to the stimulation of photosynthesis, conditioned by the elevated CO_2 and the increase in the growth and development of the root system. In particular, Norby *et al.* [30] discovered that the root system increases its activity more than twofold due to the elevated CO_2 and this tendency did not alter for six years, whereas other extension organs of plants did not respond to the elevated CO_2 as much. At present there is insufficient data about the connection between the increase in the root biomass and the nitrogen availability, which is partially explained by contradictory literature data on the correlation between the presence of nitrogen in soil and the metabolism of the root system of plants. It is probable that the atmospheric concentration of nitrogen may also affect the changes in the biomass of the root system, but neither has it been validated nor there is information on the role of the elevated atmospheric CO_2. The decrease in the root biomass is usually related to the elevated nitrogen, available in soil [31], but it is not always true [26]. In particular, the decrease in the biomass may be conditioned by the drop in the accretion of new roots or the increase in the metabolism of the existing ones. The absence of direct consecutive reaction of the root system growth for different species to the elevated nitrogen, available in soil, presupposes that life cycles of separate species and/or symbiotic systems of roots with mycorrhiza may serve as a basis for further understanding of these processes.

CONCLUSIONS

Thus, the scientific research, dedicated to the realization of the mechanisms of the formation and quantitative estimation of the interaction between plants and soil microorganisms are of exclusive relevance for the understanding of the formation of the systems of plant-microbe communities, the ecological role of these cenoses in the functioning of the ecosystems. There has been considerable progress in the study of the plant-microbe interactions in recent years; there is a new powerful instrumental basis, which allows deepening the understanding of the mechanisms of the formation of these processes. The groups of microorganisms of soil rhizosphere are known for their difference from the surrounding soil by the tempo and characteristics of the transformation cycles for nitrogen and carbon. However, modern science cannot give final answers to the questions about the formation of relations for the rhizosphere microbial communities with the differentiation of the circulation of nutrients and, eventually, the functioning of ecosystems. The researchers merely come a little closer to the understanding of the fact in what way and to what degree plants affect the physical state of soil and determine the formation of rhizosphere groups of microorganisms. What is the relative role of plants compared to the role of soil medium in the formation of the composition of rhizosphere communities of microorganisms? In what way and to what degree is the role of the plant-microbe systems of soil reflected on the physiological, population and ecological levels? How does the already formed plant-microbe system obtain the response? In what period of time is it possible to develop efficient interactions? In what way do the physical and chemical conditions of soil affect the formation of biotic interactions? What is the significance of the level and role of signaling at the intercellular interaction of the plant root system and soil microorganisms? The extension of the investigatory foundations, which would allow answering these complicated questions, requires the formation of the block of diverse data, starting with respiration, soil science and ending with biometeorology, physiology and genetics of microorganisms. Therefore, considerable progress in the field of studies on rhizosphere biology is expected on condition of complex works, covering a wide range of interdisciplinary investigations.

Агробіологія ризосфери

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Розглянуто сучасні напрямки у вивченні агробіології ризосфери відповідно до особливостей і механізмів формування природних функціонально-структурних міжвидових взаємовідносин і організаційних складових системи ґрунтоутворення, а також рослинно-мікробної взаємодії. Показано, що лише завдяки дослідженням на межі різних галузей науки (землеробство, ґрунтознавство, мікробіологія, біогеохімія та ін.) вдається розкрити особливості формування структури таксоно-функціонального різноманіття ризобактерійних угруповань як основної складової системи організації ризосфери, ефективно здійснювати інтеграцію та управління ґрунтовими процесами в агроекосистемах.

Ключові слова: ризосфера, ґрунтоутворення, рослинно-мікробні системи, агроекосистеми.

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Рассмотрены современные направления в изучении агробиологии ризосферы в соответствии с особенностями и механизмами формирования природных функционально-структурных межвидовых взаимоотношений, организационных составляющих системы почвообразования, а также растительно-микробных взаимодействий. Показано, что благодаря исследованиям на стыке

различных отраслей науки (земледелие, почвоведение, микробиология, биогеохимия и др.) удалось раскрыть особенности формирования структуры таксоно-функционального разнообразия ризобактериальных групп как составной части сложной системы организации ризосферы, эффективно осуществлять интеграцию и управление почвенными процессами в агроэкосистемах.

Ключевые слова: ризосфера, почвообразованиие, растительно-микробные системы, агроэкосистемы.

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